Delayed Density-Dependent Season Length Alone Can Lead to Rodent Population Cycles

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ABSTRACT: Studies of cyclic microtine populations (voles and lemmings) have suggested a relationship between the previous year's population density and the subsequent timing of the onset of reproduction by overwintered breeding females. No studies have explored the importance of this relationship in the generation of population cycles. Here we mathematically examine the implications of variation in reproductive season length caused by delayed density-dependent changes in its start date. We demonstrate that when reproductive season length is a function of past population densities, it is possible to get realistic population cycles without invoking any changes in birth rates or survival. When parameterized for field voles (*Microtus agrestis*) in Kielder Forest (northern England), our most realistic model predicts population cycles of similar periodicity to the Kielder populations. Our study highlights the potential importance of density-dependent reproductive timing in microtine population cycles and calls for investigations into the mechanism(s) underlying this phenomenon.

Keywords: population dynamics, *Microtus agrestis*, delayed density dependence, season length, life history, seasonality.

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Despite ever-enlarging data sets on cyclic microtine (vole and lemming) populations around the world, there is still great uncertainty over the causal mechanisms behind their population cycles (Stenseth 1999; Turchin 2003). Analysis of these data sets has led to the consensus that both direct and delayed density-dependent mechanisms operate on the populations (Stenseth 1999; Lambin et al. 2002; Turchin 2003). That is, the populations are influenced by factors that are a function of the current population density and by factors that are a function of the population density in the past. Direct density-dependent mechanisms tend to stabilize population dynamics, making them less prone to cycle, whereas delayed density-dependent mechanisms do the opposite (May 1981; Murray 2003).

There are several schools of thought concerning the cause of the delayed density dependence. The most commonly considered factors are the effects of specialist predators, resource (usually food) shortage, and intrinsic (e.g., maternal) factors (Stenseth 1999; Berryman 2002; Turchin 2003; Korpimäki et al. 2004). Studies of cyclic Fennoscandian vole populations have generally concluded that the density of specialist predators is the important delayed density-dependent factor (Hanski et al. 2001; Turchin 2003), but for most other cyclic rodent populations, less of a consensus exists. For example, studies of field vole (*Microtus agrestis*) populations in Kielder Forest, northern England, have suggested that specialist predators play no causal role in the population cycles (Graham and Lambin 2002). Perhaps the only emerging consensus from these studies is that delayed density dependence acting on the populations in the winter is a prerequisite for the population cycles (Hansen et al. 1999; Stenseth et al. 2003; Hörnfeldt 2004; Bierman et al. 2006).

Previous studies have shown that environmental influences on the length of the breeding season are important in determining whether microtine populations cycle or not (Hansen et al. 1999; Stenseth et al. 2002; Saitoh et al. 2003). However, the timing of the breeding season can also vary in relation to the different "phases" of microtine population cycles (Krebs and Myers 1974; Krebs 1996; Boonstra et al. 1998; Batzli 1999; Hansen et al. 1999). Therefore,

not only does breeding season length vary in response to external factors, but it can also vary in response to past population densities. For example, Wiger (1982) proposed that variation in the date of onset of breeding season in *Clethrionomys glareolus* may be explained by direct density-dependent territoriality in the breeding female population. Using a detail-rich population model, Stenseth and Fagerström (1986) found that this mechanism could lead to population cycles. However, those population cycles bore little resemblance to those found in natural populations. Here we will investigate the effect of past densities on reproductive timing and how this determines the population dynamics. Previous theoretical assessments have ignored this effect, perhaps because field populations are sampled too infrequently to yield reliable data on the timing of seasonal life-history events. Furthermore, many field studies have sampled at a fixed time point (or time points) in the year. This fails to adequately capture variation in the actual timing of life-history events in the studied populations.

Recent, more intensive studies of the Kielder Forest system have also shown that vole life-history traits are affected by their population density in the preceding year (Ergon et al. 2001*a*). When field voles at Kielder Forest were transferred to other sites, they rapidly took on the breeding characteristics of animals native to those sites (Ergon et al. 2001*b*). This shows that the "memory" of past densities resides in the environment, not in the voles themselves (Ergon et al. 2001*a*), and rules out maternal or genetic effects as a cause for the cycles. Shortage of food is an obvious possible external mechanism through which breeding may be suppressed. However, a recent study also revealed that microparasite loads in the Kielder Forest field voles follow the vole population dynamics in a delayed density-dependent manner (Cavanagh et al. 2004).

Regardless of the fundamental cause of the cycles in Kielder Forest, studies have shown that the external memory of past population densities influences the date at which the reproductive season starts (Ergon 2003). Specifically, Ergon (2003) found a significant positive relationship between the date that 50% of the voles had produced their first litter in one year and the population density at the start of the previous spring. In light of this, we ask whether such seasonal effects might contribute to cyclicity.

