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# Effects of density and season on the population rate of change in the meadow vole

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We developed an empirically based model of density-dependent vole population growth based on experimental data on population dynamics of *Microtus pennsylvanicus* in large field enclosures. Statistical analysis of the data indicated that both density dependent regulation and seasonal effects were important in influencing vole population growth. Together, these two factors explained approximately one-half of variance in the realized per capita rate of change exhibited by experimental vole populations. A population model assuming simple functional forms (linear for population density and sine for seasonality) provided an adequate description of the data, with more complex functional forms leading to at best minimal improvements. The natural rate of population increase, averaged over all seasons, was estimated as (mean ± SE) $r_{\max} = 6.0(\pm 0.4)$ $\mathrm{yr}^{-1}$. This estimate suggests an impressive power of population increase, implying that each female vole could be replaced by about 400 daughters a year later (assuming density-independent growth). A survey of literature, however, indicates that this is by no means the largest rate of increase observed in a vole population.

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Since Elton (1924) noticed that population numbers of voles and lemmings exhibit periodic oscillations of great amplitude, an enormous amount of empirical and theoretical work has been devoted to elucidating the mechanisms underlying this striking phenomenon (reviews in Krebs and Myers 1974, Batzli 1992, Stenseth and Ims 1993). Although much progress has been made towards this goal, a definitive synthesis still eludes us (Hansson 1987, Batzli 1992). We believe that this state of affairs is largely due to a lack of communication between theoretical and empirical ecologists working in this field. Although a large number of theoretical models has been advanced, and enormous amounts of data collected, there has been little systematic effort to parameterize the models and the test their predictions with the data (but see Hanski et al. 1993, Hanski and Korpimäki 1995).

The most basic building block of a population dynamics model is density-dependent population growth. A most-commonly followed procedure in building a population model is to assume some form of population growth (e.g., the logistic equation), and then to add to this starting point various terms for population interactions with other species in the community (and, possibly, spatial redistribution). Thus, population growth is the logical starting place in a program for systematically building empirically based models of arvicoline (microtine) population dynamics. Our goal in this paper, therefore, is to begin laying the foundation for such an empirically based theory. Specifically, we will develop a model of vole population growth based on experimental data on *Microtus pennsylvanicus* population dynamics in large field enclosures (Ostfeld and

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Canham 1993, 1995, Ostfeld et al. 1993). These data are uniquely suited for our purpose because:

1. We can employ a single-species model without time-delays in fitting these data. Although predators were not excluded from enclosures, we found no evidence of time-delays in abundance of predators or predation rate (Ostfeld and Canham 1995). Similarly, there were no lagged effects of high population density that could be mediated by long-lasting changes in vegetation (Ostfeld et al. 1993).
2. We can use a model without emigration/immigration terms because vole populations were maintained in enclosures.
3. The study provides a particularly informative data set for estimating density-dependent population regulation, because vole density was manipulated experimentally.
4. Finally, the experiment was run continuously for almost two years, which allows us to estimate seasonal changes in population dynamics.

## Methods

### Experimental design

Full details of experimental design are presented in Ostfeld and Canham (1993, 1995). Briefly, a set of nine 40 m by 40 m hardware-cloth enclosures was constructed in a lowland meadow at the Inst. of Ecosystem Studies in Millbrook, New York in spring, 1990. Primary vegetation in the meadow was a mixture of hayfield grasses (*Bromus inermis*, *Poa pratensis*, *Arrhenatherum elatius*) and forbs (*Galium mollugo*, *Solanum carolinense*, *Solidago* spp.). Vole populations within each enclosure were culled to 2–3 breeding pairs initially, and then allowed to begin population growth. The nine enclosures were arranged in a randomized block design, with three blocks, and three density treatments. Three of the enclosures were managed at low density and three at medium density by removing subadult individuals during the biweekly schedule of live-trapping. The desired targets for the low- and medium-density enclosures were about eight, and about 20 adult voles per enclosure, respectively. In the three high-density enclosures, voles were neither removed nor introduced; these populations grew to levels of about 50–90 voles enclosure$^{-1}$ (Ostfeld et al. 1993).

