

## LONG-TERM DYNAMICS OF A GRASSLAND RODENT COMMUNITY

MATTHEW J. BRADY\* AND NORMAN A. SLADE

Natural History Museum and Biodiversity Research Center and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045-7561, USA

Present address of MJB: Division of Natural Science and Mathematics, Lewis-Clark State College, 500 8th Avenue, Lewiston, ID 83501, USA

We examined long-term (1978–1999) population fluctuations and their influence on community structure in 6 species of rodents that are syntopic in old-field habitat in northeastern Kansas. Populations of all species fluctuated severalfold in abundance, with *Sigmodon hispidus*, *Peromyscus maniculatus*, and *Reithrodontomys megalotis* exhibiting annual cycles. Multiannual periodicities were evident for *Microtus ochrogaster*, *P. maniculatus* (3.5–4 years), and *P. leucopus* (7 years). Only *Synaptomys cooperi* lacked a discernable pattern in its abundance. Monthly abundances of 6 of 15 species-pairs positively covaried, suggesting similar responses to long-term environmental variation. In addition, several species-pairs showed time-lagged cross-correlations that indicate regular annual cycles, which were out of phase. Because of this variation in population dynamics within and among community members, the structure of this community varied considerably over time, indicating a nonequilibrium community. However, when looking at the community as a whole, 2 reoccurring long-term patterns in community structure emerge: an annual and a 3.5-year cycle. Annual cycles in community structure occurred because 3 of the 6 species showed annual cycles, whereas the 3.5-year cycle in community structure was probably due to the overwhelming influence of fluctuations in abundance of the numerically dominant prairie vole.

Key words: community structure, long-term dynamics, multiannual cycles, population fluctuations

Community structure varies over time as a result of fluctuations in abundances of the component species (Brown and Heske 1990). Explanations for this variation have been debated since Clements (1916) and Gleason (1917, 1926) 1st proposed their alternative concepts of communities. Clements (1916) saw communities as tightly integrated assemblages of species whose interactions (biotic factors) drove community structure. In contrast, Gleason (1917, 1926) envisioned the community as an aggregation of species reacting independently to environmental variation (abiotic factors), where coexistence occurs primarily because a site meets the requirements of all community members. Since then ecologists have considered the degree to which natural communities are integrated biological entities or somewhat random assemblages of species (Cody and Diamond 1975; Connor and Simberloff 1979; Diamond and Case 1986; Simberloff et al. 1999; Strong et al. 1984; Wiens 1977). However, this interpretation of Gleason's

concept has been recently challenged (Nicolson and McIntosh 2002). Examination of data from several recent studies suggests that most species respond individually to long-term environmental variation despite the prevalence of biotic interactions (Böhning-Gaese et al. 1994; Brown and Heske 1990; Brown and Kurzius 1989; Taper et al. 1995). This apparent paradox in community structure can be explored through the examination of the relationships among population fluctuations of the component species.

Long-term studies of community dynamics are a principal means of examining the biotic and abiotic mechanisms driving temporal variation in community structure. However, truly long-term studies are uncommon (Brouse 1999; Brown et al. 1986; Brown and Heske 1990; Cody and Smallwood 1996; Diffendorfer et al. 1996; Fryxell et al. 1998; Heske et al. 1994; Meserve et al. 1999; Swihart and Slade 1990; Whitford and Steinberger 1989). Brown and Heske (1990) provided the 1st study investigating the relationships between temporal variation in structure of a community of small mammals and long-term population fluctuations of the component species. They used time-series analysis to examine 10 years of abundance estimates for 11 species of desert rodents coexisting in the desert Southwest for repeatable patterns in population fluctuations

\* Correspondent: [mjbrady@lcsc.edu](mailto:mjbrady@lcsc.edu)

and temporal changes in community composition (Brown and Heske 1990). Despite considerable experimental evidence for interspecific competition in this system (Brown and Munger 1985; Heske et al. 1994; Munger and Brown 1981; Valone and Brown 1995), Brown and Heske (1990) discovered that these rodent populations responded independently to environmental variation, suggesting community structure to be individualistic or Gleasonian in nature (Gleason 1917, 1926). Considerable spatial variation in species composition of desert rodent assemblages also is consistent with an individualistic structure of the desert rodent community (Brown and Kurzius 1987, 1989). Brown and Kurzius (1989) suggested that this spatial and temporal variation in community composition and structure is widespread and might be evident in environments other than the desert granivore system.

Our study is the 1st to apply the methodology of Brown and Heske (1990) to a long-term data set on population fluctuations of a rodent assemblage in grassland habitat. We examined time series of monthly abundance estimates for this grassland rodent assemblage for repeatable patterns, such as annual or multi-annual fluctuations. Because climatic variables can have major influence on population fluctuations, we also explored associations between changes in abundance and monthly temperature and precipitation. In addition, we investigated whether pairs of species covaried over time and the influence of these associations and population fluctuations on temporal changes in community structure.

## MATERIALS AND METHODS

*Description of study site and rodent community.*—Since 1973, Slade and colleagues have studied the long-term dynamics of 6 species of rodents in old-field habitat (Brady and Slade 2001; Eifler and Slade 1998; Glass and Slade 1980a, 1980b; Slade and Swihart 1983; Swihart and Slade 1990) at the John H. Nelson Environmental Study Area approximately 14 km northeast (by road) of Lawrence, Kansas. The study area consists of a 2.25-ha grid with 99 trap stations approximately 15 m apart in a configuration of roughly 10 stations  $\times$  10 stations. Originally, 1 Sherman (H. B. Sherman Traps, Tallahassee, Florida) live trap and 1 modified Fitch trap (Rose 1973) were placed at each station. Later, these traps were replaced by 2 noncollapsible Sherman live traps (7.62  $\times$  8.89  $\times$  30.48 cm). Two traps per station were used to reduce trap saturation, which could bias population estimates.