We used a series of mathematical models to investigate whether the delayed density-dependent effect of population density on the timing of onset of the reproductive season can cause realistic microtine population cycles. This contrasts with the studies of Wiger (1982) and Stenseth and Fagerström (1986), who assumed that season length was directly density dependent. In addition, we use the simplest possible model to study this phenomenon (in

contrast to Stenseth and Fagerström 1986). We assume that changes in the start date of the reproductive season directly relate to the reproductive season length (the end date of the reproduction season is assumed fixed). We acknowledge that many other factors are likely to affect reproductive season length. However, here we aim to explore the implications of delayed density-dependent season length using the new data and findings derived from the Kielder Forest field vole populations.

Our theoretical study will provide crucial evidence as to whether the seasonal effects discussed above should be included in assessments of the mechanisms that lead to (rather than result from) population cycles. We contend that if the models do show appropriate population cycles, then continued neglect of these seasonal effects in studies of the causes of microtine cycles cannot be justified. Our results below support this contention for the Kielder Forest system at least.

Models

We analyze three models that differ only in the time frame over which delayed density-dependent season length operates (as illustrated in fig. 1). We refer to these models as model A (long delay), model B (medium delay), and model C (short delay). Note that we use N_T to refer to the vole population density (voles ha^{-1}) as a discrete function of time (at the end of the breeding season in year T) and $n(t)$ to refer to it as a continuous function of time.

For all models, we assume that each year is divided into a reproductive and a nonreproductive season. Within the seasons, we assume identical individuals and complete mixing. This gives

$$\frac{dn(t)}{dt} = rn(t) \tag{1}$$

in the reproductive season and

$$\frac{dn(t)}{dt} = -bn(t) \tag{2}$$

in the nonreproductive season, where $n(t)$ is the population density (voles ha^{-1}) at time t (years), r is the per capita rate of population increase in the reproductive season, and b is the per capita mortality rate in the nonreproductive season. The absence of direct density dependence in equations (1) and (2) reinforces the fact that we seek to understand the effect of one factor only, that of a variable season length.

In all three model formulations, the length of the reproductive season is a function of the population density at some time in the past ($L_T = f(n(t))$; see fig. 1). In model

Model A
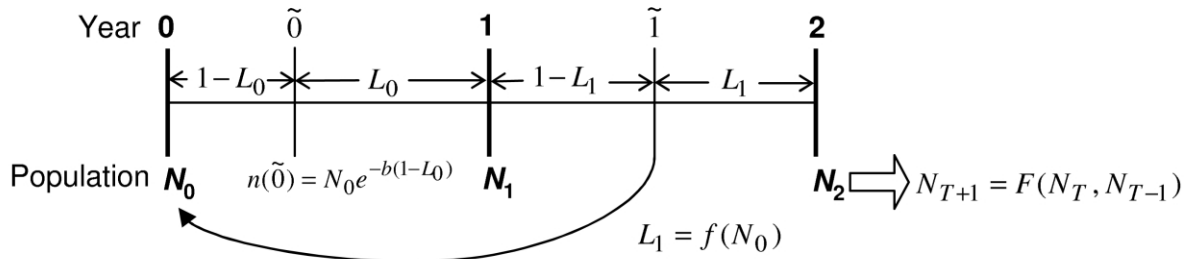
Model B
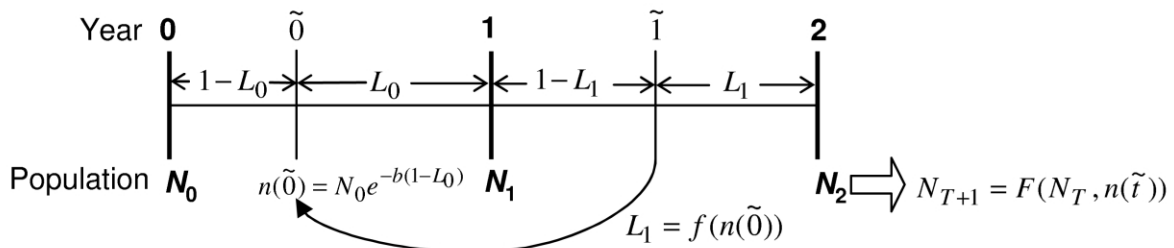
Model C
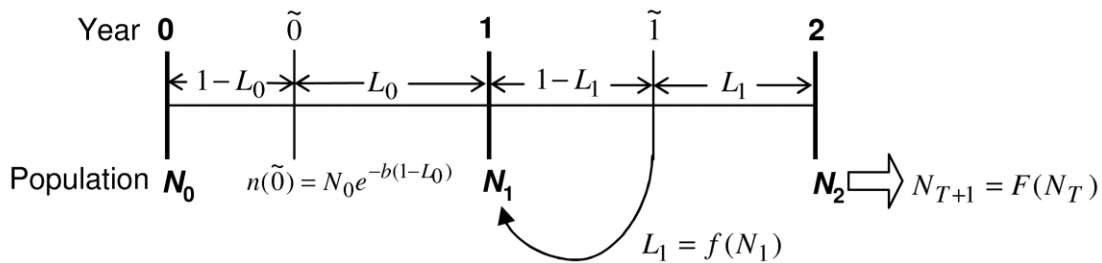
Figure 1: Schematic representation of models A–C: N_T is the population density at discrete time T, which is the end of the reproductive season; n_t is the population density at continuous time t; and L is the length of the reproductive season. Although reproductive (L) and nonreproductive $(1 - L)$ seasons have the same population dynamics for all three models (see eqq. [1] and [2]), the delay over which previous population density affects the start date of the reproductive season differs. The curved arrow indicates how the relevant population density in the past relates to the season length for the three models. The tilde indicates the transition between the reproductive and nonreproductive seasons. The arrowed functional relationship to the right of each diagram represents the general functional relationship that can be derived for each model.

