



Fast and slow dynamics of northern small mammal populations

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ARTICLE INFO

Article history:

Received 10 April 2011

Received in revised form 3 November 2011

Accepted 13 November 2011

Available online 14 December 2011

Keywords:

Climate

Life history strategy

Scale-dependent dynamics

Seasonality

Wavelet analysis

ABSTRACT

Animal populations interact with their environments in a scale-dependent manner and exhibit scale-dependent dynamics. Animals may adjust reproductive frequency and fecundity in response to fluctuating environments to maximize reproductive success. We hypothesize that populations of insectivorous small mammals undergo seasonal variations owing to predictable shortages of winter food and short breeding periods, whereas populations of herbivorous small mammals may exhibit multi-year fluctuations owing to food-induced variability in the length of the breeding period among years. We predict that omnivorous *Peromyscus* and *Reithrodontomys* species would have population dynamics patterns similar to insectivorous small mammals, if the omnivorous rodents rely on insects as winter food. Using the wavelet transform, we re-analyzed nine long-term monthly population time series of *Blarina brevicauda*, *Microtus ochrogaster*, *Microtus pennsylvanicus*, *Peromyscus leucopus*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, and *Sigmodon hispidus* from Illinois, Kansas, and Pennsylvania, United States to test our hypothesis. Populations of *B. brevicauda* in Illinois, *P. leucopus* in Pennsylvania, and *S. hispidus* and *R. megalotis* in Kansas resonated with climate change at an annual scale (8–16 months), whereas *Microtus* populations in Illinois and Kansas and *P. leucopus*, *P. maniculatus*, and *S. hispidus* populations in Kansas exhibited the greatest variability at a scale of 32 months. Our Kansas *M. ochrogaster* population cycled every 2–3 years from 1984 to 1994. Therefore, small mammal populations form a continuum of slow–fast dynamics. Variation in small mammal population abundances is related to climate dynamics only at annual scales. However, it is unlikely that long-term dynamics of local climate directly result in long-term variation in small mammal population abundances, including population cycles. Our findings demonstrate the importance of scale-specific effects of exogenous factors in the dynamics of animal populations and offer a new interpretation of complex effects of climate on population dynamics.

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1. Introduction

Patterns of population dynamics often are scale-dependent, and temporal resolutions of population data are critical to identifying scale-dependent dynamic patterns (Cazelles et al., 2008; Hastings, 2010; Levin, 1992). For instance, the dynamics of a white-footed mouse (*Peromyscus leucopus*) population were influenced more by climate variables at a scale of 2–6 months than at an annual scale (Lewellen and Vessey, 1998). Additionally, several studies have found a shift in population cyclicity in small rodents over time (Cazelles et al., 2008; Ims et al., 2008; Kausrud et al., 2008; Saitoh et al., 2006). These complex scale-dependent patterns of population dynamics suggest that animal populations may interact with their environments in a scale-dependent manner (Hastings, 2010; Keitt and Fischer, 2006).

Animal populations are subjected to the influences of both biotic (e.g., predation) and abiotic (e.g., climate) factors, exhibiting complex dynamic patterns (Previtali et al., 2009; Turchin, 2003; Twombly et al., 2007). However, the question still remains regarding the relative importance of local climate in short- and long-term dynamics of animal populations. For example, are dynamics of small mammal populations correlated with climate dynamics in only certain frequencies or timescales (i.e., monthly, annual, or multiannual scales)? Understanding scale-specific effects of climatic changes on small mammal abundances is critical to forecasting the impacts of anticipated global changes on small mammal populations.

Mammals time their reproduction to coincide with peak food availability and suitable ambient temperatures for energy balance (Bronson, 2009). Herbivorous and omnivorous small mammals in northern-temperate regions often produce multiple litters a year as opportunistic breeders, with a variable length of breeding period (Bronson, 2009; Gliwicz and Taylor, 2002; Innes and Millar, 1994). On the other hand, northern-temperate insectivorous

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shrews reproduce during spring and summer owing to increased winter energy demands and high costs of winter foraging with a low abundance of insect prey (Fournier et al., 1999). Northern-temperate shrews have predictable food shortages during winter, a time when their energy demands increase by 47% while food availability is eight times lower than during spring and summer (Merritt et al., 2001). Short breeding periods and subsequent spring decline of abundance may limit long-term increases of small-sized insectivorous mammal populations, resulting in seasonal or fast dynamics. In contrast, variable lengths of breeding periods may cause multi-annual dynamics of northern arvicoline populations (Hansen et al., 1999; Saitoh et al., 2003; Smith et al., 2006; Stenseth et al., 2002). Therefore, we hypothesize that a fast-slow dynamic continuum would exist in small mammal populations owing to different timings and lengths of breeding periods in response to variation in food availability and ambient temperatures.