The study area is located in early successional old-field habitat consisting of a variety of grasses and forbs, with patches of woody coverage, which is maintained by mowing at irregular intervals. The dominant plants of this old-field habitat include brome grass (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), Canada goldenrod (*Solidago canadensis*), and common sunflower (*Helianthus annuus*). A more detailed description of the habitat can be found in Swihart and Slade (1990).

Although 11 species of small mammals have been trapped on the study area, the study initially focused on the hispid cotton rat (*Sigmodon hispidus*) and the prairie vole (*Microtus ochrogaster*). In 1989, the study expanded to include marking 4 additional species of rodents—the white-footed mouse (*Peromyscus leucopus*), deer mouse (*P. maniculatus*), western harvest mouse (*Reithrodontomys megalotis*), and southern bog lemming (*Synaptomys cooperi*). Swihart and Slade (1990) provided a more detailed list of species caught on the grid.

*Data set.*—We used 21 years of monthly trapping records (March 1978–March 1999) to examine the time series of each resident species for long-term patterns in population dynamics as well as for interspecific associations. Each month, traps were set and checked on 3 consecutive mornings and the 2 intervening afternoons. All individuals were marked with either a numbered ear tag (Monel #1, National Band and Tag Co., Newport, Kentucky; *S. hispidus*) or by toe clipping (the other 5 species). All trapping and marking techniques followed American Society of Mammalogists guidelines (Animal Care and Use Committee 1998) and were approved by the Institutional Animal Care and Use Committee at the University of Kansas.

From these trapping records, we calculated monthly estimates of population abundance for each species, by using the heterogeneity model (model h) from the software program CAPTURE, which assumes individual variation in capture probability (White et al. 1982). However, before 1989, only *S. hispidus* and *M. ochrogaster* were systematically marked, and only numbers of captures were recorded for the other 4 species. For valid comparisons among species, the measure of abundance must be consistent among species. Consequently, we ran linear regressions on the data for the period March 1989 to March 1999 with estimated population size as the response variable and number of captures as the predictor variable for each species. These regression equations were then used to predict monthly estimates of abundance for periods before January 1989 based on number of captures for those months (Diffendorfer et al. 1996; Slade and Blair 2000). We also used this technique to predict abundance for periods after 1989 when the rate of recapture was low (Brady and Slade 2001; Slade and Blair 2000). Only trapping periods with reliable estimates of abundance (i.e., estimated numbers  $\leq$  twice their standard errors) were used to derive the regression equations used for both procedures. The average adjusted  $r^2$  values were high (87.2%, range 78.1–96%), and were comparable to those of Slade and Blair (2000).

To assess the relationship between environmental variation and population fluctuations, we used both mean monthly temperature ( $^{\circ}$ C) and total monthly precipitation (mm). These data were obtained from records at both the National Weather Station in Lawrence, Kansas, and a weather station maintained by staff at the field station at Nelson Environmental Study Area; data were similar between the 2 sites, allowing us to combine the data.

*Intraspecific patterns.*—We examined the time series of each species for annual variation, by using autocorrelation analysis (Brown and Heske 1990). Most time-series techniques, including autocorrelation, assume that the series is stationary, meaning that the series shows no tendency for increase or decrease through time (Box and Jenkins 1976). To use simple stationary models, we removed interannual fluctuations by subtracting the annual mean from each monthly value and dividing by the standard deviation for the year, and then analyzed these normalized time series (Brown and Heske 1990).

We also examined the population dynamics of each species for long-term (or interannual) patterns in abundance by inspecting the time series themselves and through the use of spectral analysis on the time series (Brown and Heske 1990).

Relationships between 2 environmental variables (mean monthly temperature and total monthly precipitation) and the population dynamics of the rodent community were investigated by using cross-correlation analysis. Cross-correlation analysis compares the degree of correlation between values of 2 variables at varying time lags (Box and Jenkins 1976). Unlike autocorrelation, cross-correlation is not symmetric about a lag of 0 months; thus, it is calculated for both negative and positive time lags (Box and Jenkins 1976).

When 2 variables both exhibit seasonal fluctuations that may be independent of one another, analyses of association (e.g., correlation)

may indicate relationships that are only coincidental. For example, monthly ambient temperature, despite its considerable within-month variation, has a regular seasonal fluctuation. Thus, correlating temperature with the population dynamics of any species that also goes through seasonal fluctuations might lead to the spurious conclusion that temperature at some time lag is associated strongly with fluctuations in population abundance. Consequently, we removed seasonal fluctuations from time series of temperature, precipitation, and abundance estimates of 6 species of rodents by performing 1-way analyses of variance (ANOVAs) with month as the factor variable for all 21 years combined. We then ran cross-correlation analysis on the residuals (deviations from monthly means) from the ANOVAs. This approach allowed us to examine associations between environmental variables and population estimates for a species after adjusting for seasonal variation. We then qualitatively compared these results with those from cross-correlations performed on the unadjusted data.

*Interspecific associations and community-level patterns.*—We investigated long-term patterns of association among populations of the community members with cross-correlation in 2 ways (Brown and Heske 1990). First, time series of the monthly abundance were correlated for all 15 species-pairs. Second, we correlated yearly averages to examine similarities between annual fluctuations of the species' populations (Brown and Heske 1990). Annual averages were based on a year beginning in April and ending in March, with the exception of the 1st year, which began in March 1978.

We followed the procedure described by Brown and Heske (1990) to assess temporal variation in community structure, with 1 exception. We used principal components analysis instead of detrended correspondence analysis to quantify common variation among the 6 species as a measure of monthly community composition, because the 2 techniques are similar and we had access to software for principal components analysis but not detrended correspondence analysis. The presence of repeating patterns or stability in community structure was explored with spectral analysis on monthly scores on the first 2 principal component axes (Brown and Heske 1990).

