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Richard S. Ostfeld; Charles D. Canham

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## DENSITY-DEPENDENT PROCESSES IN MEADOW VOLES: AN EXPERIMENTAL APPROACH<sup>1</sup>

RICHARD S. OSTFELD AND CHARLES D. CANHAM

*Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545 USA*

**Abstract.** Patterns of population dynamics are determined by the interaction between density-dependent and density-independent processes. To examine the responsiveness of various demographic and behavioral processes to population density, we maintained replicate meadow vole (*Microtus pennsylvanicus*) populations at low, medium, and high densities inside field enclosures in southeastern New York. Density was manipulated by removing subadults during biweekly live-trapping sessions. Under higher density conditions voles exhibited: (1) a truncated breeding season; (2) reduction in growth rates of individuals; (3) increase in age (but not size) at sexual maturity; and (4) reduction in movement distances of individuals. Extremely large-bodied voles were most frequent in low-density enclosures and least common in high-density ones. Survival rates of adults were delayed density-dependent. Reproductive rates during the middle of the breeding season and survival rates of juveniles and subadults were not affected by vole density. We conclude that vole populations are stabilized by density-dependent reductions in reproductive rate and recruitment, but destabilized by density-independent survival rates of young, and by density-dependent compression of individual movements, which accommodates population growth. The time delay in the effects of density on survival of adults may provide a mechanism for vole cycles in which lagged density-dependent mortality plays a central role.

**Key words:** age at sexual maturity; breeding season length; density vs. individual performance; density vs. space use; enclosure; field experiment; individual growth; movement distance vs. density; reproductive rates; survival rates.

### INTRODUCTION

The arvicoline (=microtine) rodents are perhaps best known for their population cycles. Many populations fluctuate in size an order of magnitude or more, with  $\approx 2$ –4 yr between peaks (Krebs and Myers 1974, Hansson and Henttonen 1988, many others). In attempting to explain this unusual pattern of population dynamics, ecologists have searched unsuccessfully for features unique to arvicolines (Elton 1942, Chitty 1967, Finerty 1980, Cockburn 1988, Batzli 1992). The predominant approach has been to treat the vole cycle as a single, unitary phenomenon, and to provide a unifying hypothesis to explain most or all phases, i.e., increase, peak, decline, and low phases, as well as their rhythm (reviewed by Cockburn [1988]; see also Lidicker [1988]). There is widespread disagreement among researchers on arvicolines about the accuracy and utility of the resulting models, and because they are specifically intended to explain vole cycles, the models have limited applicability to animal populations in general.

Any pattern of population dynamics, including a cycle, is caused by an interplay between density-dependent and density-independent processes. Unfortunately, relatively little attention has been paid by vole ecologists to disentangling which population processes are more or less sensitive to population density. Density-dependent processes, acting with little or no delay,

tend to stabilize population size, and density-independent processes will destabilize it (Royama 1992). Thus, density-independent, or delayed density-dependent processes should be important in strongly fluctuating populations.

Many investigators have monitored demography and space use of freely fluctuating vole populations. It is often claimed that rates of natality, mortality, or dispersal are not density dependent (Krebs and Myers 1974, Finerty 1980, Gaines and McClenaghan 1980, Bondrup-Nielsen 1987), only weakly so (Krebs and Myers 1974, Mihok et al. 1985), or delayed density-dependent (Schaffer and Tamarin 1973, Stenseth and Antonsen 1988, Hanski et al. 1991, 1993, Turchin 1993). For instance, reproductive rates may remain high even in high-density populations (Batzli and Pitelka 1971, Lidicker 1973, Rodd and Boonstra 1984), and survival rates can be low at either low or high density (Krebs et al. 1973, Boonstra and Rodd 1983, Mihok et al. 1985). Sharp declines in numbers can follow a period of high or only moderate density (Krebs and Boonstra 1978). Emigration rates are not observed to be density dependent (Gaines and McClenaghan 1980, Lidicker and Stenseth 1992). It is argued that vole demography is sensitive to the phase of the cycle (Krebs et al. 1973, Krebs and Myers 1974, Chitty 1987), but not necessarily to density per se.

However, the effects of density itself on demographic processes can be difficult to determine in freely fluctuating populations for three primary reasons. First,

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establishing cause-and-effect relationships is problematic. Investigators must apply correlational methods to assess the relationship between density and rates of natality, mortality, and dispersal, but often it is difficult to determine the polarity of the causal relationship and to eliminate spurious correlations caused by unmeasured factors and unknown time lags. Second, many vole populations pass through density levels very quickly, making the effects of current density on current or future demographic performance difficult to detect. Finally, time-series approaches to examining the strength and timing of density dependence in population growth rates (Hanski et al. 1993, Turchin 1993) rarely allow exploration of the demographic or behavioral mechanisms of any observed density dependence.