A, L_T is a function of the population density at the start of the previous year (N_{T-1}). In model B, L_T is a function of the population density at the start of the previous reproductive season, occurring at some time (e.g., $\tilde{t}$) between $T - 1$ and T. In model C, L_T is a function of the population density at the end of the previous reproductive season (N_T). The delayed density dependence in model B corresponds to the field data from Kielder Forest (Ergon 2003) discussed above. We chose to analyze all three models to see how plausible delays of different lengths affect our results.

Equations (1) and (2) have simple analytical solutions

for $n(t)$. These can be combined with the framework for models A, B, and C (fig. 1) to derive mathematical expressions for the three models (see appendix): in model A,

$$N_{T+1} = N_T e^{-b+(r+b)f(N_{T-1})}; \qquad (3a)$$

in model B,

$$N_{T+1} = N_T e^{-b+(r+b)f(n(\tilde{t}))}; \qquad (3b)$$

and in model C,

$$N_{T+1} = N_T e^{-b+(r+b)f(N_T)}. \tag{3c}$$

For equations (3a)–(3c), this means that the population density next year is equal to the population density in the current year multiplied by the net per capita growth from the reproductive season and proportional survival through the nonreproductive season. N_T

There are insufficient data to produce an accurate functional relationship for the delayed density dependence of season length for the field voles in Kielder Forest. Therefore, we use the negative sigmoid relationship between reproductive season length and population density:

$$f(n(t)) = \alpha\left(\frac{1+\beta}{\beta}\right)\left(1 - \frac{1}{1+\beta e^{-n(t)/\tau}}\right) + (\kappa - \alpha), \tag{4}$$

where κ is the maximum reproductive season length, $\kappa - \alpha$ is the minimum reproductive season length (here $1 > \kappa > \alpha$), and β and τ scale the slope of the sigmoid function. In equation (4), $n(t)$ is the population density at the appropriate time (see fig. 1). Using equation (4), we can then explore the effects of different-shaped functional relationships on the model dynamics. Figure 2 illustrates equation (4) for various values of α, β, and τ.

The nontrivial steady state solution for all three models (eqq. [3]) is

$$f(n^*) = \frac{b}{r+b}$$

$$\Rightarrow n^* = \ln\left\{\frac{\beta[\kappa(r+b)-b] + \alpha(r+b)}{b - (\kappa - \alpha)(r+b)}\right\}^\tau. \tag{5}$$

Here n^* is the population density that gives repeated and identical annual cycles. It corresponds to the population density at time T in models A and C and at time $\tilde{t}$ in model B (fig. 1). For realistic population densities, this requires that $(\kappa - \alpha)(r+b) < b < (\beta\kappa + \alpha)(r+b)/\beta$ and $\beta[\kappa(r+b) - b] + \alpha(r+b) > b - (\kappa - \alpha)(r+b)$.

It is possible to derive stability criteria for the annual cycles for all three models (see appendix). This gives the criteria for the local stability of n^* as

$$S_{\text{crit}} < S < 0, \tag{6a}$$

where

$$S = (r+b)n^*f'(n^*)$$

$$= \frac{\{\beta[\kappa(r+b)-b] + \alpha(r+b)\}[b-(\kappa-\alpha)(r+b)]}{(\alpha+\alpha\beta)(r+b)} \tag{6b}$$

$$\times \ln\left\{\frac{b-(\kappa-\alpha)(r+b)}{\beta[\kappa(r+b)-b] + \alpha(r+b)}\right\}.$$

Here, $f'(n^*)$ is the first-order derivative of $f(n(t))$ with respect to $n(t)$ at n^*, and S is an index of stability. Given the conditions for a positive equilibrium population density in equation (5), S must be negative. $S_{\text{crit}} = -1$ for model A and $S_{\text{crit}} = -2$ for model C. For model B, S_{crit} depends on r and b and varies between -1 and -3 (see appendix). Our stability analysis (appendix) shows that the parameter τ has no effect on the stability of the equilibrium solution (eq. [6b]); however, it does affect the equilibrium population density (eq. [5]).