## RESULTS

*Intraspecific patterns.*—Substantial temporal variation was evident in the population dynamics of all 6 species in the community. Population dynamics of *R. megalotis* displayed regular seasonal fluctuations, whereas the occurrence of *S. cooperi* was sporadic with prolonged periods of low abundance or apparent local extinction on the grid (Fig. 1). Although the population of *S. hispidus* also experienced periods of very low abundance, fluctuations were less sporadic than those of *S. cooperi* and reached peaks each autumn and winter when they were present (Fig. 1). *Peromyscus maniculatus* consistently occurred on the grid in relatively low numbers, but experienced peaks in abundance in 6 of the years during the study (Fig. 1). With the exception of a 5-month period (December 1983–April 1984), individuals of *M. ochrogaster* were consistently found on the grid with considerable variation in abundance (Fig. 1). *Peromyscus leucopus* varied widely in abundance, but was present throughout the study.

Annual cycles, as indicated by significant negative autocorrelations at lags of 6 months and significant positive autocorrelations at 12 months, were apparent in the population dynamics of 3 of the 6 species (Fig. 2). Populations of both *S. hispidus* and *R. megalotis* experienced strong annual cycles,

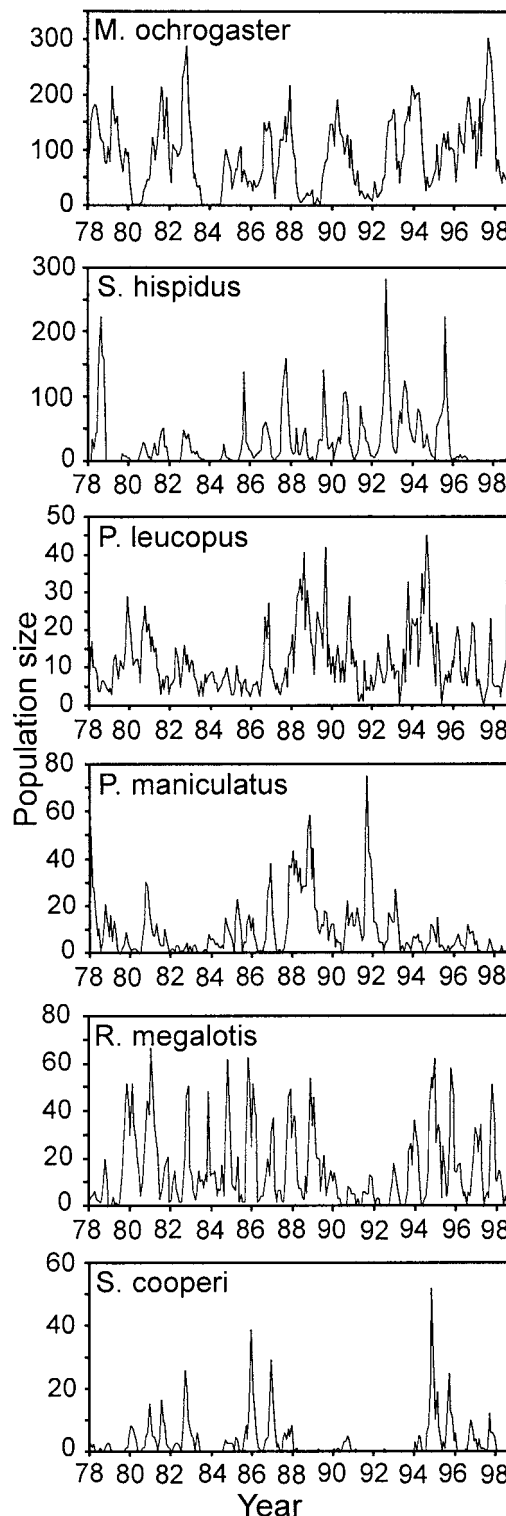


FIG. 1.—Time series of monthly estimates of abundance for 6 species of rodents found in an old field at the Nelson Environmental Study Area northeast of Lawrence, Kansas, over a 21-year period (March 1978–March 1999). Yearly designations on graphs begin in April of each year after 1978.