Trapping was conducted for two consecutive days every second week from June 1990 to May 1992, using Longworth live-traps set in a five-by-five array with 7.5 m between traps. Two regular trapping sessions were canceled due to cold weather. All rodents were given individually numbered metal eartags for identification, and standard data on sex, body mass, and reproductive condition were recorded. Capture probabilities of voles averaged 86% over the course of the study (Ostfeld and Canham 1995); thus, population density was estimated by calculating the minimum number known alive (Krebs 1966).

### Statistical analysis

The per capita rate of population change is defined as $r = dN/Ndt = d/dt(\ln N)$. A discrete approximation of $r$, which is referred to as the realized per capita rate of population change, is

$$r_t = \frac{1}{T}\ln\frac{N_{t+T}}{N_t}, \qquad (1)$$

where $N_t$ is the population density at time $t$, and $T$ is the finite time interval over which population change is measured. Because in two experimental treatments (medium- and low-density) voles were removed, the formula (1) needs to be modified as follows:

$$r_t = \frac{1}{T}\ln\frac{N_{t+T}+R_{t+T}}{N_t}, \qquad (2)$$

where $R_{t+T}$ is the number of voles removed at $t+T$.

The value of $T$ used in the analysis must be a multiple of time intervals at which data were collected in the experiment (2 weeks). $T$ should be short enough for environmental conditions (population density and season) not to change too much. On the other hand, if $T$ is too short, the population density will not have enough time to change during this period, and the ratio of change in population numbers to the measurement error ("the signal/noise ratio") may be unacceptably low. Preliminary examination of the data suggested to us that $T = 4$ weeks, or 1/13th of a year (since the units of $r_t$ are yr$^{-1}$) was the optimal choice given these conflicting demands. An additional consideration is that on two occasions a biweekly census was missed, leading to two intervals of 4 weeks each. Using $T = 4$ weeks allowed us not to have to exclude these data. Finally, $T = 4$ weeks seems a good choice on biological grounds, since it approximates time between litters for a female under favorable conditions, as well as time from birth to sexual maturity (Hasler 1975, Keller 1985).

Two periods during the experiment yielded biased estimates of $r_t$. First, because the experiment was started by reducing the vole density in each enclosure to two pairs of breeding adults, there were no young voles present at the beginning of the experiment. An estimate of the intrinsic rate of population increase assumes that the population is close to a stable age distribution. It is unlikely that the experimental vole populations ever achieved a truly stable age distribution, being continuously affected by variable field environment. Nevertheless, we felt that such obvious gross departures from this state, as heavy predominance of mature adults during the first month, should be eliminated. Thus, the first month's data were omitted. Second, a severe drought (<40% of long-term monthly mean rainfall) occurred in the summer of 1992, depressing both population growth rates and densities of voles in enclosures. To avoid a negative estimation bias due to such a rare event, the data for 12 weeks starting with week 51 were excluded from the analysis. This left 162 data points for analysis.

Estimated $r_t$ (for each 4-week period in each enclosure) were the dependent variable in all analyses. We explored the influence of population density by regression, and combined effects of density and season were investigated with the analysis of covariance. Next, a model of seasonally affected population growth was fitted to the data using nonlinear methods (see below). Possible effects of serial correlation between sequential values of $r_t$ from the same enclosure were investigated by submitting residuals from the fitted model to time-series analysis. Autocorrelation coefficient between subsequent values of residuals was estimated as 0.146. Because this correlation coefficient was small (and not significantly different from zero), our statistical analyses treated each $r_t$ as an independent data point. All the analyses were performed using the software package Statistica.

## Results

A linear regression of $r_t$ on $N_t$ provided strong evidence for density-dependent regulation of vole populations in enclosures (Fig. 1). However, although the effect of population density was statistically highly significant ($F = 54.13$, $P < 0.000001$), this factor alone explained only one-quarter of variation in $r_t$. The unexplained variation is due to demographic stochasticity, observation errors, and environmental influences. Demographic effects are expected to be a prominent source of variability, since many values of $r_t$ were based on populations consisting of only 10–20 individuals (note how variance around the regression line appears to decrease as $N_t$ increases). On the other hand, measurement errors probably were not a large source of variation, since the experimental technique ensured that >80% of post-weaning voles present in enclosures were captured during biweekly trapping censuses, and this high capture probability did not change seasonally (R. S. Ostfeld, unpubl.).