In this study we used an experimental approach to examine the relationship between population density and demographic and behavioral processes in meadow voles (*Microtus pennsylvanicus*). By maintaining vole populations at different levels of density through time, we attempted to isolate density and its immediate consequences as causes of variation in demographic processes. We do not attempt to explain vole cycles, but rather ask which demographic processes will act to maintain vole populations near an equilibrium, and which may be responsible for wide divergences from equilibrium.

## MATERIALS AND METHODS

### *Study site and experimental design*

We performed our experiment in a fertile, mesic, old field on the property of the Institute of Ecosystem Studies in Dutchess County, southeastern New York (41°50' N, 73°45' W). The field had been mown every 1–2 yr since abandonment from corn cultivation in the early 1970s. Mown vegetation was not removed, and the field had a well-developed litter layer. Dominant plants included the grasses *Bromus inermis*, *Poa pratensis*, *Arrhenatherum elatius*, and *Phleum pratense* and the forbs *Galium mollugo*, *Solanum carolinense*, *Glechoma hederacea*, *Oxalis repens*, *Potentilla* spp., *Hieracium pratense*, and *Solidago* spp.

We employed a randomized block design to study the effects of vole density on demography, individual performance, and space use. In May and June 1990 we constructed nine 40 × 40 m fenced enclosures. Fences were made of 1.3 m wide galvanized hardware cloth (1.3-cm mesh), with 0.5 m belowground and 0.8 m aboveground. The nine enclosures were divided into three blocks. Blocks 1 and 2 were contiguous, and were separated from block 3 by a hedgerow (see Ostfeld and Canham 1993: Fig. 1). The plant species composition of blocks 1 and 2 were similar, whereas block 3 was more mesic and had a higher percentage cover of sedges (*Carex* spp.) and goldenrods (*Solidago* spp.). The three enclosures within each block were assigned randomly to either a low, medium, or high vole-density

treatment giving us three replicates of each density level. Enclosures were closely juxtaposed and experienced similar abiotic and biotic conditions. Mammalian and avian predators were not excluded by the fences.

### *Monitoring and manipulating vole populations*

Live-trapping grids were established in June 1990 within each enclosure. In addition, two 0.16-ha unenclosed (control) trapping grids were established adjacent to the enclosures in August 1991. Each grid consisted of 25 trap stations 7.5 m apart, with 5 m between the outermost trap stations and the fence. Initially, one Longworth live trap was placed at each station; when vole density grew such that ≥80% of traps contained voles on any single trapping day, a second trap was placed at each station within that enclosure. Thus, for most of the study, high-density enclosures had two traps per station. Traps were supplied with crimped oats and cotton batting, and were covered with a masonite board for protection from rain and snow. Traps were set for two consecutive nights every 2nd wk from June 1990 to April 1992. Due to cold temperatures, one scheduled trapping session was missed in December 1990, and one in December 1991. All small mammals captured (except shrews) were given individually numbered metal ear tags on first capture. On all captures we recorded tag number, body mass, sex, reproductive condition, and trap station. Females were considered reproductive if they had enlarged nipples, an open vulva, or were obviously pregnant. Males were considered in breeding condition if their testes were scrotal rather than abdominal. All small mammals were released at the point of capture after handling. Traps were locked open between trap sessions. In addition to meadow voles, low numbers of shrews (*Blarina brevicauda* and *Sorex cinereus*), white-footed mice (*Peromyscus leucopus*), meadow jumping mice (*Zapus hudsonius*), and eastern chipmunks (*Tamias striatus*) were captured. Since these species are granivorous or insectivorous, none of them competes directly with folivorous meadow voles for food.

In late June 1990 the vole density in all enclosures was reduced to two breeding pairs by removing adults and independent young. Vole density was subsequently managed at three different levels. In designated high-density enclosures we neither introduced nor removed voles throughout the remainder of the experiment. In low- and medium-density enclosures vole numbers were regulated by removing subadults (20 to 30 g) during the biweekly every-second-week trapping sessions. The subadult class is the primary age of dispersal in meadow voles (Gaines and McClenaghan 1980, Lidicker 1985). Approximate vole density was ascertained on day 1 of each trapping session, and targeted voles were removed and released several kilometres away on day 2. For medium-density enclosures, voles were removed whenever ≥15 adult plus subadult voles were captured on day 1. For low-density enclosures,