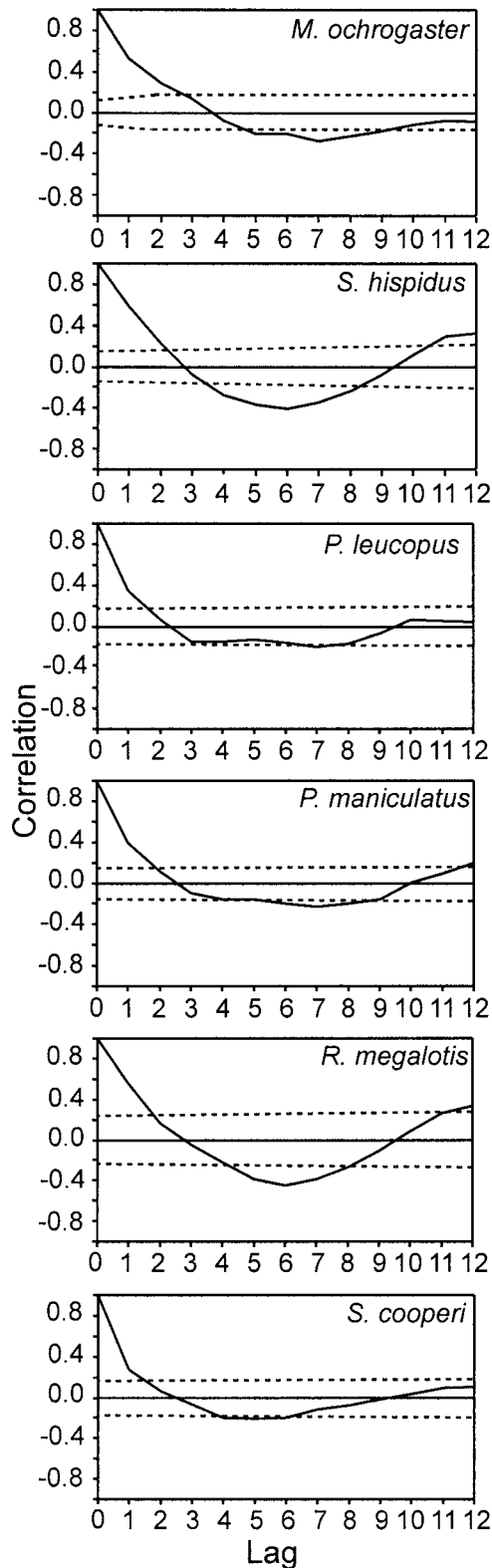


FIG. 2.—Autocorrelograms for 6 species of grassland rodents from northeastern Kansas. Before analysis, all time series were normalized by subtracting the annual mean from each monthly value and dividing by *SD* for the year. The dashed lines represent significance levels; any coefficient above the dashed line is significantly different from 0 at  $P < 0.05$ .

whereas *P. maniculatus* had a significant but less pronounced annual cycle. No indication of annual cycles was found in the other 3 species (Fig. 2).

Spectral analysis corroborated the seasonal fluctuations in populations of *S. hispidus*, *P. maniculatus*, and *R. megalotis*. Of these 3, only the population of *P. maniculatus* had any indication of a longer-term pattern to its dynamics. Populations of *M. ochrogaster* and *P. maniculatus* showed 42-month (3.5-year) periodicities (peaks in their spectrograms), whereas *P. leucopus* experienced an 84-month (7-year) period. No clear long-term patterns emerged for *S. cooperi*, which might be a result of its sporadic occurrence on the grid (Fig. 1).

Fluctuations in both mean monthly temperature and total monthly precipitation were seasonal; however, the seasonal pattern of precipitation was less pronounced than that of temperature (Brady 2001). Consequently, cross-correlations of temperature with monthly abundance for 6 species indicated some annual covariation (Fig. 3), more so for *S. hispidus*, *R. megalotis*, and *P. maniculatus*, whose populations experienced seasonal fluctuations (Figs. 2 and 3). Associations with precipitation were less clear, which might be a result of the weaker seasonal fluctuation in precipitation (Brady 2001), although the general pattern was similar to that of temperature (Fig. 3). After accounting for seasonality, abundances of only 2 species had consistent associations with precipitation or temperature. Abundance of *M. ochrogaster* was negatively correlated with mean monthly temperature for lags of 1 through 8 months (Fig. 4). Thus, vole numbers tended to be lower than average for a month after times of above normal temperatures and to be higher after relatively cool temperatures. In contrast, abundance of *P. maniculatus* was positively correlated with mean monthly temperature at lags ranging from 6 to 14 months (Fig. 4). No other species had consistent associations with deviations from mean monthly temperature. When using either the original time series or seasonally adjusted values, patterns between monthly variation in total precipitation and population dynamics for the 6 species were less clear. Strong associations seen in unadjusted precipitation with population dynamics of *R. megalotis* disappeared when seasonality was taken into account.

*Interspecific patterns.*—Fewer than one half of the pairwise comparisons resulted in significant patterns of covariation between monthly population fluctuations of the different species-pairs (Fig. 5 and Table 1). Six species-pairs, 3 of which involved the 3 species (*S. hispidus*, *P. maniculatus*, and *R. megalotis*) that exhibited annual cycles (Fig. 2 and Table 1), had positive associations (Table 1) but with different intra-annual dynamics (Fig. 5). However, monthly abundance numbers of *M. ochrogaster* and *P. maniculatus* were associated negatively at lags of 0 to 9 months (Fig. 5 and Table 1). The only apparent long-term association between numbers of *S. hispidus* and *M. ochrogaster* was a significant positive association at lag 0 (Table 1 and Fig. 5), despite evidence indicating that *S. hispidus* negatively influences the spatial and temporal activities of *M. ochrogaster* (Glass and Slade 1980a, 1980b; Terman 1974). However, the correlation coefficients for both monthly and yearly averages at lag 0 for *S. hispidus* and