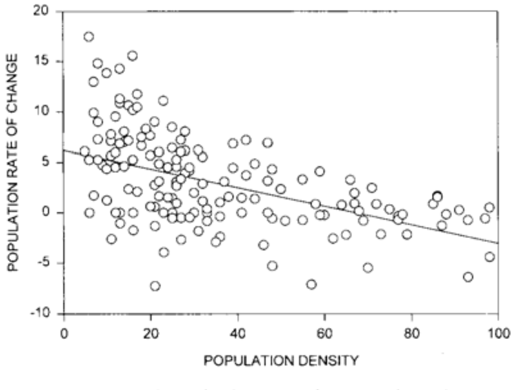

Fig. 1. A plot of realized rates of population change vs population density, combining all seasons. The straight line is fitted by linear regression, $r_t = 6.20 - 0.092N_t$, ($R^2 = 0.25$, $P < 0.001$).

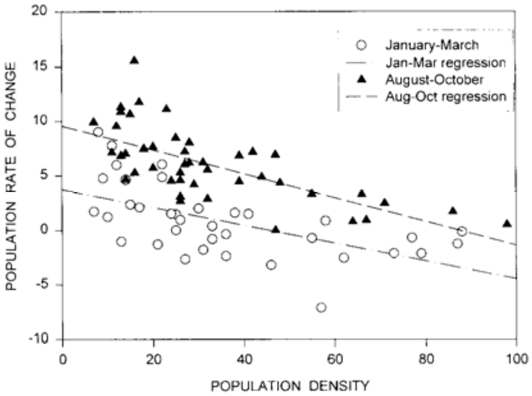

Fig. 2. The relationship between the realized rates of population change and population density during the most favorable (August–October) and least favorable (January–March) seasons. Straight lines are fitted by linear regression (the proportion of variance explained by linear regression is $R^2 = 0.47$ and 0.34 for the most favorable and least favorable season, respectively). The difference between the slopes of the two regressions is not statistically significant.

One systematic environmental factor affecting population growth is seasonality, as suggested by annual increases and decreases in vole populations (see Fig. 1 in Ostfeld and Canham 1995). This potential influence was investigated by the analysis of covariance (ANCOVA), with $r_t$ as the dependent variable, time (or season) as the independent variable, and $N_t$ as the covariate. "Season" was a qualitative (class) variable that varied from 1 to 13. It corresponded to each 4-week period, starting in January, and ending in December.

The results of this analysis indicated that both the effects of season ($F = 10.01$, $P < 0.001$) and population density ($F = 45.04$, $P < 0.001$) were highly significant. Peak increase rates were observed during late summer–early fall, and $r_t$ was lowest during late winter–early spring. Plotting $r_t$ vs $N_t$ for these two seasons separately shows a cleaner relationship between these two variables (Fig. 2).

Our next step was to fit a seasonally modified logistic model to the data:

$$r_t = r_{\max}[1 + \varepsilon \sin 2\pi(t + \omega)] - gN_t. \qquad (3)$$

The independent variables in this model are time $t$ (in units of yr) and $N_t$ (voles in the enclosure). Estimated parameters are $r_{\max}$, the rate of increase at low population density averaged over all seasons (this parameter corresponds to the natural rate of population increase in the unmodified logistic equation); $\varepsilon$, the amplitude of seasonal oscillation in the rate of population increase; $\omega$, the phase; and $g$, the strength of density dependence. Fitting model (3) to the data by nonlinear least-squares, we found that both the seasonal ($\varepsilon$) and density-dependent ($g$) effects were highly significant (in both cases $P < 0.001$). The least-squares estimates ($\pm$standard errors) of parameters were as follows:

$$r_{\max} = 6.0(\pm 0.4)\ \mathrm{yr}^{-1}, \quad \varepsilon = 0.53(\pm 0.08),$$

$$\omega = 0.08(\pm 0.02)\ \mathrm{yr}, \quad \text{and } g = 0.08\ (\pm 0.01)\ \mathrm{yr}^{-1}\ \mathrm{vole}^{-1}.$$

The model explained 48% of variance in $r_t$.