Traditional time series analysis of population dynamics in the time domain that averages across all temporal scales may miss opportunities for identifying the primary scale-specific interactions between populations and environments. Here we take advantage of continuous wavelet transform (CWT) and discrete wavelet transform (DWT) to identify the timescales at which population abundances exhibit the greatest variability and the strongest correlation with climate variables. The main objective of the current study was to test the following three hypotheses concerning slow-fast dynamics of northern small mammals: (1) that populations of small insectivorous species resonate quickly with seasonal climatic fluctuations in a time horizon of less than a year, owing to substantial within-year variability in the availability of insect prey; (2) that populations of small herbivorous species fluctuate slowly in a multi-annual scale, owing to environmental stochasticity or inter-annual variability in the length of breeding periods; and (3) that omnivorous species exhibit dynamics more similar to insectivorous species than to herbivorous species, if omnivores rely on insects for winter food. To test these hypotheses, we re-analyzed nine long-term monthly population time series of one insectivorous species (short-tailed shrew, *Blarina brevicauda*), three omnivorous species (white-footed mouse; deer mouse, *Peromyscus maniculatus*; and western harvest mouse, *Reithrodontomys megalotis*) and three herbivorous species (prairie vole, *Microtus ochrogaster*; meadow vole, *Microtus pennsylvanicus*; and cotton rat, *Sigmodon hispidus*) from Illinois, Kansas, and Pennsylvania, United States of America (USA; Fig. A1).

2. Methods

2.1. Study sites and monthly live trapping data of small mammals

We analyzed nine monthly population time series of small mammals, including populations of short-tailed shrews, meadow voles, and prairie voles collected by L.L. Getz near Urbana, Illinois, USA (Getz et al., 2004), populations of prairie voles, white-footed mice, deer mice, western harvest mice, and cotton rats collected by N.A. Slade near Lawrence, Kansas, USA (Slade and Blair, 2000), and a population of white-footed mice collected by A.V. Linzey and M.H. Kesner in Pennsylvania, USA (Kesner and Linzey, 1997). The Urbana populations were monitored by 3-day live trapping sessions at monthly intervals: short-tailed shrew population, May 1972–December 1996 ($N=296$); meadow vole population, October 1975–May 1997 ($N=260$); and prairie vole population, May 1972–May 1997 ($N=301$). Trapping was conducted using multiple-capture live traps (placed in a 10 m grid pattern) in 1.0–1.4 ha alfalfa sites, 0.5–2.0 ha restored tallgrass prairie habitats, and 0.8–2.0 ha bluegrass sites located in the University of Illinois Biological Research Area (“Phillips Tract”) and Trelease Prairie,

both 6 km northeast of Urbana, Illinois (40°15'N, 88°28'W). The white-footed mouse population at Yellow Creek State Park, Pennsylvania (40°51'N, 79°05'W) was monitored from September 1984 through April 1996 ($N=140$), using bluebird nest boxes (Kesner and Linzey, 1997). Mice were captured weekly using 36 nest boxes spaced 30–90 m apart, covering an area about 2.54 ha. The vegetation on the Pennsylvania site included a heavy cover of grasses, forbs and shrubs (Kesner and Linzey, 1997). The rodent populations near Lawrence, Kansas (39°03'N, 95°12'W) were monitored using a 2.5-ha grid of 99 trap stations approximately 15 m apart in a configuration of roughly 10 stations \times 10 stations. Two traps (originally one Sherman live trap and one modified Fitch trap and later two non-collapsible Sherman live traps) were placed at each station. The vegetation was an old field mixture of forbs. Trapping was conducted for three consecutive days each month from 1973 through 2003. We used data from October 1980 to July 2003 for cotton rats, prairie voles and white-footed mice ($N=274$), to June 2003 for harvest mice ($N=273$), and to April 2003 for deer mice ($N=271$), respectively, to minimize missing data. There were 12 missing months, one or more in nine of the 24 years, in the Kansas rodent population time series.

We used minimum number of animals known alive (MNA) as an index of monthly population abundance for the Illinois and Pennsylvania populations (Krebs, 1999). We combined MNA over the three Illinois sites to generate an overall abundance index for each of the three species. Population size was estimated by the Jackknife estimator supplemented by regression on number of captures in eastern Kansas (Brady and Slade, 2004; Slade and Blair, 2000). We estimated the 12 missing values of the Kansas rodent populations, using a basic structural model, a state-space time series model, following Wang (2009). Wengert (2009) compared the Jolly-Seber (JS) estimates of population sizes and MNA's of a white-footed mouse population in Ohio (Lewellen and Vessey, 1998) and found that MNA was positively related to the JS estimate with a R^2 value of 0.68, which is consistent with the findings in meadow voles in Ontario, Canada (Boonstra, 1985) and deer mice in Montana, USA (Luis et al., 2010). Therefore, MNA is a sufficient index for studying the trends of population dynamics, although MNA underestimates population abundances more than do the JS estimates.

Zeros existed in the population time series of short-tailed shrews ($n=2$) and prairie voles ($n=21$) in Illinois and all rodent time series in Kansas. We conducted square root transformations to normalize time series data (Fig. A2). In addition, we conducted wavelet analysis on both the square root transformed and log-transformed population time series of white-footed mice in Pennsylvania and meadow voles in Illinois (the two time series without zeros). The results of scale-based analysis of variance (ANOVA) and wavelet cross correlations were consistent between the two transformations. Therefore, we used the square root transformations of time series in our final analysis.

2.2. Climate data

Climate data for the Illinois site were recorded at a weather station at Urbana (station ID = 118,740, 6.6 km from the study site), and were obtained from the Illinois State Water Survey.

Climate data were recorded at the weather station Indiana 3SE for the Pennsylvania site (about 9 km from the study site) and at a weather station in Lawrence for the Kansas site (about 12 km from the study site), and were obtained from the US NOAA National Climate Data Center. To derive a comprehensive index of climate changes, we applied principal component analysis (Khattree and Naik, 2000) to monthly average temperature, monthly minimum temperature, monthly maximum temperature, and total monthly precipitation for each of the three study sites. The first principal component explained 79%, 81%, and 76% of the total variability of

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