Parameterization

To investigate the stability and dynamics of the models above, we need estimates for six parameters (r, b, α, β, κ, and τ). Therefore, we define representative parameter values from Kielder Forest data and explore model stability
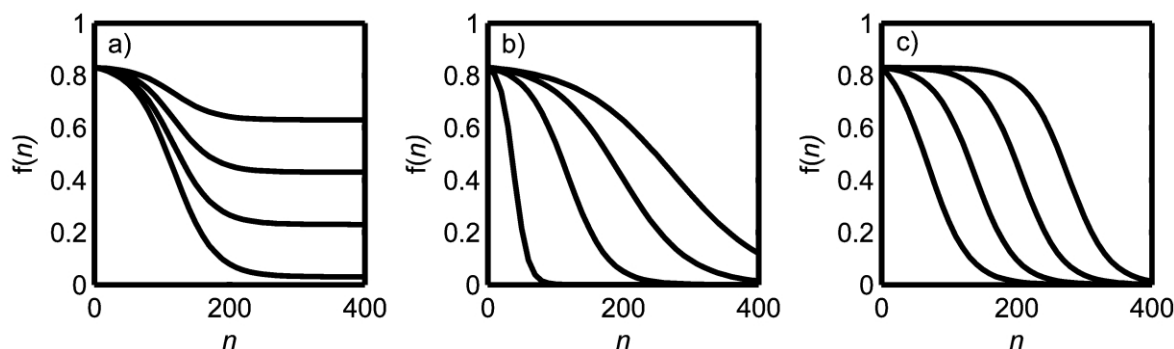
Figure 2: Functional form of equation (4) plotted against population density, where for *a*, $\kappa = 0.83$ (10 months), $\beta = 50$, $\tau = 30$, and $\alpha = 0.2$, 0.4, 0.6, and 0.8 (top to bottom); *b*, $\kappa = 0.83$, $\beta = 50$, $\alpha = 0.83$, and $\tau = 10$, 30, 50, and 70 (left to right); and *c*, $\kappa = 0.83$, $\tau = 30$, $\alpha = 0.83$, and $\beta = 10$, 100, 1,000, and 10,000 (left to right).
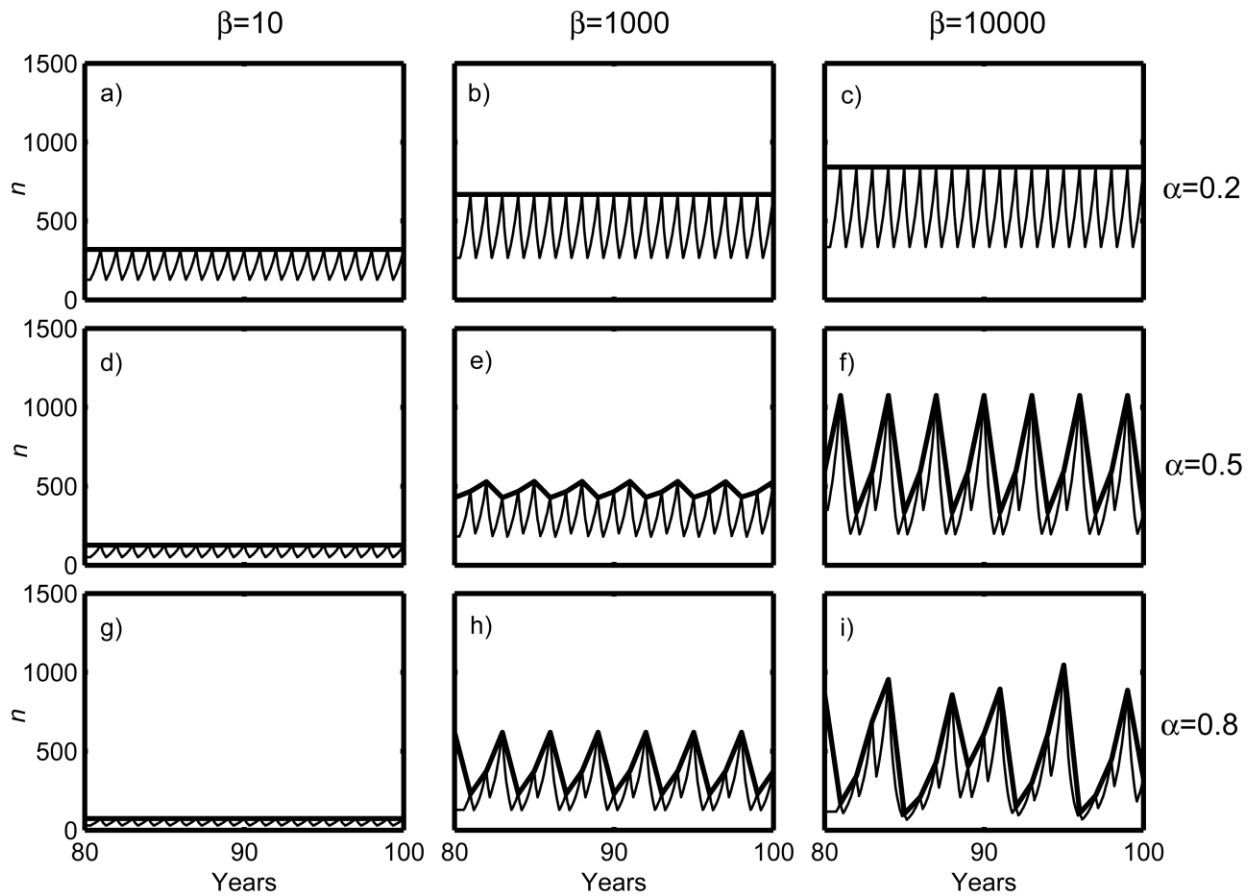
Figure 3: Numerical results for model B between 80 and 100 years, where initial population density $= 50$, $r = 1.4$, $b = 2.7$, $\tau = 30$, and $\kappa = 0.83$, for different values of α (0.2, 0.5, and 0.8, top to bottom, respectively) and β (10, 1,000, and 10,000, left to right, respectively). The thin line shows the within-year dynamics. The thick line connects the population densities at the end of each reproductive season to illustrate whether dynamics are stable or show multiyear population cycles.