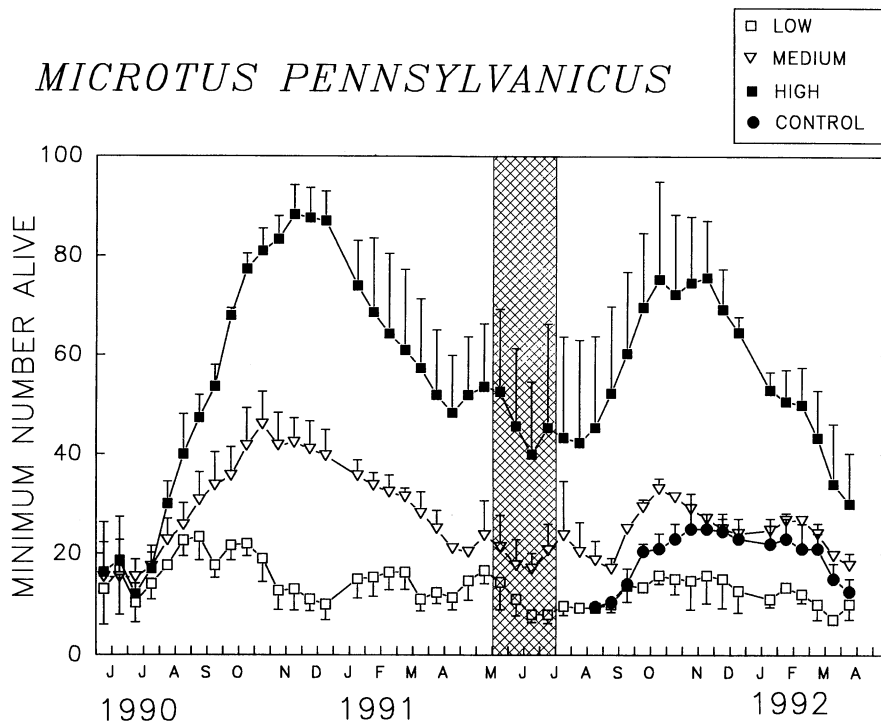


FIG. 1. Population densities (minimum number alive per 0.16 ha) of voles in the three density treatments (fenced populations) and controls (unfenced). Values are means ( $\pm 1$  SE) for the three replicates of each density level and the two replicate control grids. Shading indicates the drought period (<40% of long-term monthly mean rainfall). Sampling every 2nd wk gives some months three samples.

voles were removed whenever  $\geq 5$  adult plus subadult voles were captured on day 1. During some seasons, rapid population growth in low- and medium-density enclosures necessitated trapping each week in order to maintain targeted densities. We avoided removing adults ( $>30$  g) in order to reduce disruption of social organization, which is dominated by interactions among adults (Wolff 1985). We did not remove dependent young (juveniles, defined as  $<20$  g) in order to minimize direct impacts on endocrine and behavioral state of lactating females.

Capture probabilities of voles averaged 86% over the study, and therefore we used the minimum-number-alive method (Krebs 1966) to estimate vole density.

#### *Statistical analyses*

Our general approach was to test for the effects of vole-density treatment (low, medium, high) on various demographic and behavioral features. We were interested in the effects of density on: (1) reproduction (proportion of adult females and males in breeding condition); (2) recruitment (rate of appearance of unmarked individuals); (3) survival of juveniles, subadults, and adults (instantaneous survival rate per 14 d); (4) growth in body mass of different age categories (percentage growth rate per day); (5) median mass (in grams) at sexual maturity for both sexes (minimum

body mass at which half the individuals are in breeding condition); (6) frequency distribution of body mass; and (7) movement distances (in metres) of both sexes and all age classes (distance between successive captures 2 or 4 wk apart). Movement distances were used as an indicator of home range size. These parameters were measured for each trapping session, every 2 wk, to account for seasonal and annual changes. Therefore, we used repeated-measures analysis of variance (SAS Institute 1987) to analyze the effects of density treatment on population and individual performance. Because the three enclosures at each density level maintained independent populations of voles, we used the enclosures, not individual voles, as the unit of replication. Percentages for reproduction and survival were subjected to an angular transformation before analysis. We also used ANOVA to test for effects of season and block.