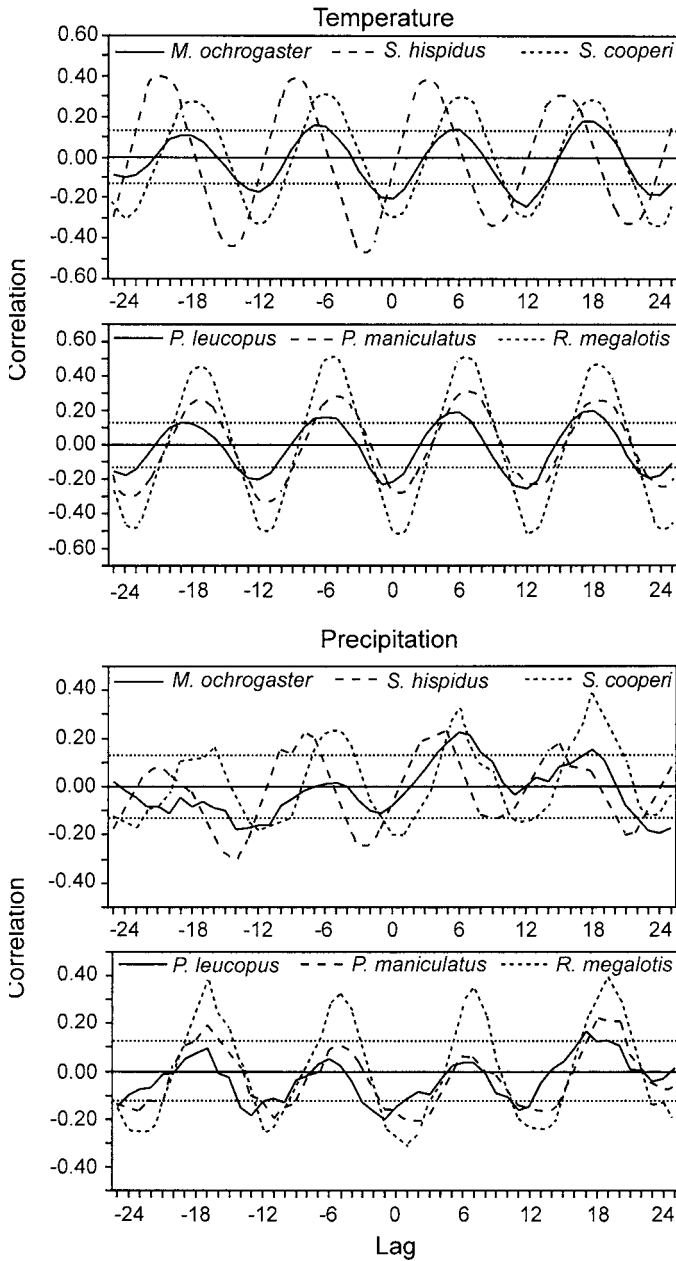


FIG. 3.—Cross-correlograms between mean monthly temperature and total monthly precipitation and monthly abundance for 6 species of grassland rodents in northeastern Kansas unadjusted for seasonality in the variables. Coefficients above 0.126 or below -0.126 are significantly different from 0 at  $P < 0.05$ .

*R. megalotis*, although not significant, were negative (Table 1). Comparisons of yearly averages of abundance resulted in only 1 significantly positive relationship and no significantly negative relationships (Table 1).

**Community structure.**—Community structure varied substantially over time (Fig. 6). The first 2 principal components accounted for 63% of the monthly variation in community composition (Table 2) and were easily interpretable. The 1st principal component was a contrast, with strong positive loadings for *M. ochrogaster* and negative loadings for *P. leucopus*, *P. maniculatus*, and *R. megalotis* (Table 2). The

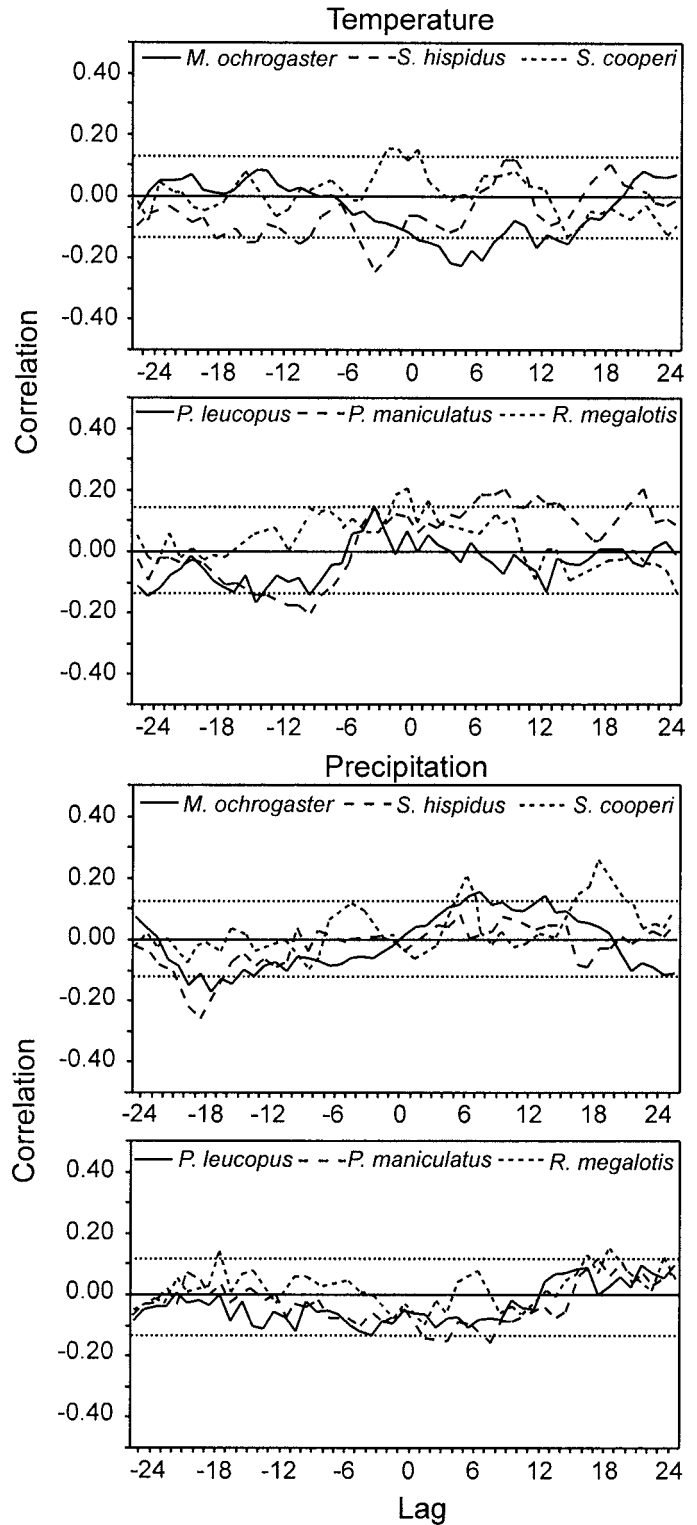


FIG. 4.—Cross-correlograms between mean monthly temperature and total monthly precipitation and monthly abundance for 6 species of grassland rodents in northeastern Kansas adjusted for seasonality in the variables. Coefficients above 0.126 or below -0.126 are significantly different from 0 at  $P < 0.05$ .

