Intrinsic density-dependent regulation of vole populations

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CONSIDERABLE controversy exists over the role of density-dependent processes in controlling animal population size. In populations that fluctuate cyclically or erratically, for example many voles and insects[1,2], theory predicts that either density-dependence is weak[1,3], or that density-dependent responses lag behind density[4–6]. One key mechanism for lagged density-dependence is a delay in regeneration of food resources following heavy exploitation. Here we show that meadow vole (*Microtus pennsylvanicus*) populations respond immediately to high density by reducing breeding effort and hence population growth, disproving the hypothesis that density-dependence is weak. In addition, vole populations do not show a delay in growth following marked reduction in plant biomass (their source of food and cover). We conclude that intrinsic density-dependence processes tend to stabilize vole populations, and that cyclic dynamics are not caused by lagged effects of resource exploitation.

Vole populations often fluctuate cyclically, with 3–5 years between peaks[7,8]. To mimic different points in the natural cycle, we established three replicates each of meadow vole populations held chronically at low, medium and high density in nine field enclosures. Populations averaged about 70, 180 and 380 voles per hectare, respectively (Fig. 1), maintained at targeted densities by removing subadults (the primary age of dispersal[9,10]). Enclosures were closely juxtaposed and therefore experienced similar abiotic and biotic conditions. Avian and mammalian predators were not excluded by the fences.

Correlational studies of vole population dynamics have shown that neither mortality rates nor emigration rates are density-dependent[9–11]. Instead, typical populations appear to be characterized by catastrophic declines after the achievement of a peak. Peaks are usually preceded by atypically high rates of winter breeding, which are critical to vole population dynamics[7,12]. The determinants of winter breeding, however, have until now not been established[11,12].

In our study, population density determined the rate of autumn, winter and spring breeding in both 1990–1991 and 1991–1992 (Fig. 2*a*, *b*). Females and males on high-density grids became non-reproductive 2–4 weeks earlier in the autumn, and reproductive four weeks later in the spring than voles on medium-density grids. On low-density grids, although there was a reduction in the proportion of voles breeding between October and May, roughly half bred throughout this period, resulting in continuous recruitment (Fig. 2*c*). High-density treatments resulted in 2–3 fewer generations per year than medium-density treatments, and up to 5 fewer generations per year than low-density treatments. As vole generation times are short (3–4 weeks[13,14]; typically 5–10 generations per year) and litter size is large (~4–5; refs 13,14), the loss of several generations per year would sharply curtail population growth rate.

Vole density had little effect on juvenile survival probabilities as determined by repeated measures analysis of variance in both breeding and non-breeding seasons of both years of the study. Similarly, analysis of variance on median mass at sexual maturity for both sexes and all seasons only revealed a significant effect of density for females during the 1991–1992 non-breeding season ($F = 6.02$; d.f. = 2; $P = 0.038$; ranking, low < medium < high). Therefore the number, but not the quality, of offspring appears to be strongly density-dependent.

Female (but not male) voles under all density treatments curtailed breeding during an unusual summer drought during June and July 1991 (Fig. 2*a*, *b*). Thus, voles gave a density-independent response to an unpredictable change in resource availability, namely the drying of their principal food, grasses and forbs. Despite an apparent consensus that both density-dependent and density-independent processes affect population dynamic patterns[3,15–20], clear examples of both processes acting on the same population are few.

Above-ground plant biomass in spring was significantly reduced in high- and medium-density enclosures compared with low-density enclosures, but recovered by late summer or autumn; moreover, food quality was reduced by the elimination of some preferred plant species and the reduction of others (R.S.O., manuscript submitted). Thus, the effects of voles on plants seemed likely to cause lagged density-dependence. Models incorporating lags of about nine months produce cyclic dynamics with a period and magnitude virtually identical to those of microtine populations[4,21].

Lagged density-dependence has been detected in time series

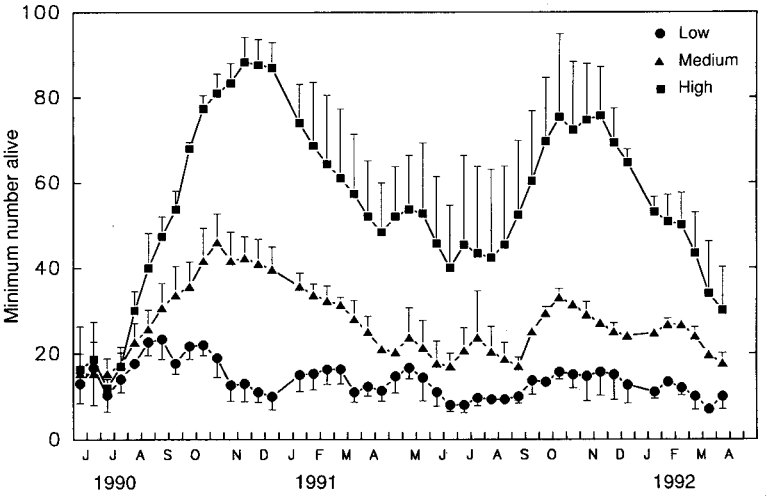

FIG. 1 Densities of the experimental vole populations expressed as minimum number alive per 0.16 hectare enclosure. Symbols show means (±1 s.e.) of the 3 replicates of low-, medium-, and high-density treatments, which were arranged in a randomized block design, in an old field in south-eastern New York state. The data set consists of 11,282 capture records of 3,094 individuals in the enclosures. The densities maintained represent the range of naturally occurring densities for unenclosed populations of this species[8,11]. Low- and medium-density enclosures were maintained at desired levels by removing selected subadults (body mass, 20–30 g) during normal biweekly live trapping. Subadults, independent of their mothers, were targeted to minimize disruption of social structure of the populations, and to simulate dispersal that occurs primarily in subadults[9–11]. Individuals were not removed from designated high-density enclosures. Sex ratios of removed individuals were equalized within and among enclosures. Owing to high reproductive rates in low-density enclosures, and to the necessity of preserving realistic genetic diversity and sex ratios, we were unable to maintain densities more typical of nadirs in cyclic vole populations (≤50 animals per hectare[11]).