The model (3) assumes that the slope of density dependence, $g$, does not vary with season. To test this assumption, we fitted to data the model (3) with an additional term $[1 + \varepsilon \sin 2\pi(t + \omega)]N_t$ expressing the interaction between seasonal and density-dependent effects. However, this term increased the proportion of explained variance only to 49%, and was not statistically significant ($P = 0.18$), suggesting that the model (3) provides an adequate description of the data (this is further supported by approximate parallelism of slopes in Fig. 2). The consequence of the constant slope $g$ is that the "carrying capacity" will oscillate with season, since

$$K(t) = r_{\max}[1 + \varepsilon \sin 2\pi(t + \omega)]/g$$

(this can be seen in Fig. 2 by observing how the intersect of the fitted line with the abscissa shifts with season). $K(t)$ is the population equilibrium density set by a combined effect of resource limitation and social interactions. In the seasonal logistic model, population density eventually converges to $K$ (and fluctuates around it, if the system is subject to density-independent perturbations). In the seasonal model (3), by contrast, $K(t)$ changes with time, and the population density never converges to it. Instead, population density is tracking a "moving target", attempting to catch up to $K(t)$ as it is increasing, and overshooting it when it starts to decrease. The seasonally averaged $K(t)$ is estimated as $g/r_{\max} = 75.7$ voles per enclosure, or 473 vole $\mathrm{ha}^{-1}$.

Another assumption of model (3) is that the effect of $N_t$ on $r_t$ is linear. This assumption was tested by fitting a model in which $N_t$ was transformed using the Box-Cox transformation (Sokal and Rohlf 1981). The effect of including an extra parameter on the proportion of variance explained by the model was minimal (it increased from 48% to 52%), suggesting that the linear form provides a reasonable approximation.

Model (3) also assumes that a sine function is an appropriate description of the effects of seasonality on the intrinsic rate of increase. Smooth trigonometric functions are often used in the mathematical literature (e.g., Rinaldi et al. 1993). By contrast, Hanski et al. (1993, Hanski and Korpimäki 1995) employed a discontinuous step-function. The adequacy of these two choices as functional forms for seasonal effects can be visually assessed by subtracting density-dependent effects from each data point, and then plotting each resulting estimate of the rate of increase at $N_t = 0$, $r_t^0 = r_t + gN_t$, against time (Fig. 3). A discontinuous change in $r_t^0$ with season appears not to be supported (Fig. 3), although the amount of variation present in the data precludes any strong conclusions. Similarly, although some other smooth function may provide a better fit to the data than the sine, given the degree of scatter in the data such an improvement is likely to be marginal. Since the sine form has a virtue of simplicity and is widely used in modeling literature, there appears to be little reason to reject it in favor of some other more complicated alternative.

## Discussion

Our major results can be summarized as follows. Two factors, density-dependent regulation and seasonal influences, together accounted for one-half of variance in realized per capita rate of population growth exhibited by vole populations. A population model assuming simple functional forms, linear for population density and sine for seasonality, provided an adequate description of the data, since more complex functional forms yielded minimal improvements in the proportion of variance explained. The unexplained variance is probably due to the effects of demographic stochasticity and

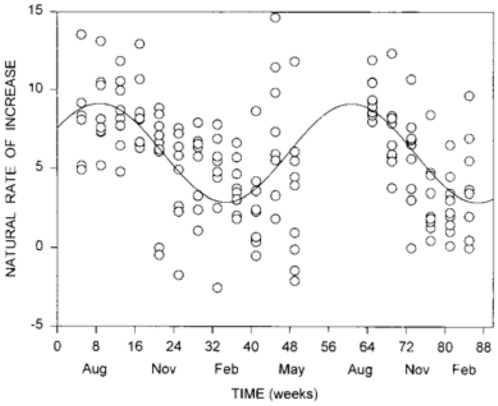

Fig. 3. The relationship between the intrinsic rate of population change and season. Each point corresponds to a transformed data point $r_t^0 = r_t + gN_t$ plotted against time. The curve is the sine function fitted to the data using nonlinear least squares.

environmental factors other than density and season. These stochastic factors are clearly an important source of fluctuations in vole numbers, because they were responsible for about half of variance in $r_t$. In addition, episodic severe fluctuations of climate can have a profound effect on vole populations, as was demonstrated by the drought during the summer of 1992.

