

Synergistic influences of phase, density, and climatic variation on the dynamics of fluctuating populations

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Abstract. Although ecologists have long recognized that certain mammalian species exhibit high-amplitude, often multiannual, fluctuations in abundance, their causes have remained poorly understood and the subject of intense debate. A key contention has been the relative role of density-dependent and density-independent processes in governing population dynamics. We applied capture–mark–recapture analysis to 25 years of monthly trapping data from a fluctuating prairie vole *Microtus ochrogaster* population in Illinois, USA, to estimate realized population growth rates and associated vital rates (survival and recruitment) and modeled them as a function of vole density and density-independent climatic variation. We also tested for phase dependence and seasonality in the effects of the above processes. Variation in the realized population growth rate was best explained by phase-specific changes in vole density lagged by one month and mean monthly temperatures with no time lags. The underlying vital rates, survival and recruitment, were influenced by the additive and interactive effects of phase, vole density, and mean monthly temperatures. Our results are consistent with the observation that large-scale population fluctuations are characterized by phase-specific changes in demographic and physiological characteristics. Our findings also support the growing realization that the interaction between climatic variables and density-dependent factors may be a widespread phenomenon, and they suggest that the direction and magnitude of such interactive effects may be phase specific. We conclude that density-dependent and density-independent climatic variables work in tandem during each phase of density fluctuations to drive the dynamics of fluctuating populations.

Key words: capture–mark–recapture (CMR) analysis; density-dependent and density-independent processes; *Microtus ochrogaster*; population growth; Pradel's temporal symmetry CMR model; prairie vole; recruitment; survival.

INTRODUCTION

Pronounced multiannual density fluctuations, characteristic of certain mammalian species, have captured the attention of ecologists over several decades. The causal mechanisms of such fluctuations, particularly those observed in microtine rodent populations, have been hotly debated (Krebs et al. 1973, Krebs 1996, Oli 2003, Ozgul et al. 2004) and extensively researched (Batzli 1992, Stenseth et al. 1999). A major point of contention has been the role of density-dependent (vs. density-independent) mechanisms in driving observed fluctuations: a recurring debate that began with the pioneering work of Lotka, Volterra, and Elton in the 1920s, and climaxed in the 1950s with Nicholson advocating the deterministic (density-dependent) process and Andrewartha and Birch championing the stochastic (density-independent) school (Coulson et al. 2004). It is now

recognized that both processes can act synergistically within the same population (Turchin 2003). However, density-dependent and environmental factors can exert variable levels of influence on the population dynamics of a species (Coulson et al. 2000, Reed and Slade 2008). Multiannual fluctuations in small mammal populations have, by and large, remained an enigma despite over 80 years of research (Stenseth 1999); disentangling the individual effects of density-dependent and density-independent processes may well be the key to understanding the mechanisms that govern the dynamics of such populations.

Clearly, population fluctuations are a function of changes in population growth rates, which in turn are influenced by demographic factors (Oli and Dobson 2001, Ozgul et al. 2004). Temporal variation in the demographic rates that underlie population growth, namely survival (including deaths and emigration) and recruitment (including births and immigration), can be associated with both density-dependent and density-independent processes (Coulson et al. 2000). A negative feedback between density and either survival or recruit-

Manuscript received 2 December 2010; revised 25 February 2011; accepted 3 March 2011. Corresponding Editor: W. D. Koenig.

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ment may bring about density-dependent changes in population growth rates (Reed and Slade 2008). Furthermore, density may drive phase-related changes in demographic, behavioral, and physiological characteristics that are typical of fluctuating populations (Krebs 1996, Oli and Dobson 1999). However, intrinsic factors such as age, sex, and reproductive stage may lead to dynamics that depend on the phase rather than population density per se (Framstad et al. 1997). Among density-independent processes, much attention has been directed toward climatic forcing in recent years (Previtali et al. 2009). It is widely recognized that broad climatic phenomena such as the North Atlantic Oscillation (NAO), the Arctic Oscillation, and the El Niño Southern Oscillation (ENSO), can have a far-reaching and deep-rooted impact on ecological systems (Stenseth et al. 2002, Hallett et al. 2004). In addition, there is growing evidence that global warming can affect population dynamics and ecosystem functioning (Sæther et al. 2000, Walther et al. 2002, Ozgul et al. 2010). Finally, seasonal variations in local weather conditions may be a potential driver of population dynamics (Ozgul et al. 2004), and these can work in concert with broad long-term climatic phenomena to shape the trajectory of a fluctuating population (Previtali et al. 2009).

A majority of studies that have explored the influence of density-dependent and density-independent processes on population dynamics have relied on time series analyses whereby autoregressive models are fitted to log-transformed population size data (Coulson et al. 2000). Under such a framework, a time series of population abundance is essentially deconstructed into a deterministic skeleton representing endogenous processes (Coulson et al. 2004, 2008), while the exogenous component is characterized by the variation explained by environmental covariates around this skeleton (Forchhammer et al. 1998, Grenfell et al. 1998). Although theoretical and empirical time series deconstructions have proven useful in demonstrating the importance of density-dependent and density-independent processes in governing population dynamics (Coulson et al. 2008), there are limitations to this approach. First, the choice of the deterministic skeleton is contentious; it is “usually selected as a matter of personal taste, regardless of its appropriateness for the system, and unexplained variation is mopped up by environmental drivers including weather” (Coulson et al. 2008). Second, using this framework, it is impossible to infer which vital rates are influenced by current or past densities. Finally, a drawback that applies to small mammals in particular, is that time series data typically are composed of annual estimates of abundance while the average life span of a number of arvicoline rodent species is about 2–3 months (Getz et al. 1997).

Capture–mark–recapture (CMR) theory has grown in flexibility, power, and sophistication over the years (Williams et al. 2002), and presents an alternative to conventional time series analysis in modeling the effects

of density-dependent and density-independent processes on population dynamics. One CMR modeling framework that is particularly useful in discerning the effect of various extrinsic and intrinsic environmental factors on population dynamics is Pradel’s reverse time (or temporal symmetry) models (Pradel 1996, Nichols et al. 2000, Nichols and Hines 2002). This approach confers several advantages: (1) it assumes no underlying autoregressive process; (2) the realized population growth rate can be estimated and modeled directly as a function of various covariates, including population density and weather variables with and without time lags; (3) it allows direct evaluation of the role of density dependence (or lack thereof) in driving observed variation in population growth rate as well as vital rates such as survival and recruitment.