and dynamics for variation in each parameter while keeping the remaining parameters fixed at their mean values.

We estimate the per capita rate of increase *r* by assuming that the "increase phase" of the vole density cycle represents maximum annual growth rate. Any subsequent change in the annual population growth rate is therefore a result of the delayed density-dependent season length function. Data from Burthe (2005) for various trapping sites in Kielder Forest gave $1 < r < 1.7$. Using data from Graham and Lambin (2002) and Burthe (2005) gave monthly survival probabilities between 0.6 and 0.9. For our analysis, we assume an instantaneous rate $b = 2.7$ (monthly survival $\cong 0.8$) and $r = 1.4$.

We assume $\kappa = 0.83$ ($= 10/12$) because the maximum reproductive season length for field voles in Kielder Forest is 10 months (MacKinnon 1998; Ergon et al. 2001*a*), and $\tau = 30$ (τ does not affect the stability of the models). The calculation of α and β and the determination of the pa-

rameter ranges for the sensitivity analysis for all six parameters are detailed and discussed in the results below.

Results

Stability analysis of all three models, using equations (6) with the parameters defined in the previous section, showed that the equilibrium population density (eq. [5]) becomes unstable to small perturbations above critical α and β values. For certain realistic parameter combinations, the models predict regular or quasiperiodic multiyear cycles (cyclic dynamics with a dominant but slightly variable period). Numerical analysis of model B (fig. 3) illustrates the effect of changing α and β values on the population dynamics. For low α values in the range analyzed (fig. 3*a*–3*c*), β does not affect the overall stability, and stable population dynamics are predicted (the dynamics are stable in discrete time and show an annual periodicity in con-

tinuous time). For higher α values (fig. 3*d*–3*i*), there is a threshold value of β above which model B produces multiyear cycles. Qualitatively similar dynamics are produced by models A and C. Therefore, all three models predict that delayed density-dependent season length can result in multiyear population density cycles. We next consider whether the predicted cycles are similar to those found in the Kielder Forest field voles and whether their dominant period is sensitive to changes in parameter values.