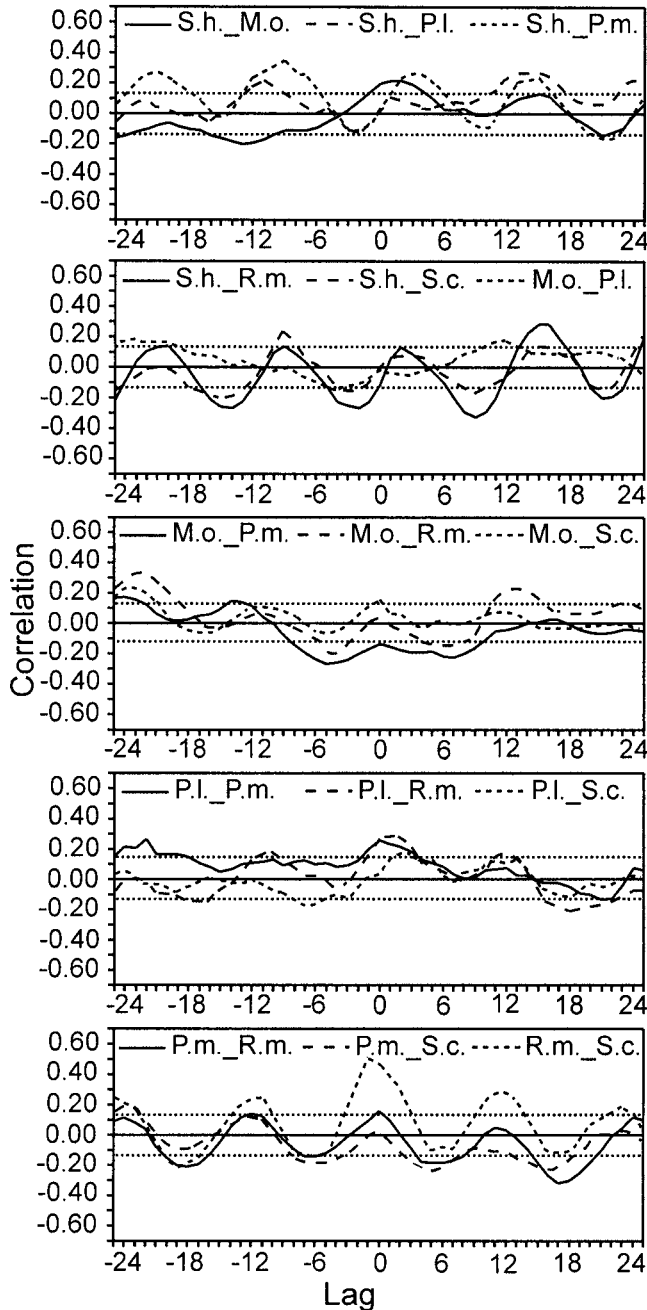


FIG. 5.—Cross-correlograms for pairwise comparisons between monthly population dynamics for 6 species of rodents found in old-field habitat in northeastern Kansas. Coefficients above 0.126 or below  $-0.126$  are significantly different from 0 at  $P < 0.05$ . Each species is indicated by the 1st letter of the generic and specific epithet (e.g., S.h. = *Signodon hispidus*). See the text for the other species designations.

2nd principal component also was a contrast, with strong positive loadings for *R. megalotis*, *M. ochrogaster*, and *S. cooperi* and negative loadings for *S. hispidus* and *P. maniculatus* (Table 2).

Spectral analysis of the 2 principal components revealed 2 long-term patterns in community structure (Fig. 6). The 1st principal component shows a 3.5-year cycle, whereas the dominant pattern in community structure revealed in the 2nd principal component is an annual cycle.

## DISCUSSION

*Intraspecific patterns.*—Despite the variable nature of the population dynamics of the 6 species of rodents in old-field habitat at the Nelson Environmental Study Area (Fig. 1), a few similarities in long-term population fluctuations emerged among the 6 species (Fig. 2 and Table 1). The population of *M. ochrogaster* experienced multiannual fluctuations with a periodicity of 3.5-years (Table 1). Previous studies reported varying results when assessing cyclicity in the population dynamics of *M. ochrogaster* in temperate climates (Abramsky and Tracy 1979; Gaines and Rose 1976; Taitt and Krebs 1985) and other species of *Microtus* (Birney et al. 1976; Garsd and Howard 1981, 1982; Gilbert and Krebs 1991; Meserve and Klatt 1985; Taitt and Krebs 1985). Abramsky and Tracy (1979) found that populations of *M. ochrogaster* in their short-grass prairie plots cycled annually, but not multiannually. However, their plots were small and the low ground cover between plots probably impeded immigration, which might have resulted in noncycling populations (Abramsky and Tracy 1979; Krebs 1978). A recent spectral analysis of a long-term data set found that populations of *M. ochrogaster* in east-central Illinois experienced 3- to 4-year cycles (Getz et al. 2001). Additional studies using time-series analyses on long-term data sets of abundance of *Microtus* might reveal that multiannual patterns are common at lower latitudes (Abramsky and Tracy 1979; Garsd and Howard 1981, 1982).

The populations of the 2 species of *Peromyscus* were unusual in that they both experienced multiannual fluctuations (Table 1), which are not typical of populations of *Peromyscus* (Terman 1968). One other known instance of *P. maniculatus* experiencing a multiannual cycle was in an insular population, where it also cycled annually (Drost and Fellers 1991). A possible explanation to the pattern seen in the population of *P. maniculatus* is the potential relationship between this species and *M. ochrogaster*. Populations of *P. maniculatus* have been shown in other studies to be negatively affected by or associated with populations of *M. ochrogaster* (Abramsky et al. 1979; Diffendorfer et al. 1996; Gaines et al. 1992; Swihart and Slade 1990). Consequently, if these 2 species compete, changes in the abundance of *P. maniculatus* could be a response to the multiannual cycle of *M. ochrogaster*. Both species also differed in their lagged responses to mean monthly temperature. *M. ochrogaster* increased after cooler than average temperatures, whereas *P. maniculatus* increased after warmer temperatures. These opposite responses suggest that these 2 species might respond differently to long-term climatic changes. Negative covariation in abundances thus might reflect opposing responses to temperature and associated environmental changes rather than negative interspecific interactions (Table 1).