In this paper, we apply a CMR modeling approach to a detailed data set collected from a fluctuating prairie vole *Microtus ochrogaster* (Wagner, 1842; see Plate 1) population that was monitored once a month for 25 years (1972–1997). We hypothesized that (1) density-dependent and density-independent processes would act in concert to drive observed fluctuations through their influences on vital rates that underlie population growth and (2) the influence of density and climatic factors would be phase specific. We tested these hypotheses by first estimating the realized population growth rate, as well as vole survival and recruitment rates, and modeling them as a function of direct and delayed density dependence and density-independent climatic variation with and without time lags. We then evaluated whether the influence of density-dependent and density-independent processes revealed signatures that are specific to different phases of density fluctuations. Finally, we tested for the synergistic, phase-specific effects of vole density and climatic variation on survival and recruitment rates to better understand the mechanisms that drive density fluctuations in our study population.

METHODS

Study area and field methods

The study was carried out from May 1972 to May 1997 in five 1.0–1.4-ha *Medicago sativa* (alfalfa) sites in the University of Illinois Biological Research Area (Philips Tract), 6 km northeast of Urbana, Illinois, USA (40°15' N, 88°28' W). Further details about the study site are provided in Getz et al. (2001).

We monitored the *M. ochrogaster* population once a month using live traps. Trapping was conducted in two adjacent sites (Getz et al. 2001). At each site, we established a grid system with a 10-m interval, and placed one wooden multiple-capture trap (Burt 1940) at each grid station. Trapping was continued in one site until the alfalfa plants began to be crowded out by invading grasses and forbs (4–6 years). One year before trapping was terminated in a site, the other was planted with alfalfa so that the plants would be mature at the time of trapping. Each month, a 2-day pre-baiting

period was followed by a 3-day trapping session. Traps were set in the afternoon and checked at about 08:00 and 15:00 on the following three days. The trapped voles were individually marked by toe clipping (< 2 toes/foot) at first capture. New animals were weighed at first capture; animal ID, sex, body mass, and reproductive condition were recorded at each capture. For males, testes were recorded as abdominal (non-reproductive) or scrotal (reproductive); females were recorded as vagina closed (non-reproductive) or vagina open, lactating, or pregnant (reproductive). See Getz et al. (2001) for a more complete description of the field procedures.

We used the minimum-number-known-alive method (MNA: Krebs 1999) as an index for population density (D). Phase and season definitions followed Getz et al. (2000) and included the following phases: increase, peak, decline, and trough, and the four seasons: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). We further partitioned the population fluctuations into “cycles” where each cycle was defined as starting with the increase phase. Therefore, any given cycle would follow a sequence of increase to peak to decline to trough phases, with the next increase representing a new cycle. Data on weather variables were obtained from a National Weather Station maintained by the Illinois State Water Survey within the University of Illinois campus, 6.6 km from the study sites. These included monthly estimates of mean temperature ($^{\circ}\text{C}$), as well as precipitation and snow fall (in inches).

Capture-mark-recapture (CMR) analyses

We used the temporal symmetry approach of Pradel to estimate and model realized population growth rate and its components, survival and recruitment rates (Nichols and Hines 2002). A reparameterization of the original Jolly-Seber model, the temporal symmetry approach comes with the same basic set of assumptions, including homogenous capture probabilities, no tag loss, instantaneous sampling periods, permanent emigration, and independent fates of individuals with respect to capture and survival (Hines and Nichols 2002). In addition, possible limitations include biases in parameter estimates if the study area expands over time or if there is permanent trap response (Hines and Nichols 2002). We used two alternative parameterizations of the model, whereby the first provided estimates of apparent survival (ϕ), recapture probability (p), and realized population growth rate (λ), while the latter estimated recruitment (f) instead of realized population growth rate. Thus, we were able to make inferences about (1) the processes that drive population growth in our system and (2) the underlying demographic mechanisms by which these processes influence population growth. The analyses were performed using Program MARK (White and Burnham 1999), implemented in R (R Development Core Team 2008) using the RMark library (Laake and Rexstad 2007).

Survival rates can vary over time (Ozgul et al. 2004) and may also be influenced by intrinsic factors such as age, sex, and reproductive stage (Sinclair 1989, Jorgenson et al. 1997, Farand et al. 2002). Therefore, we first tested for temporal variation and the influence of sex on survival using the standard Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965). We did not consider age and reproductive stage as covariates since subsequent models used are based on single age and stage classes. Similar to Ozgul et al. (2004), sex did not have a significant influence on survival (Appendix A), and we did not differentiate between the sexes in latter models.

We began analyses under the temporal symmetry approach using the ϕ and λ parameterization of Pradel's (1996) model which estimated apparent survival (ϕ), recapture probability (p), and realized population growth rate (λ). First, we determined the appropriate model structure for recapture probability, and thereafter fixed it to the identified covariate for subsequent analyses. Model definitions for this analysis are included in Appendix B. Akaike's information criterion corrected for small sample size (AIC_c) was used for all model comparisons. Second, we tested for phase and season dependence by evaluating models without phase and season effects, and with independent, additive, and interactive effects of phase (P) and season (S) on apparent survival and realized population growth rates. In addition, we evaluated whether the strength of phase-dependence varied among cycles by testing for the additive effects of phase and cycle (C). We did not include the interactive effect of phase and cycle because a model where survival and population growth rates are different for every phase and every cycle did not seem biologically meaningful. However, we did model recapture rates as a function of these covariates. Third, we evaluated the effects of vole density and climatic variation (with and without time lags) independently on survival and population growth rates. Since the prairie vole has an average life span of about two months (Getz et al. 1997), we used delays of one month and two months to model time lags. Further, we combined covariates from the best supported models in the above evaluation with the most parsimonious phase-dependent model to investigate if dependence of survival and population growth rates on density and climatic variation demonstrated phase-specific signatures. We then used the same set of covariates to test for the relative influence of density-dependent and density-independent processes on survival and recruitment. These analyses were based on the survival (ϕ) and recruitment (f) parameterization of Pradel's (1996) model, and helped us identify the mechanism by which density-dependent and density-independent processes influence population growth, and thereby drive the dynamics of our study population.