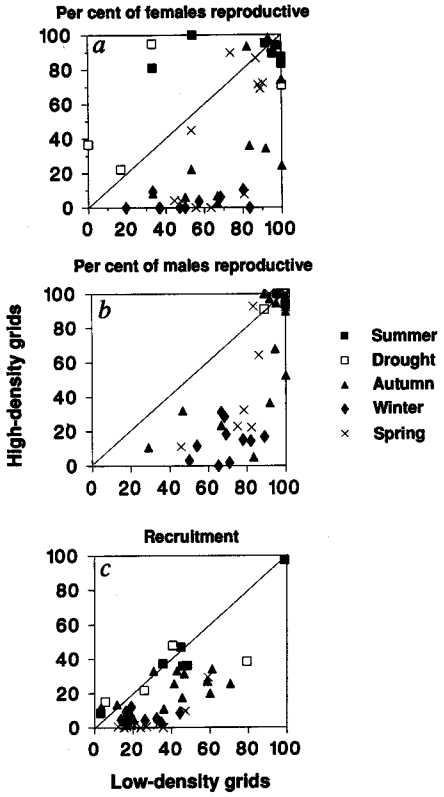

FIG. 2 Phase diagrams comparing high-density and low-density treatments with respect to: *a*, per cent of females in breeding condition; *b*, per cent of males in breeding condition; and *c*, recruits as a per cent of the total adult population. Females were considered to be in breeding condition if the vaginal orifice was open[29]; and males were considered to be in breeding condition if their testes were descended into the scrotum[14]. Each data point is the combination of the mean of three replicates of high density and the mean of three replicates of low density for a given trapping session. Trapping sessions are distinguished by season: June–August, summer; September–November, autumn; December–February, winter; March–May, spring. In addition, the four summer data points taken during the 1991 drought (in which mean monthly rainfall was <40% of the 1951–1980 average for this site) are distinguished. Diagonal line indicates an equivalent proportion of individuals breeding (or recruiting) at high and low density; points below the diagonal line indicate density-dependence.

of insects[5,22], and of voles[23], but the mechanisms causing delayed density-dependence are poorly understood and controversial. Four primary hypotheses have been put forward to explain delayed density-dependence in voles: behavioural polymorphism[11], maternal effects[24], predation[8], and herbivore–resource[8,11,21]. Recent experimental and theoretical studies[24–27] substantially weaken the first two hypotheses. Moreover, the lack of a strong density effect on either survival or maturation rates of juveniles does not support the prediction of the maternal effects hypothesis, that high population density causes stress to females, reducing the quality of their offspring. This leaves predator–prey and herbivore–resource dynamics as the most plausible mechanisms for lagged density-dependence. We therefore tested whether the depression of resource quantity and quality, resulting from high vole density, caused a time lag in the ability of vole populations to recover.

In April 1992, after 20 months of chronically different densities among treatments, all voles from the experimental enclosures were removed and one week later two pairs of voles, caught 2 km away, were introduced into each enclosure. One week later, missing voles were replaced to equalize sex and age composition among enclosures. The timing of the removal and introduction simulated the annual 'spring decline'[11] characteristic of North American voles. Populations were then allowed to grow freely to November 1992, after which the study ended.

A time lag in the growth of populations introduced into enclosures that were previously high-density was not observed; dynamics were similar to those in enclosures previously of low- or medium-density. Although there were no statistically significant differences in density or growth rate among the experimental treatments, voles introduced into formerly medium-density treatments maintained the highest density levels on average (Fig. 3). This result suggests that a moderate degree of grazing by voles may stimulate plant growth, whereas high and low grazing intensity are less stimulating.

Our demonstration of instantaneous density-dependent reproduction supports the hypothesis that intrinsic (demographic and behavioural) features of vole populations tend to be stabilizing, and that extrinsic features (predators and disease agents) may be necessary to cause the dramatic population fluctuations often observed[25,27,28]. Our experimental results indicate that a consumer–resource lag is unlikely to contribute to cyclic popula-

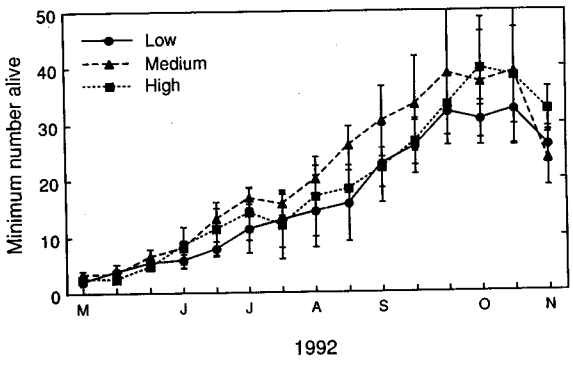

FIG. 3 Population growth trajectories of the vole populations inhabiting enclosures that had previously experienced high, medium or low population density for 20 months. Symbols represent the means (minimum number alive per 0.16 hectare) of the three replicates of each prior-density treatment. Repeated measures analysis of variance revealed no significant differences in density among prior-density treatments during any trapping session.

tion dynamics in this system, and are consistent with analyses[23] supporting a key role for delayed density-dependence resulting from predator–prey dynamics. □

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