Sensitivity analysis of the dominant period of the population dynamics to parameter variation is shown in figure 4. We used $\alpha = 0.5$ and $\beta = 10,000$ when not varying these parameters (see fig. 3*f* for example dynamics for model B). The parameter values for the sensitivity analysis were picked using sensible ranges from the Kielder Forest field vole population data but additionally restricting the ranges to those that did not violate the conditions for a positive population density in equation (5). The sensitivity analysis clearly illustrates that delayed density-dependent season length can result in multiyear population fluctuations over a range of parameter values. Where the models do predict such cycles (dominant period > 1), model A predicts periodicities of 6–10 years, whereas models B and C predict periodicities of 3–4 years. The periodicity of the Kielder Forest cycles is about 3–4 years (fig. 5*b*; Lambin et al. 2000). Thus, only models B and C predict periodicities similar to the observed cycles. Furthermore, model B predicts periodicities that are similar to the Kielder Forest cycles over the largest range of parameter variation. For certain parameter combinations, the dynamics of model
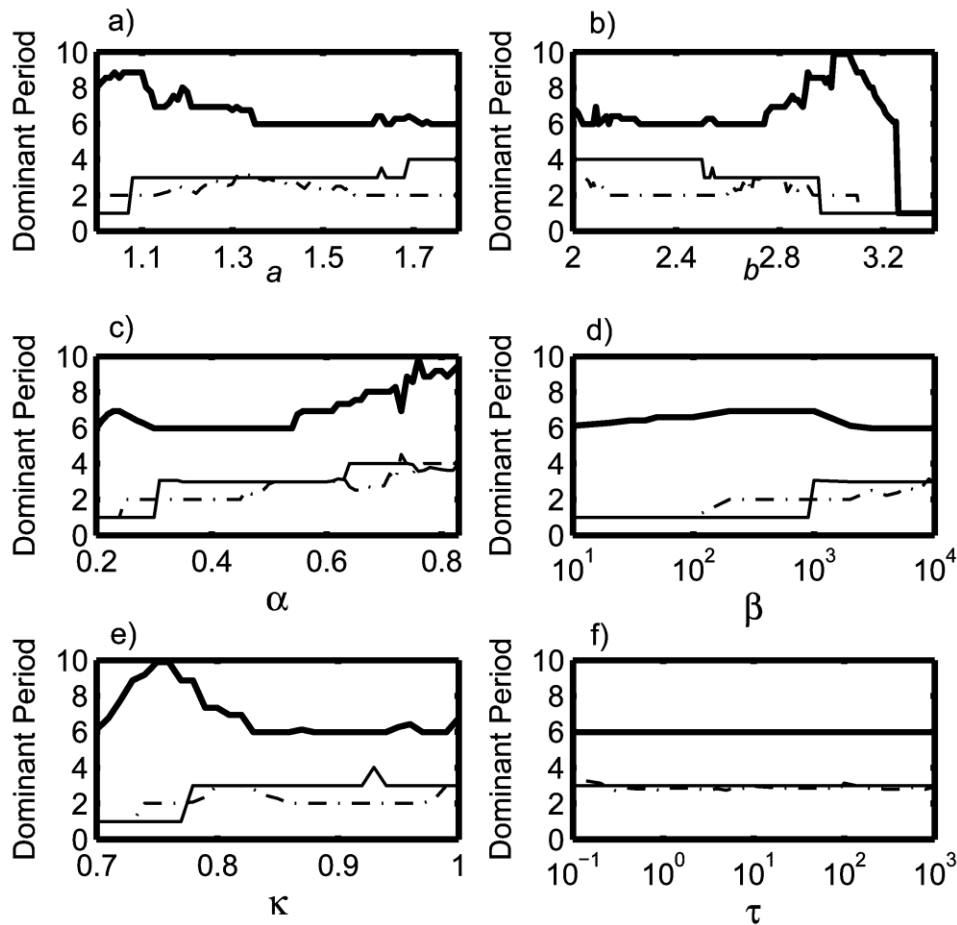
Figure 4: Sensitivity analysis of the dominant period of population fluctuations to variation in parameter values. Dominant period was determined using power spectrum analysis. The constant parameters (other than when an individual parameter was varied in the analysis) are $r = 1.4$, $b = 2.7$, $\alpha = 0.5$, $\beta = 10,000$, $\tau = 30$, and $\kappa = 0.83$. The lines correspond to model A (*thick*), model B (*thin*), model C (*dashed*). When the dominant period equals 1, the populations are at equilibrium and do not show multiyear population cycles. Minor fluctuations in the lines represent either small chaotic windows in parameter space that otherwise predicts stable oscillations or regions of parameter space giving chaotic dynamics but where the dominant period is sensitive to minor parameter variation.
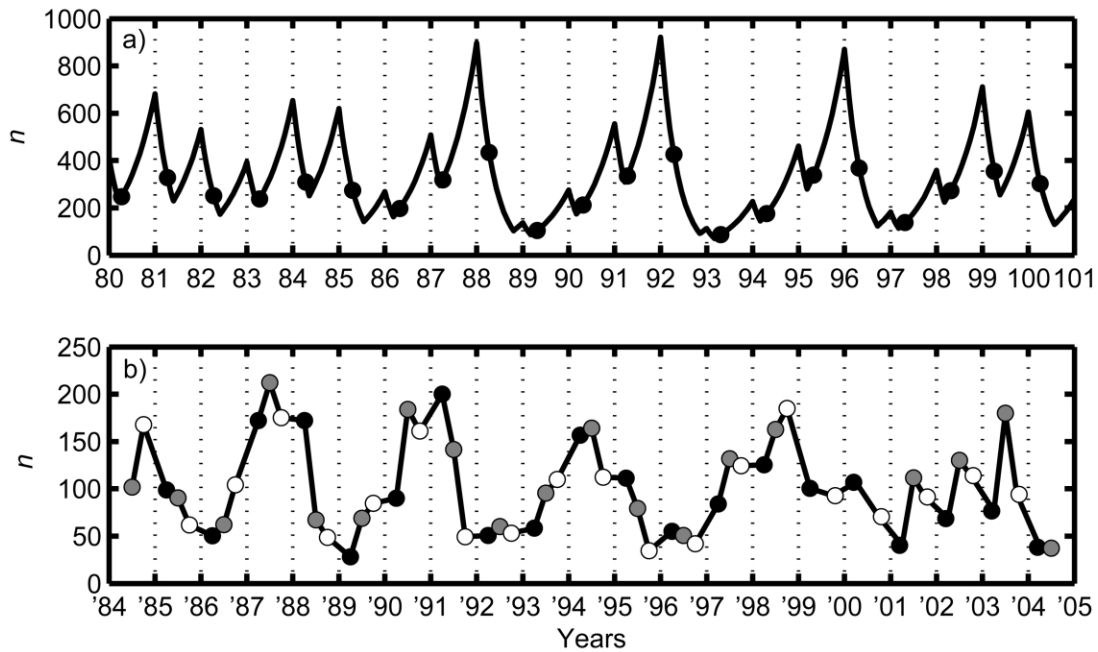
Figure 5: *a*, Population dynamics from model B between years 80 and 100 where initial population density is 50, $r = 1.4$, $\alpha = 0.8$, $\beta = 4{,}779$, $\tau = 30$, and $\kappa = 0.83$. The dots represent the population density when measured at the same point (one quarter of the year or the start of April) in each year. Clearly, sampling at only this fixed time in the year would fail to reveal the variable onset of reproductive season length, an important clue toward the mechanism underlying the dynamics. These dynamics appear qualitatively similar to the Kielder Forest field vole data shown in *b*. The data in *b* are estimated average field vole densities between 1984 and 2004 for spring (*black*), summer (*gray*), and autumn (*white*), for the 14–18 sites in Kielder Forest. Vole densities were derived using sign indices at each site that were calibrated with capture-recapture estimates of vole density (see Lambin et al. 2000 for further details).