The presence of a multiannual cycle in *P. leucopus* is unusual given that this species is considered to have relatively stable populations in other habitats (Terman 1968). Consequently, the 7-year cycle found in this study should be viewed with some caution. However, Kesner and Linzey (1997) found populations of *P. leucopus* in Pennsylvania to have a 3-year

**TABLE 1.**—Cross-correlation coefficients at lag 0 for all 15 pairwise species comparisons of monthly estimates (below diagonal) and yearly averages (above diagonal) of abundance for 6 species of grassland rodents. An asterisk next to a value indicates that value to be significantly different from 0 at the 0.05 level.

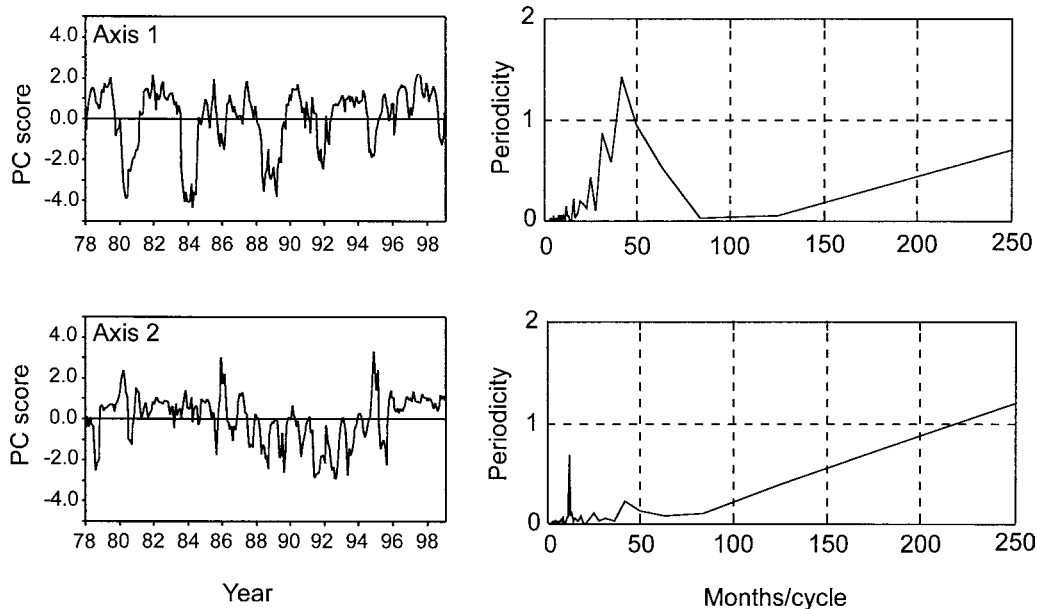
	<i>Sigmodon hispidus</i>	<i>Microtus ochrogaster</i>	<i>Peromyscus leucopus</i>	<i>P. maniculatus</i>	<i>Reithrodontomys megalotis</i>	<i>Synaptomys cooperi</i>
<i>Sigmodon hispidus</i>		0.161	−0.046	0.226	−0.383	0.050
<i>M. ochrogaster</i>	0.199*		−0.117	−0.397	−0.142	0.202
<i>P. leucopus</i>	0.032	−0.018		0.285	0.341	0.070
<i>P. maniculatus</i>	0.027	−0.137*	0.256*		−0.155	−0.305
<i>R. megalotis</i>	−0.105	0.043	0.275*	0.159*		0.572*
<i>Synaptomys cooperi</i>	0.037	0.146*	0.055	0.013	0.462*	

cycle, and Wolff (1985) reported that populations of both *P. leucopus* and *P. maniculatus* in Virginia fluctuated in a cyclic pattern with a 4- to 6-year periodicity. Populations of *P. leucopus* in the eastern United States track mast (e.g., acorn) production (Ostfeld et al. 1996), and the repeating pattern found in this study might be linked to long-term fluctuations in mast production. Unfortunately, we have no data on mast production in secondary forests bordering the successional habitats at the Nelson Environmental Study Area to address this relationship. Alternatively, multiannual fluctuations in populations of *P. leucopus* (or other rodents) might be related to the old field in this study being mowed to maintain an early successional stage. However, mowing events were irregularly spaced over time, and appeared to have no obvious long-term affect on the population fluctuations of these species (Brady 2001).

*Interspecific patterns.*—Interspecific variation in long-term population dynamics, along with the small number of significant interspecific correlations of population dynamics

(Table 1), suggests that the members of the rodent community at our study site are responding independently to environmental variation (Brown and Heske 1990). However, 6 pairs of species did have strong positive correlations among numbers, indicating that some species respond similarly to long-term environmental variation (Table 1). Despite similarities in response to environmental variation, only 2 species (*M. ochrogaster* and *P. maniculatus*) had significant associations with either mean monthly temperature or total monthly precipitation, after adjusting for seasonality (Fig. 4). Clearly, our 2 simple measures of temperature and precipitation do not reflect the entirety of climatic variation, and even species that show similar population dynamics might not be responding to the same environmental factor (Böhning-Gaese et al. 1994; Brown and Heske 1990; Brown and Kurzius 1989; Taper et al. 1995).

Temporal variation in structure of this rodent assemblage, as revealed by our principal components, suggests a nonequilibrium community (Chesson and Case 1986; Swihart and Slade 1990).