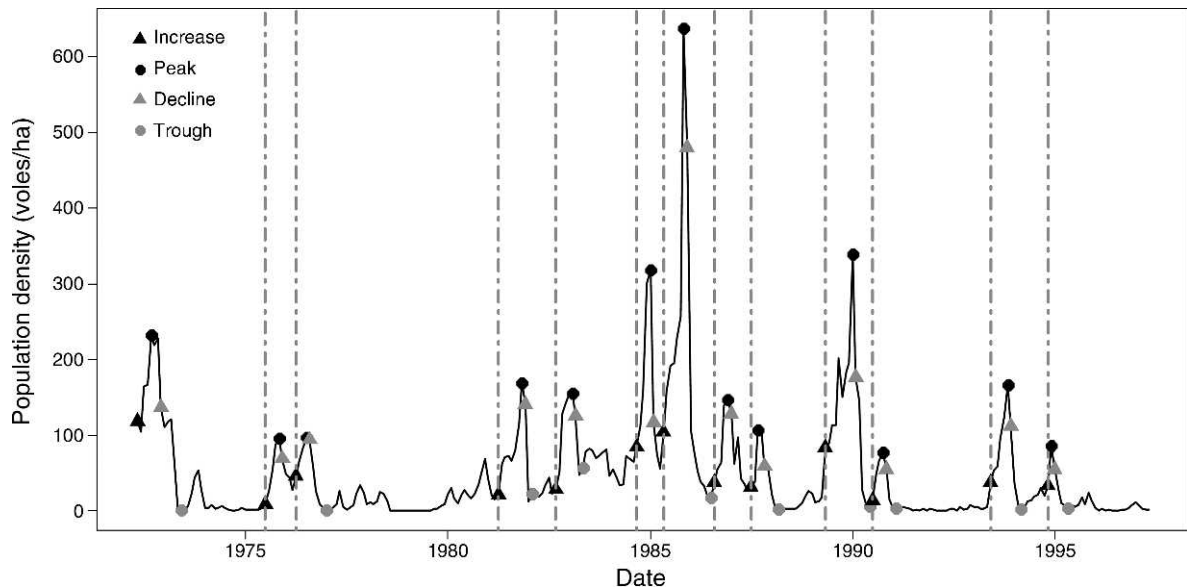


FIG. 1. Observed density fluctuations in our study population of prairie voles (*Microtus ochrogaster*) between May 1972 and May 1997. The start of each phase of the density fluctuations is indicated by triangles and circles. Dotted vertical lines represent the beginning of a new cycle coinciding with the start of the increase phase.

RESULTS

Population fluctuations

In 25 years, the prairie vole population experienced a total of 13 population fluctuations (defined as cycles in our analyses; Fig. 1). During this period, densities ranged from 9 to 301 voles/ha (mean \pm SE = 102.2 ± 8.64) in the increase phase, 77 to 638 (mean \pm SE = 198.6 ± 35.45) in the peak phase, 2 to 480 (mean \pm SE = 66.5 ± 10.08) in the decline phase, and 0 to 82 (mean \pm SE = 14.6 ± 1.51) in the trough phase. The increase phase largely coincided with warmer seasons as 80.4% of all increases occurred in the summer and fall. Peak phases were also more frequent (68.8%) in the same seasons. Conversely, 84.9% of all declines in vole density coincided with the winter and spring. The trough phase was more evenly distributed across time, with colder months accounting for 51.1% of all troughs. Average mean temperatures in the four seasons were as follows: spring, 10.8°C; summer, 23.0°C; fall, 12.0°C; and winter, -2.6°C.

Recapture probability

Our data set for CMR analyses included a total of 14 565 monthly captures of 7660 individuals. Variation in recapture probability of individual voles was best explained by a time-varying model. However, we encountered a parameter identifiability problem whereby only eight of the 307 parameters were estimable. We therefore ignored time as a covariate in our analyses, and fixed the model structure for recapture probability to that in the next best model, which included interactive effects of phase and cycle (i.e., $p(P \times C)$; model in boldface type, Appendix B). It is important to note that

this model is essentially a time-dependent model at a coarser scale. As such, we avoided parameter unidentifiability while still accounting for temporal variation in recapture probability in a meaningful way.

Drivers of population growth

We tested for the effects of phase, vole density, and climatic variation on realized population growth rate. The best model structure for phase-dependent variation in population growth rate included the additive effects of phase and cycle, $\phi(P + C)$, $\lambda(P + C)$ (Appendix C: Table C1a). Phase-specific estimates of growth rates as per this model were as follows: (a) increase phase, $\hat{\lambda} = 1.39$ (95% CI = 1.32–1.46); (b) peak phase, $\hat{\lambda} = 0.94$ (95% CI = 0.88–1.01); (c) decline phase, $\hat{\lambda} = 0.64$ (95% CI = 0.63–0.65); (d) trough phase, $\hat{\lambda} = 1.01$ (95% CI = 0.96–1.05). In addition, we found evidence for seasonality in phase-specific variation in population growth rates (Appendix C: Table C1a). Among density-dependent processes, there was strongest support for a model wherein realized population growth rate showed direct density dependence (model $\phi(D_{t-1})$, $\lambda(D_t)$; Appendix C: Table C1b); realized population growth rate demonstrated a weak positive relationship with density (slope parameter, $\beta = 0.0001$, 95% CI = 0.00008–0.00013). Results from density-independent models indicated that population growth was influenced by mean monthly temperature without time lags $\phi(T_t)$, $\lambda(T_t)$ (Appendix C: Table C1c), whereby mean temperatures contributed positively to population growth rate ($\beta = 0.008$, 95% CI = 0.007–0.008).

We then tested for phase dependence in the effects on population growth rates of density-dependent and