B qualitatively resemble those of the Kielder Forest field vole population cycles (fig. 5). In particular, note how the model results and field observations display pronounced cycles every 3–4 years with smaller fluctuations on an annual timescale.

Discussion

The models analyzed here show clearly that delayed density-dependent season length alone could play an important role in the generation of rodent population cycles. The sensitivity analysis (fig. 4) indicates that this effect is robust to changes in parameter values of the system. Indeed, Stenseth's (1999, p. 449) comment, "The relative fraction of exposure to winter and summer conditions may keep the key to the enigma of the rodent cycle," is strongly supported by this study. For the Kielder Forest field voles in particular, our analysis confirms that the significant positive correlation found between the population density at the start of the previous year's breeding season and the date in the year that the breeding season starts (Ergon 2003) could point toward a mechanism that can result in population cycles. In further support, model B, which

most closely matches the field data, predicted periodicities within the 3–4-year range observed in the data for the largest range in parameter values (fig. 4).

Analysis of the character of the population cycles, including the within-year dynamics, reveals further features common to model output and real data. In addition to a qualitative resemblance to the observed trajectories (fig. 5), the dynamics also show the characteristic delay in recovery following a population decline (Boonstra et al. 1998). As we have deliberately chosen the most parsimonious model, we need not expect such characteristics to match the population data, and further studies, incorporating delayed density-dependent season length into more realistic models, are needed to indicate the causal agents behind particular characteristics of the population cycle. Numerical analysis also indicates that sampling populations at a few fixed points in the year (common practice) may miss important details of the true character of the annual population dynamics. To illustrate this, consider figure 5*a*, a typical numerical realization of model B. In figure 5*a*, the densities at the beginning of April in years 81, 87, and 95 are similar. However, in year 81, the population density continues to drop, reaching a trough

3 months later; in year 87, it is at its trough, and in year 95, the population density has been increasing from a trough for almost 2 months. Only capture-recapture studies with short sampling intervals provide accurate estimates of the timings of key life-history events in the breeding season and provide clues as to the importance of density-dependent seasonality in reproduction (Yoccoz et al. 1998). It is also striking that, if sampled at fixed time intervals, simulated trajectories include periods with ill-defined cyclicity. This is a feature shared by more complex predator-prey vole population models (Hanski et al. 1993; Hanski and Henttonen 1996). Our analyses also indicated that populations should tend to show cyclic dynamics when the potential variation in season length (α) is high and population densities over which season length varies (β) are large (e.g., fig. 3). These model predictions could be tested with field data.

Our study highlights several avenues for future research. What causes the start date of the reproductive season to be delayed density-dependent in Kielder Forest remains to be determined, as does the frequency of this phenomenon in other populations. For example, a similar phenomenon has been observed in smallmouth bass (*Micropterous dolomieui*) populations in the United States (Wiegmann et al. 1997). The shape of the functional relationship between past densities and when the breeding season starts also requires further investigation. It also remains to be shown whether season length in Kielder Forest (and elsewhere) is delayed density dependent. However, our study suggests that the omission of this phenomenon from future attempts to fully comprehend the cycles may be unwise.