Our results provide a clear indication that vole dynamics can be affected by strong density-dependent feedback operating with little, or no delay. This conclusion about an overall pattern of density dependence is supported by the analyses of density dependence in specific demographic parameters (Ostfeld and Canham 1995). Ostfeld and Canham (1995) found that high density had an immediate effect on individual growth and reproduction (shorter breeding seasons, lower rates of recruitment, and older age at sexual maturity). However, population density did not affect reproductive activity during the height of the breeding season or survival rates of juveniles and subadults (survival of adults was slightly affected by density during the second half of the experiment). Our analysis here suggests that density dependence in individual growth, maturation rates, and reproduction was enough to impose an overall pattern of density dependence, even though other demographic parameters were unaffected. Density independence in survival and reproductive rate during the mid-breeding season may contribute to the unexplained variation in per capita rate of population growth.

To maintain experimental populations under different density levels, we had to enclose voles within fences. As the fences restricted both immigration and emigration, we could not examine the effects of population density on per capita rate of dispersal, nor of dispersal rates on realized rates of population growth. However, a large literature on dispersal in small rodents indicates that per capita dispersal rates are rarely density dependent (reviewed by Gaines and McClenaghan 1980, Stenseth and Lidicker 1992, but see Krebs 1992). Instead, dispersal rates typically are highest during the increase phase of a multiannual cycle, and lowest during the peak and decline phases, and dispersal generally is thought to be a nonregulating, or even antiregulating, factor in rodent population dynamics (Lidicker 1975, Gaines and McClenaghan 1980). Thus, the absence of dispersal from our data set may have strengthened our ability to detect density dependence in rate of population growth. The lack of emigration also may have contributed to the very high $K$ (473 ha$^{-1}$) observed in our populations (Ostfeld 1994).

## General implications

One of the most important parameters determining qualitative dynamics of ecological models (such as stable equilibria, limit cycles, or chaos) is the natural rate of population increase. Our estimate of this parameter (averaged over all seasons) was $r_{\max} = 6.0$ yr$^{-1}$. This estimate suggests an impressive power of population increase, since it implies that each female will be replaced by about 400 daughters a year later (assuming that no density-dependent factors will come into play). How well does this estimate correspond to the theoretical maximum rate of population increase, and to increase rates observed in other studies and other species?

The theoretical $r_{\max}$ can be calculated as follows. Under favorable conditions (low population density, abundant food, and no predators), females in the genera *Microtus*, *Clethrionomys*, or *Lemmus* produce a litter of 4–8 offspring every 20–30 d. The age to sexual maturity is also 20–30 d, and a female may produce 4–6 litters during her lifetime (Hasler 1975, Keller 1985). We can represent the exponential growth of a vole population with the following simple stage-structured model:

$$\begin{aligned} J_{t+T} &= (L/2)F_t \\ F_{t+T} &= RJ_t + PF_t, \end{aligned} \tag{4}$$

where $J_t$ and $F_t$ are the numbers of juvenile and reproductive females at time $t$, $L$ is the litter size, and $T$ is the time step (both the time between successive litters and the maturation time of juveniles). $P$ is the proportion of breeding females that survives to reproduce again, and $R$ is the proportion of juvenile females that becomes reproductive. Because model (4) is linear (there is no density dependence), population growth obeying this model will be exponential. The exponential rate of increase is $r = (1/T) \ln \lambda_1$, where $\lambda_1$ is the dominant eigenvalue of the projection matrix associated with the model (4), and is related to the model parameters in the following way:

$$\lambda_1 = (P + \sqrt{P^2 + 2LR})/2$$

(for mathematics of such stage-structured population models see, e.g., Caswell 1989). Now, assuming conservative values of parameters (since we are interested not in a theoretical maximum, but in a seasonal average of $r$), let $T = 30$ d or 1/12 yr and $L = 6$. If 70% of newly-born survive the juvenile stage, and 70% of juveniles become mature females (Hansson 1987), then $R = 0.5$. If each female has 4 litters, then at each time step, one-fourth of females will be lost to the population of reproducing females, therefore $P = 3/4$. For these values of parameters, $r = 6.05$ yr$^{-1}$. This is very close to the value of $r_{\max}$ estimated by us for *M. pennsylvanicus*. We can compare these estimates with previously published estimates of yearly production per female. Koshkina (1970) calculated that a single *L. lemmus* female will leave at least 1500–2000 descendants after one year (this estimate accounts for seasonal effects on