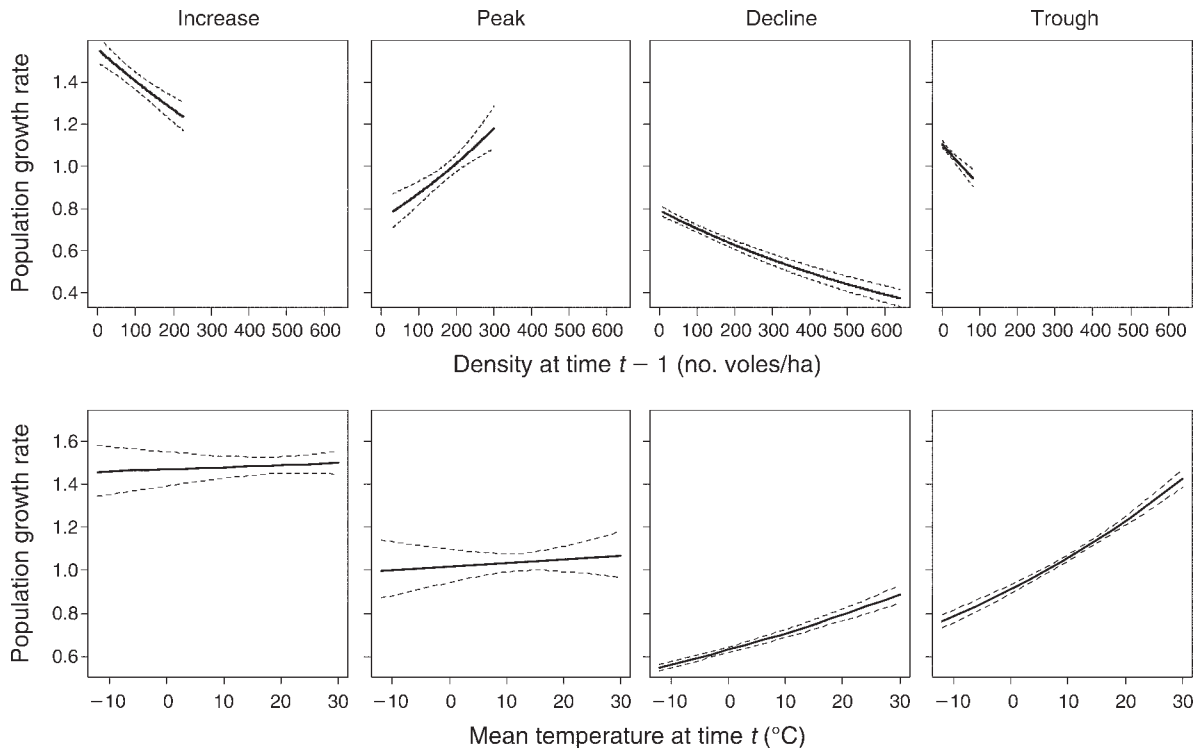


FIG. 2. Phase-specific effects of population density (voles/ha) lagged by one month and mean temperature ($^{\circ}\text{C}$) with no time lags on the realized growth rate of the prairie vole population. Dotted lines indicate 95% confidence intervals.

density-independent covariates, and found evidence for phase-specific mechanisms (Appendix C). In the increase phase, population growth rates were high ($\hat{\lambda} = 1.45$, 95% CI = 1.37–1.53) but declined with increasing density in the previous month (Fig. 2a). During the peak phase, the population continued to grow ($\hat{\lambda} = 1.13$, 95% CI = 1.04–1.21) but only when lagged density was 192 voles/ha or more. Mean monthly temperatures did not influence growth rates in the peak and increase phases (Fig. 2b). Population growth was reversed in the decline phase ($\hat{\lambda} = 0.71$, 95% CI = 0.69–0.72), and lagged density contributed negatively to the growth rate. However, the growth rate improved with increasing mean temperature. Finally, the trough phase witnessed a modest population growth ($\hat{\lambda} = 1.02$, 95% CI = 0.97–1.08) but only at low densities and when mean temperatures exceeded 4.4°C .

The demographic mechanisms that govern population dynamics

We were also interested in discerning demographic mechanisms underlying density-dependent and density-independent influences on population growth. Variation in apparent survival rates was explained by a delayed-density effect (Appendix C: Table C1b and Appendix D: Table D1a), and by mean temperature with no time lags (Appendix C: Table C1c and Appendix D: Table D1b). As per the top models in Appendix C: Table C1b and c, respectively, apparent survival rates were negatively affected by lagged vole density ($\beta = -0.003$, 95% CI =

-0.0033 to -0.0027) but were positively influenced by mean monthly temperature ($\beta = 0.015$, 95% CI = 0.013 to 0.017). In contrast to vole survival, recruitment into our study population experienced direct density dependence (Appendix D: Table D1a). These trends were reversed with density-independent processes whereby the best-supported model suggested that recruitment rate was influenced by mean monthly temperatures in the previous month (Appendix D: Table D1b). Recruitment rate was positively influenced by both density ($\beta = 0.0018$, 95% CI = 0.0017 to 0.0019) and lagged mean temperatures ($\beta = 0.021$, 95% CI = 0.019 to 0.022).

On closer inspection of the mechanisms that govern the dynamics of our study population, we found that models with the effects of density and climatic variables alone were not as strongly supported as those that included the synergistic effects of phase and the two aforementioned processes (Appendix D: Table D1c). The covariates for survival in the top model included the main effects of density at time $t - 1$, phase, and temperature at time t , and the interactive effects of the density with the phase and temperature ($\phi[D_1 \times P + D_{t-1} \times T_t]$). In contrast, recruitment rates were influenced by phase, density (without time lags), and mean monthly temperature at time $t - 1$, as well as the interactive effects of phase with the density and mean monthly temperature ($f[P \times D_t + P \times T_{t-1}]$).

Contour plots of survival rates based on the above model provided evidence for the following phase-specific

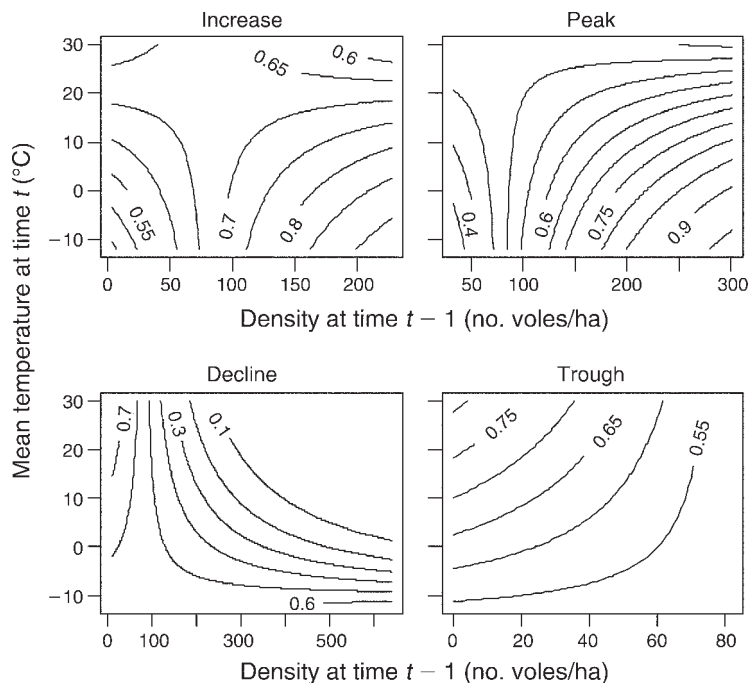


FIG. 3. Phase-specific interactions of population density (voles/ha) lagged by one month and mean temperature ($^{\circ}\text{C}$) with no time lags that governed prairie vole survival in the study population. Contour lines represent survival rate estimates.