Acknowledgments

APPENDIX

Derivation and Stability Analysis of Models A–C

Derivation of the Three Discrete Models

Equations (1) and (2) have simple analytical solutions ($n(t) = n(0)e^{rL}$ and $n(t) = n(0)e^{-b(1-L)}$, respectively, where $n(0)$ is the population density at the start of the respective season). For models A–C, the product of these solutions is

$$N_{T+1} = N_T e^{rL} e^{-b(1-L)} \equiv N_T e^{-b+(r+b)L}, \qquad (A1)$$

which calculates the population change for exactly 1 year in the future from the initial population size at the start of the previous year. Models A–C differ only in that L is a function of population density at different times in the past (fig. 1). These are incorporated separately to give the three equations for each model, as shown in equations (3).

Stability Analysis

Here we summarize the derivation of the stability condition for the three models. In each case, we express the conditions in terms of the constant $S = (r + b)N^* f'(N^*)$.

Model C is the simplest case. The model is the first-order difference equation $N_{T+1} = N_T e^{-b+(r+b)f(N_T)}$. The steady state $N_T \equiv N^*$ is therefore stable if and only if $|d/dN[Ne^{-b+(r+b)f(N)}]_{N=N^*}| < 1$, which simplifies to

$$0 > S > -2. \qquad (A2)$$

Model A is the second-order difference equation, $N_{T+1} = N_T e^{-b+(r+b)f(N_{T-1})}$. This can be written as a system of two first-order difference equations, where

$$N_{T+1} = Y_T,$$
$$Y_{T+1} = Y_T e^{-b+(r+b)f(N_T)}. \qquad (A3)$$

These have a stability matrix at $N_T \equiv N^*$, given by

$$J_A = \begin{bmatrix} 0 & 1 \\ S & 1 \end{bmatrix}. \qquad (A4)$$

The standard conditions for the stability of J_A are $2 > 1 + \det(J_A) > |Tr(J_A)|$ (see, e.g., Edelstein-Keshet 1988). This simplifies to

$$0 > S > -1. \qquad (A5)$$

Model B is the most difficult of the three cases because equations (1) and (2) do not immediately reduce to a difference equation. This makes it necessary to solve the underlying differential equations. The annual cycles predicted by the model have a reproductive season length $b/(r + b)$; the population density is n^* at the start of the reproductive season and $N_S = n^* e^{rb/(r+b)}$ at the end. To consider the deviation from these annual cycles, we define ψ_i to be the length of the reproductive season in year i and γ_{i+1} to be the population density at its end.

In the nonreproductive season in year i, the population density is initially $N = \gamma_i$ and evolves according to equa-

tion (2). Straightforward integration shows that the density at the start of the reproductive season is $\gamma_i e^{-b(1-\psi_i)}$. To continue the solution, we solve equation (1) for the reproductive season. This gives the population density at the end of this season as $\gamma_i e^{-b+(r+b)\psi_i}$. The reproductive season length and the population density are related by the feedback function f (eq. [4]). Therefore, the model reduces to two coupled difference equations where

$$\gamma_{i+1} = \gamma_i e^{-b+(r+b)\psi_i},$$

$$\psi_{i+1} = f(\gamma_i e^{-b(1-\psi_i)}). \tag{A6}$$

The stability of the steady state $\gamma_i = N_s$, $\psi_i = b/(r+b)$, corresponding to annual cycles, can be found from the stability matrix

$$J_B = \begin{bmatrix} 1 & (r+b)N_S \\ S/(r+b)N_S & Sb/(r+b) \end{bmatrix}. \tag{A7}$$

The standard stability conditions (as for model C above) imply that n^* is stable if and only if $2 > 1 + Sb/(r+b) - S$ and $1 + Sb/(r+b) - S > -1 - Sb/(r+b)$.

This further implies that $(1 - b/(r+b))S > -1$, $S < 0$, and $(2b/(r+b) - 1)S > -2$.

We therefore see that $S_{\text{crit}} < S < 0$, where

$$S_{\text{crit}} = \begin{cases} -1/[1 - b/(r+b)] & 0 < b/(r+b) \leq 3/4 \\ -2/[2b/(r+b) - 1] & 3/4 < b/(r+b) < 1 \end{cases}. \tag{A8}$$

Note that S_{crit} is a nonmonotonic function of the ratio $b/(r+b)$. As $b/(r+b)$ is increased from 0, S_{crit} decreases from -1, reaching -4 at $b/(r+b) = 3/4$. Then S_{crit} increases as $b/(r+b)$ is increased further, reaching -2 at $b/(r+b) = 1$.

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