Table 1. Maximum increase rates observed in field populations of *Microtus* voles (*penn.* = *pennsylvanicus*, *calif.* = *californicus*, *town.* = *townsendii*, *ochr.* = *ochrogaster*, *agre.* = *agrestis*). In all entries (except Erlinge 1974) increase rate was determined by locating a period of approximately linear increase of log-transformed numbers. Only sustained increases beginning at low population densities and occurring during the most favorable season are reported. Time period column indicates the length of the period of approximately exponential growth. Numbers column indicates population numbers at the beginning and the end of this period, as measured by investigators (usually, the minimum number alive). The last entry is an estimate by Erlinge (1974) based on quantitative information about vole reproduction.

| Species | Reference | Numbers | Time period | Season | $r$ (yr$^{-1}$) |
|---|---|---|---|---|---|
| *M. penn.* | Krebs et al. 1969 | 3.5–22.5 | 6 weeks | Aug.–Sep. | 16.1 |
| *M. penn.* | Gaines and Krebs 1971 | 2.5–25 | 4 weeks | Aug.–Oct. | 10.0 |
| *M. penn.* | Boonstra and Boag 1987 | 15–75 | 6 weeks | Jul.–Aug. | 13.9 |
| *M. penn.* | Ostfeld and Canham 1995 | 12–30 | 4 weeks | Jul. | 11.9 |
| *M. calif.* | Krebs and Delong 1965 | 42–79 | 2 weeks | Nov. | 16.2 |
| *M. calif.* | Krebs 1966 | 1.5–20 | 10 weeks | Feb.–May | 12.4 |
| *M. town.* | Boonstra 1977 | 10–90 | 10 weeks | Aug.–Nov. | 11.4 |
| *M. town.* | Beacham 1980 | 10–100 | 10 weeks | Sep.–Oct. | 12.0 |
| *M. ochr.* | Myers and Krebs 1971 | 3–12 | 6 weeks | Sep.–Oct. | 12.0 |
| *M. agre.* | Erlinge 1974 | – | – | Summer | 13.8 |
| Average | | | | | 13.0 |

reproduction), which corresponds to $r_{\max} = 6.62–6.90$ yr$^{-1}$. Batzli et al. (1980) arrived at a similar estimate $r_{\max} = 7.17$ yr$^{-1}$ for *L. sibiricus*. While these estimates are somewhat higher than our estimate $r_{\max} = 6.0$ yr$^{-1}$, this should be expected, since lemmings tend to have slightly faster generation times and larger litter sizes, compared to voles.

It is also interesting to consider what the theoretical maximum of $r$ may be. Assuming ideal conditions (that is, the peak of reproductive season), $T = 20$ d (1/18 yr), 100% survival and recruitment of juveniles, $R = 1$, and 8 litters per female, $P = 7/8$. This combination of parameters results in $r = 14.39$ yr$^{-1}$. To put this number in perspective, the population characterized by such an $r$ would double every 2.5 weeks. We would expect that conditions conducive to such an enormous rate of increase would be rarely achieved, and when achieved, extremely transitory. Nevertheless, there is a number of documented cases in which vole populations have increased almost as rapidly (Table 1). Thus, a seasonal peak of $r = 12$ yr$^{-1}$ would not be an unrealistic value for most vole and lemming populations.

We believe that further progress in understanding the causes of fluctuations in populations of arvicoline rodents will be enhanced by the creation and testing of empirically based models that integrate the effects of a variety of extrinsic and intrinsic factors. Here we have provided a foundation for further model development by estimating the relative importance of density-dependent regulation and seasonality in influencing the realized rate of population growth. A more complete synthesis can be attempted by including density-independent factors (probably including dispersal) and lagged density-dependent factors in future empirical and theoretical efforts.

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