mechanisms: (a) in the increase phase, survival rates showed a positive relationship with density of the previous month when mean temperatures at month t were relatively low (-12 to $+16^{\circ}\text{C}$) but declined at higher mean temperatures (Fig. 3a). Further, the curvature of the plot indicated that density had a greater effect at low temperatures and that temperature had the least effect at intermediate densities (~ 70 – 100 voles/ha). (b) The peak phase showed similar trends whereby survival rates increased with density of the previous month, but for a given density, survival rates were lower at higher temperatures and the effect of density diminished at higher temperatures ($\sim 21^{\circ}\text{C}$) than the increase phase (Fig. 3b). (c) In the decline phase, survival rates were generally low (0.1 – 0.6), and declined further with increasing lagged density (D_{t-1}) and mean temperature (Fig. 3c). In addition, temperature had a greater effect at high densities and the influence of density was more pronounced when temperatures were relatively high. (d) When the population was in the trough phase, survival rates were lowered with higher densities in the previous month but showed a positive relationship with increasing mean temperatures at month t (Fig. 3d).

Recruitment into our study population was highest during the increase phase, but declined with increasing density at time t and mean temperature at time $t - 1$ (Fig. 4). In the peak and decline phases, recruitment was low although density at time t contributed to a marginal increase in the former and a decline of almost 30% in the latter. Interestingly, as mean temperatures exceeded

10°C , recruitment rates showed a dramatic rise from near 0 to about 1.5 during the peak phase. Mean temperatures did not have any influence on recruitment rates in the decline and trough phases. However, we found indications of a steep increase in recruitment in the trough phase with increasing density.

DISCUSSION

Fluctuating populations are characterized by phase-specific changes in demographic and physiological characteristics (Krebs 1996, Oli and Dobson 1999). During the decline phase, age at maturity is delayed, juvenile survival and fertility are reduced, adverse social interactions (aggressive and spacing behaviors) increase, and the mean age of reproductive females increases (Boonstra 1994, Krebs 1996). In the increase phase, trends in the above life history variables are reversed (Oli and Dobson 1999, 2001). While density, either directly or through its influence on behavioral or demographic attributes, can influence these phase-specific changes, intrinsic factors may also contribute to phase dependence (Framstad et al. 1997). Our results support the above expectations, whereby: (1) all top models included phase-specific variation in the realized population growth rate as well as underlying vital rates; (2) apparent survival rates were lower during the decline phase than the increase phase, as has been previously reported (Krebs et al. 1995, Getz et al. 2000, Ozgul et al. 2004); (3) recruitment rate estimates based on our final model in Appendix D: Table D1c also showed similar

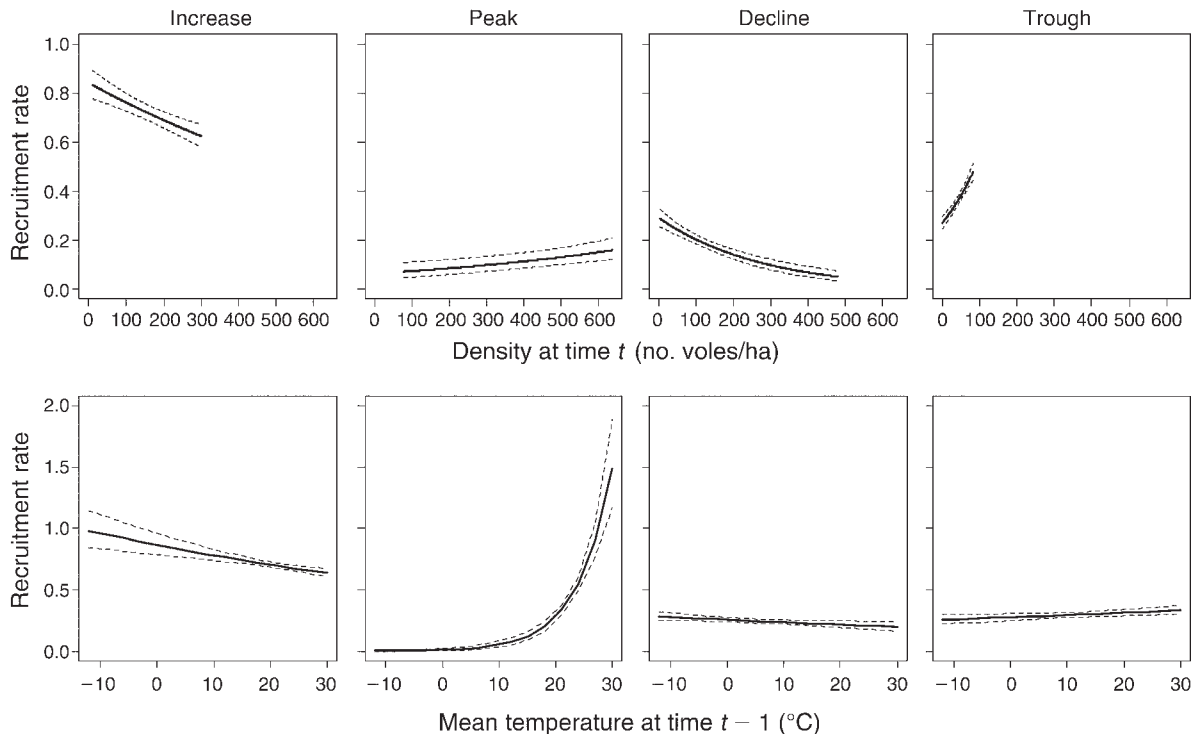


FIG. 4. The influence of phase-specific changes in population density (voles/ha) and lagged mean temperature ($^{\circ}\text{C}$) on recruitment rates in the study population. Dotted lines indicate 95% confidence intervals.

trends [decline phase, $\hat{f}(\hat{SE}) = 0.14$ (0.01); increase phase, $\hat{f}(\hat{SE}) = 0.72$ (0.01)].