**FIG. 6.**—Long-term patterns in community structure of a grassland rodent assemblage in northeastern Kansas. The graphs on the left are the time series of scores on the first 2 principal components (PC) axes, and the 2 on the right are the spectrograms from fast Fourier transformation on the principal component scores of the respective PC axes. Major peaks in the spectrograms represent long-term patterns in community structure. Yearly designations on graphs begin in April of each year after 1978.

**TABLE 2.**—Eigenvalues for the first 2 principal components (PC) of population fluctuations for 6 grassland rodent species in northeastern Kansas.

	PC 1	PC 2
Eigenvalue	2.377	1.381
Cumulative proportion	0.396	0.626
<i>Microtus ochrogaster</i>	0.582	0.281
<i>Sigmodon hispidus</i>	0.038	-0.723
<i>Peromyscus leucopus</i>	-0.516	0.020
<i>P. maniculatus</i>	-0.382	-0.259
<i>Reithrodontomys megalotis</i>	-0.492	0.390
<i>Synaptomys cooperi</i>	-0.077	0.423

Constant relative abundances of species would produce a “size” component having loadings of the same sign for all species, but the largest 2 principal components were contrast axes indicating that the dominant features of this community were fluctuations in relative abundances over time (Fig. 6). Scores along principal components 1 and 2 exhibited long-term structure, with recurring periods of 3.5 years and 1 year, respectively (Fig. 6). The 1st principal component was a contrast between abundances of 3 species (*P. leucopus*, *P. maniculatus*, and *R. megalotis*) and *M. ochrogaster*, which supports the hypothesis that multiannual shifts in the structure of this grassland community might be strongly influenced by fluctuations in abundance of the numerically dominant *M. ochrogaster* (Table 2; Diffendorfer et al. 1996) and opposing fluctuations in numbers of *P. maniculatus*. Temporal variation in the 2nd most prominent component of variation in abundances reflected weakly synchronous annual periodicities in abundances of *S. hispidus* and *P. maniculatus*, and out-of-phase periodicities of *R. megalotis*.

*Comparison to the desert granivore system.*—The grassland rodent community at the Nelson Environmental Study Area exhibits a number of similarities and differences when compared with the desert rodent community studied by Brown and colleagues (Brown and Heske 1990; Heske et al. 1994; Valone and Brown 1995). One difference is how the dominant species of the 2 habitats influence other community members. In a previous study (Brady and Slade 2001), we found that the 2 dominant species (*M. ochrogaster* and *S. hispidus*) in this old-field habitat had little direct effect on the long-term diversity of the resident community of rodents. However, during a short period of time (a 4-year period) when *S. hispidus* had a consistently high abundance, a strong negative association existed between fluctuations in abundance of *S. hispidus* and community diversity in the form of decreased species richness and relative abundance of the other community members (Brady and Slade 2001). In contrast, kangaroo rats (*Dipodomys*), the dominant species in desert rodent assemblages, exert considerable influence on the dynamics of other granivorous rodents in the community (Heske et al. 1994; Valone and Brown 1995). A 2nd difference is seen in the population dynamics of 2 species (*P. maniculatus* and *R. megalotis*) found in both habitats. In the old field, both species exhibit annual fluctuations in abundance (Fig. 1), whereas in

the desert system, no evidence was found of annual patterns (Brown and Heske 1990:293, figure 1), despite both environments having well-defined growing seasons. One difference might be that seed crops are better preserved in arid environments, and hence are more constantly available in the desert. However, we have no data to support this conjecture.

Along with these differences, a number of similarities in community structure are apparent. Strong associations among community members do not predominate in either community (Table 1; Brown and Heske 1990:297, table 3), and the majority of significant associations in both systems are positive (6 of 7 = 85.7% our study and 25 of 30 = 83.3% from the study of Brown and Heske [1990]). Also, no evidence exists of a single environmental variable having a pervasive effect on the population dynamics of members of either community (our study; Brown and Heske 1990).

As a whole, the similarities and differences lend support for the argument of Brown and Kurzius (1989) that the considerable spatial and temporal variation seen in desert communities is most likely widespread among habitat types, and this variation in community structure is probably a result of component species responding individually to local environmental variation. A case in point is the differences in population dynamics of *P. maniculatus* and *R. megalotis*. Both species are widely distributed and occur in a variety of habitats. Given this wide geographic range, it is not surprising that both species exhibit varying population dynamics among habitats.

*Implications for community structure.*—Although some community members interact (our study; Diffendorfer et al. 1996; Glass and Slade 1980a, 1980b; Swihart and Slade 1990), the structure of the community at our study area as a whole seems to be individualistic in nature. Other studies, mostly on desert granivore systems, have shown that community composition is typically individualistic in nature despite considerable evidence for interspecific competition (Brown and Heske 1990; Brown and Kurzius 1989; Taper et al. 1995). How then does this reconcile with the considerable evidence from field experiments suggesting that interspecific competition is prevalent in nature and represents a major factor in structuring communities? First, the above studies do not claim that interspecific competition does not influence community structure. However, they suggest that interspecific competition is one of many factors involved in determining the structure of communities (Brown and Kurzius 1989). Competition might occur in most communities, but might affect community structure only when resources are limiting (Wiens 1977; but see Heske et al. 1994). Consequently, competition might affect community structure at smaller scales (both temporal and spatial), whereas stochastic or abiotic processes (e.g., environmental variation) operate at larger scales (Brady and Slade 2001; Heske et al. 1994). Populations that covary over time as a result of shared conditions and resources would be those of species most likely to exhibit intense competition for those very resources (Heske et al. 1994). For example, the populations of *S. hispidus* and *M. ochrogaster* positively covary (Table 1), most likely as a result of their similar dietary and habitat needs, which also lead to competitive interactions between the 2

species (Glass and Slade 1980a, 1980b; Terman 1974). Together, these studies highlight the need to carefully consider spatial and temporal scale when gauging the relative roles of biotic and abiotic forces in structuring ecological communities.

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