Species ranging from mammals to insects demonstrate some form of negative feedback between population density and growth rate (Sibly et al. 2005). Initially, we did not find any evidence for density dependence; only a positive, albeit weak, relationship between lagged vole density and population growth rate was observed. However, phase-specific trends indicated a negative feedback between lagged density and population growth rate in all phases except the peak phase. Delayed density dependence, which was evident in phase-specific growth rates, is suggested to be a necessity for multiannual population cycles (Korpimäki et al. 2004). Arguments of cyclicity aside, lagged vole densities through its influence on one of the underlying vital rates (i.e., apparent survival) did appear to substantially influence the dynamics of our study population. Such a delayed effect of density on survival can potentially result from interactions with diminishing food supply or with natural enemies including predators, parasites, and diseases (Korpimäki et al. 2004). Although we did not directly test for predation effects, experimental studies in northern England conclusively demonstrate that predation is not a necessary or sufficient cause for population fluctuations in voles (Lambin et al. 2000, Graham and Lambin 2002). Delayed density dependence might also be induced by intrinsic factors (Boonstra et al. 1998),

but this idea has not been supported by theoretical, observational, or experimental studies of fluctuating small mammal populations (Ergon et al. 2001, Klemola et al. 2002, Turchin 2003).

Recruitment, a vital rate which includes immigration and births, demonstrated direct density dependence and was negatively influenced by density in the increase and decline phases. These results were consistent with the findings of Reed and Slade (2008) who report a negative feedback between density and recruitment for the prairie vole population in Kansas. At high densities, immigration tends to be reduced as individuals are unlikely to disperse if new territories are sparse (Lin and Batzli 2001), and also immigrants are less successful at colonizing a patch (Gundersen et al. 2002). Recruitment through births can also be impeded with increased intraspecific competition and food limitation at high densities. For one, sexual maturation and thereby reproduction may be suppressed in a hostile social environment (Boyce and Boyce 1988, Rodd and Boonstra 1988, Boonstra 1994). For another, environmental stress can reduce the success of females in raising young to weaning (Lambin and Yoccoz 1998, Koskela et al. 1999), or result in lower body mass (Webb et al. 2005) and potentially lower quality of the offspring (Rossiter 1994). In contrast, conspecific attraction and the benefits of conspecific presence when densities are low, can lead to improved recruitment in colonial species



PLATE 1. The prairie vole, *Microtus ochrogaster*, displays behavioral monogamy and pair territoriality. Here, a male *M. ochrogaster* is defending his pair territory from entry by an unfamiliar male. Photo credit: L. L. Getz.

such as the prairie vole (Stephens and Sutherland 1999). Thus, the positive relationship between density and recruitment evident in the low-density trough phase may have resulted because of the Allee effect (Stephens and Sutherland 1999, Stephens et al. 1999).

Stenseth et al. (2002, 2004) posit that the interaction between climatic variables and density-dependent factors may be a widespread phenomenon. Our results add to the findings of other studies (Grenfell et al. 1998, Coulson et al. 2001, Previtalli et al. 2009) that support the above contention, and suggest that direction and

magnitude of such interactive effects may be phase specific. In fact, ours is one of the first studies to directly test for the effects of various density- and climate-related factors on population growth rates through the application of CMR modeling techniques to long-term field data. Underlying demographic mechanisms suggest that the interaction between density and mean temperatures strongly influence vole survival (Appendix D: Table D1c). In the increase and peak phases, survival rates increased with lagged density while the reverse was true for the decline and trough phases (Fig. 3). Importantly,

with the exception of the trough phase, survival rates (1) declined with increasing mean temperatures at relatively high densities (> 100 voles/ha) and (2) increased with mean temperature when densities were comparatively low (lower than ~ 70 voles/ha). These results seem to suggest that density-dependence is expressed more profoundly when temperatures are high. This is further evidenced by the finding that survival rates increased with mean temperature in the trough phase where densities were less than ~ 70 voles/ha.

Despite the difficulties of interpreting results that include interactive effects, the above findings are fairly intuitive. At high temperatures, prairie voles active outside their burrows may be susceptible to hyperthermia leading to lowered life expectancy (Getz et al. 1997). In addition, it is conceivable that resource competition and other external factors that may depress survival rates at high densities (Korpimäki et al. 2004) are more influential when mean temperatures are high. In fact, our results suggest that when temperatures are low, increasing densities help boost survival rates. Prairie voles nest communally (Getz et al. 1993, Getz and McGuire 1997), and high densities in the colder months may indeed help improve survival via improved thermoregulation.

The results of our study come from a long-term data set on a fluctuating prairie vole population. Previous analyses of these data tested the role of changes in survival and reproduction in relation to (1) initiation of, and intervals between, population fluctuations (Getz et al. 2006b), (2) amplitudes of observed fluctuations (Getz et al. 2006a), (3) temporal and phase-related changes (Ozgul et al. 2004), (4) comparisons among phases of fluctuations (Getz et al. 2007b), and (5) phase homogeneity (Getz and McGuire 2009). These analyses involved primarily density-dependent factors. In addition, Getz et al. (2007a) evaluated the effect of weather extremes on amplitudes of population fluctuations while Wang and Getz (2007) investigated the role of environmental stochasticity and density dependence on population dynamics. In this paper, we add to the above findings by highlighting the role of vole density and density-independent climatic variation in driving demographic mechanisms that underlie the fluctuations in this population. We note that an exploratory analysis on a five-year subset of the data did not reveal all of the same patterns (V. R. Goswami, *unpublished analysis*), highlighting the importance of long-term data sets in teasing apart the effects of density-dependent and density-independent factors on population dynamics.

Our understanding of the factors that drive the dynamics of fluctuating populations will be further strengthened if similar trends are found from other such populations. Therefore, we hope that the relationships we report are tested on other species or populations for which long-term demographic and weather data are available. It is now well recognized that the impact of

broad climatic phenomena such as the NAO, the Arctic Oscillation, and the ENSO, as well as global climate change can be extensive and deep rooted (Sæther et al. 2000, Stenseth et al. 2002, Walther et al. 2002, Hallett et al. 2004, Ozgul et al. 2010). Thus, the implications of climatic forcing on the dynamics of fluctuating populations are likely to be substantial in the future. However, we conclude by restating that both density dependence and density-independent climatic variables are important determinants of population fluctuations; it is their synergistic effects during each phase of density fluctuations that will shape the fate of such populations over time.

ACKNOWLEDGMENTS

This study was supported in part by grants NSF DEB 78–25864 and NIH HD 09328 (to L. L. Getz) and by the University of Illinois School of Life Sciences and Graduate College Research Board. Data analysis and manuscript preparation were supported by a grant from the NSF DEB-0224953 (to M. K. Oli) and the University of Florida Alumni Fellowship (to V. R. Goswami and J. A. Hostetler). Assistance in the field was provided by: D. Tazik, B. McGuire, J. Hofmann, P. Mankin, T. Pizzuto, M. Snarski, S. Buck, K. Gubista, S. Vanthornout, W. Holmgren, P. Malmberg, B. Klatt, L. Gavish, and B. Frase. M. Snarski entered the data sets into the computer. Two anonymous reviewers provided many helpful comments. We record our gratitude to all institutions and individuals mentioned above.

LITERATURE CITED

- Batzli, G. O. 1992. Dynamics of small mammal populations: a review. Pages 831–850 in D. R. McCullough, and R. H. Barrett, editors. *Wildlife 2001: populations*. Elsevier Applied Science, London, UK.
- Boonstra, R. 1994. Population-cycles in microtines—the senescence hypothesis. *Evolutionary Ecology* 8:196–219.
- Boonstra, R., C. J. Krebs, and N. C. Stenseth. 1998. Population cycles in small mammals: the problem of explaining the low phase. *Ecology* 79:1479–1488.
- Boyce, C. C. K., and J. L. Boyce. 1988. Population biology of *Microtus arvalis*. 1. Lifetime reproductive success of solitary and grouped breeding females. *Journal of Animal Ecology* 57:711–722.
- Burt, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. *University Michigan Museum of Zoology Miscellaneous Publications* 45:1–58.
- Cormack, R. M. 1964. Estimates of survival from sighting of marked animals. *Biometrika* 51:429–438.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292:1528–1531.
- Coulson, T., T. H. G. Ezard, F. Pelletier, G. Tavecchia, N. C. Stenseth, D. Z. Childs, J. G. Pilkington, J. M. Pemberton, L. E. B. Kruuk, T. H. Clutton-Brock, and M. J. Crawley. 2008. Estimating the functional form for the density dependence from life history data. *Ecology* 89:1661–1674.
- Coulson, T., E. J. Milner-Gulland, and T. Clutton-Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society B* 267:1771–1779.
- Coulson, T., P. Rohani, and M. Pascual. 2004. Skeletons, noise and population growth: the end of an old debate? *Trends in Ecology and Evolution* 19:359–364.
- Ergon, T., J. L. MacKinnon, N. C. Stenseth, R. Boonstra, and X. Lambin. 2001. Mechanisms for delayed density-dependent

- reproductive traits in field voles, *Microtus agrestis*: the importance of inherited environmental effects. *Oikos* 95:185–197.
- Farand, E., D. Allaine, and J. Coulon. 2002. Variation in survival rates for the alpine marmot (*Marmota marmota*): effects of sex, age, year, and climatic factors. *Canadian Journal of Zoology* 80:342–349.
- Forchhammer, M. C., N. C. Stenseth, E. Post, and R. Langvatn. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proceedings of the Royal Society B* 265:341–350.
- Framstad, E., N. C. Stenseth, O. N. Bjornstad, and W. Falck. 1997. Limit cycles in Norwegian lemmings: tensions between phase-dependence and density-dependence. *Proceedings of the Royal Society B* 264:31–38.
- Getz, L. L., J. E. Hofmann, B. McGuire, and T. W. Dolan. 2001. Twenty-five years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in three habitats in east-central Illinois. *Journal of Mammalogy* 82:22–34.
- Getz, L. L., J. E. Hofmann, M. K. Oli, and B. McGuire. 2007a. Vole population dynamics: influence of weather extremes on stoppage of population growth. *American Midland Naturalist* 158:461–466.
- Getz, L. L., and B. McGuire. 1997. Communal nesting in prairie voles (*Microtus ochrogaster*): formation, composition, and persistence of communal groups. *Canadian Journal of Zoology* 75:525–534.
- Getz, L. L., and B. McGuire. 2009. Demography of fluctuating vole populations: phase homogeneity of demographic variables. *Basic and Applied Ecology* 10:170–177.
- Getz, L. L., B. McGuire, T. Pizzuto, J. E. Hofmann, and B. Frase. 1993. Social-organization of the prairie vole (*Microtus ochrogaster*). *Journal of Mammalogy* 74:44–58.
- Getz, L. L., M. K. Oli, J. E. Hofmann, and B. McGuire. 2006a. Vole population dynamics: factors affecting peak densities and amplitudes of *Microtus ochrogaster* population fluctuations. *Basic and Applied Ecology* 7:97–107.
- Getz, L. L., M. K. Oli, J. E. Hofmann, and B. McGuire. 2006b. Vole population fluctuations: factors that initiate and determine intervals between them in *Microtus ochrogaster*. *Journal of Mammalogy* 87:387–393.
- Getz, L. L., M. K. Oli, J. E. Hofmann, and B. McGuire. 2007b. Demography of fluctuating prairie vole populations: comparison of demographic variables among phases of fluctuations. *Acta Theriologica* 52:291–298.
- Getz, L. L., L. E. Simms, and B. McGuire. 2000. Nestling survival and population cycles in the prairie vole, *Microtus ochrogaster*. *Canadian Journal of Zoology* 78:1723–1731.
- Getz, L. L., L. E. Simms, B. McGuire, and M. E. Snarski. 1997. Factors affecting life expectancy of the prairie vole, *Microtus ochrogaster*. *Oikos* 80:362–370.
- Graham, I. M., and X. Lambin. 2002. The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. *Journal of Animal Ecology* 71:946–956.
- Grenfell, B. T., K. Wilson, B. F. Finkenstadt, T. N. Coulson, S. Murray, S. D. Albon, J. M. Pemberton, T. H. Clutton-Brock, and M. J. Crawley. 1998. Noise and determinism in synchronized sheep dynamics. *Nature* 394:674–677.
- Gundersen, G., H. P. Andreassen, and R. A. Ims. 2002. Individual and population level determinants of immigration success on local habitat patches: an experimental approach. *Ecology Letters* 5:294–301.
- Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and B. T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* 430:71–75.
- Hines, J. E., and J. D. Nichols. 2002. Investigations of potential bias in the estimation of lambda using Pradel's (1996) model for capture–recapture data. *Journal of Applied Statistics* 29:573–587.
- Jolly, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic model. *Biometrika* 52:225–247.
- Jorgenson, J. T., M. Festa-Bianchet, J. M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology* 78:1019–1032.
- Klemola, T., E. Korpimäki, and M. Koivula. 2002. Rate of population change in voles from different phases of the population cycle. *Oikos* 96:291–298.
- Korpimäki, E., P. R. Brown, J. Jacob, and R. P. Pech. 2004. The puzzles of population cycles and outbreaks of small mammals solved? *BioScience* 54:1071–1079.
- Koskela, E., T. Mappes, and H. Ylonen. 1999. Experimental manipulation of breeding density and litter size: effects on reproductive success in the bank vole. *Journal of Animal Ecology* 68:513–521.
- Krebs, C. J. 1996. Population cycles revisited. *Journal of Mammalogy* 77:8–24.
- Krebs, C. J. 1999. *Ecological methodology*. Addison-Wesley, New York, New York, USA.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
- Krebs, C. J., M. S. Gaines, B. L. Keller, J. H. Myers, and R. H. Tamarin. 1973. Population cycles in small rodents. *Science* 179:35–41.
- Laake, J. L., and E. A. Rexstad. 2007. RMark. Appendix C in E. G. Cooch and G. C. White, editors. Program MARK: a gentle introduction. (<http://www.phidot.org/software/mark/docs/book/>)
- Lambin, X., S. J. Petty, and J. L. MacKinnon. 2000. Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology* 69:106–118.
- Lambin, X., and N. G. Yoccoz. 1998. The impact of population kin-structure on nestling survival in Townsend's voles, *Microtus townsendii*. *Journal of Animal Ecology* 67:1–16.
- Lin, Y. T. K., and G. O. Batzli. 2001. The influence of habitat quality on dispersal demography, and population dynamics of voles. *Ecological Monographs* 71:245–275.
- Nichols, J. D., and J. E. Hines. 2002. Approaches for the direct estimation of lambda, and demographic contributions to lambda, using capture–recapture data. *Journal of Applied Statistics* 29:539–568.
- Nichols, J. D., J. E. Hines, J. D. Lebreton, and R. Pradel. 2000. Estimation of contributions to population growth: a reverse-time capture–recapture approach. *Ecology* 81:3362–3376.
- Oli, M. K. 2003. Population cycles of small rodents are caused by specialist predators: or are they? *Trends in Ecology and Evolution* 18:105–107.
- Oli, M. K., and F. S. Dobson. 1999. Population cycles in small mammals: the role of age at sexual maturity. *Oikos* 86:557–565.
- Oli, M. K., and F. S. Dobson. 2001. Population cycles in small mammals: the alpha-hypothesis. *Journal of Mammalogy* 82:573–581.
- Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466:482–485.
- Ozgul, A., L. L. Getz, and M. K. Oli. 2004. Demography of fluctuating populations: temporal and phase-related changes in vital rates of *Microtus ochrogaster*. *Journal of Animal Ecology* 73:201–215.
- Pradel, R. 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- Previtali, M. A., M. Lima, P. L. Meserve, D. A. Kelt, and J. R. Gutierrez. 2009. Population dynamics of two sympatric

- rodents in a variable environment: rainfall, resource availability, and predation. *Ecology* 90:1996–2006.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (www.r-project.com)
- Reed, A. W., and N. A. Slade. 2008. Density-dependent recruitment in grassland small mammals. *Journal of Animal Ecology* 77:57–65.
- Rodd, F. H., and R. Boonstra. 1988. Effects of adult meadow voles, *Microtus pennsylvanicus*, on young conspecifics in field populations. *Journal of Animal Ecology* 57:755–770.
- Rossiter, M. 1994. Maternal effects hypothesis of herbivore outbreak. *BioScience* 44:752–763.
- Sæther, B. E., J. Tufto, S. Engen, K. Jerstad, O. W. Rostad, and J. E. Skatan. 2000. Population dynamical consequences of climate change for a small temperate songbird. *Science* 287:854–856.
- Seber, G. A. F. 1965. A note on multiple-recapture census. *Biometrika* 52:249–259.
- Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the regulation of populations of mammals, birds, fish, and insects. *Science* 309:607–610.
- Sinclair, A. R. E. 1989. Population regulation in animals. Pages 197–241 in J. M. Cherratt, editor. *Ecological concepts: the contribution of ecology to an understanding of the natural world*. Blackwell Scientific Publications, Oxford, UK.
- Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87:427–461.
- Stenseth, N. C., K. S. Chan, G. Tavecchia, T. Coulson, A. Mysterud, T. Clutton-Brock, and B. Grenfell. 2004. Modelling non-additive and nonlinear signals from climatic noise in ecological time series: Soay sheep as an example. *Proceedings of the Royal Society B* 271:1985–1993.
- Stenseth, N. C., K. S. Chan, H. Tong, R. Boonstra, S. Boutin, C. J. Krebs, E. Post, M. O'Donoghue, N. G. Yoccoz, M. C. Forchhammer, and J. W. Hurrell. 1999. Common dynamic structure of Canada lynx populations within three climatic regions. *Science* 285:1071–1073.
- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* 297:1292–1296.
- Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution* 14:401–405.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos* 87:185–190.
- Turchin, P. 2003. *Complex population dynamics: a theoretical/empirical synthesis*. Princeton University Press, Princeton, New Jersey, USA.
- Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Wang, G., and L. L. Getz. 2007. State space models for stochastic and seasonal fluctuations of vole and shrew populations in east central Illinois. *Ecological Modelling* 207:189–196.
- Webb, R. E., D. M. Leslie, R. L. Lochmiller, and R. E. Masters. 2005. Impact of food supplementation and methionine on high densities of cotton rats: support of the amino-acid-quality hypothesis? *Journal of Mammalogy* 86:46–55.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, California, USA.

APPENDIX A

Results from the Cormack-Jolly-Seber models used to evaluate the relative effects of time and sex on survival rates of prairie voles at the University of Illinois Biological Research Area from 1972 to 1997 (*Ecological Archives* E092-142-A1).

APPENDIX B

Model selection statistics used to determine appropriate model structure for recapture probability under the survival–population-growth rate parameterization of Pradel's model (*Ecological Archives* E092-142-A2).

APPENDIX C

Model comparison tables evaluating the relative influences of phase-dependent, density-dependent, and density-independent processes on vole survival and population growth rate. Also presented are the phase-specific effects of density and climate on ϕ and λ (*Ecological Archives* E092-142-A3).

APPENDIX D

Model selection statistics under the survival–recruitment parameterization of Pradel's model used to evaluate the relative influences of density-dependent and density-independent processes, as well as the synergistic effects of phase, density and climate on prairie vole survival and recruitment rates (*Ecological Archives* E092-142-A4).