## RESULTS

### *Effects of the density manipulation*

Within 2 mo of the establishment of the enclosures (i.e., August 1990), vole densities in the three experimental treatments had begun to diverge, and for the remainder of the study average densities were distinctly different (Fig. 1). For part of the summer of 1991, density in one of the high-density enclosures declined

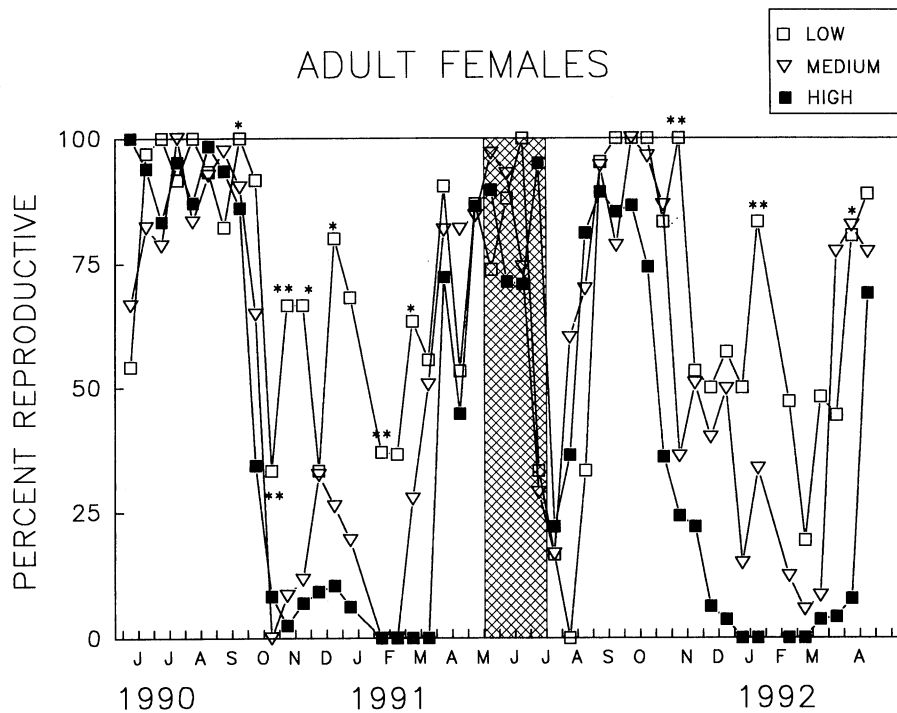


FIG. 2. Percentage of adult vole females in breeding condition, as indicated by condition of the vulva (perforate or nonperforate). Values are means for the three replicates of each density level. For the entire study, repeated-measures ANOVA showed statistically significant effects of density ( $F_{2,6} = 27.02$ ,  $P = 0.001$ ), time ( $F_{45, 270} = 11.74$ ,  $P < 0.0001$ ) and density  $\times$  time ( $F_{90, 270} = 1.96$ ,  $P < 0.0001$ ). For individual trapping sessions, statistically significant effects of density on proportion reproductive (angular transformed) are indicated by \* =  $P < 0.05$ , \*\* =  $P < 0.01$ . Shading indicates the drought period. Sampling every 2nd wk gives some months three samples.

to a level similar to those in the medium-density enclosures, but it then increased substantially in the autumn. Populations in all three high-density enclosures declined gradually in the winter of 1991–1992. The unfenced control grids maintained density levels quite similar to those in the medium-density enclosures (Fig. 1). On the 11 trapping grids we captured a total of 3271 individuals 11 601 times over the course of the study.

#### Reproduction and recruitment

Vole density had a strong effect on reproductive activity of both females and males in the autumn, winter, and spring of both years, but not in summer (Figs. 2 and 3). For both sexes, a high proportion of individuals in low-density treatments remained in breeding condition even in winter, which typically is considered the nonbreeding season for this species (Tamarin 1977). In medium-density enclosures, voles of both sexes continued to breed later in the autumn, and returned to breeding condition earlier in the spring, than did those in high-density enclosures (Figs. 2 and 3).

During May and June 1991, rainfall was  $< 40\%$  of the long-term (1951–1989) monthly mean for this site. For females but not males, breeding activity dropped sharply in response to this drought (Figs. 2 and 3). The abrupt decline in breeding activity occurred in all en-

closures, irrespective of population density. A delay of  $\approx 2$  mo was observed between the onset of the drought and the decline in breeding, presumably as a result of a lag in drying of the vegetation, which serves as food and cover for voles (Batzli 1985).

Differences among treatments in reproductive activity appeared to cause the strong density effect on per capita recruitment (Fig. 4). For most of the study, recruitment rates were highest in low-density enclosures, intermediate at medium-density, and lowest in high-density enclosures. However, the differences were statistically significant primarily in autumn, winter, and spring. For  $\approx 2$  mo following the 1991 drought, recruitment rates dropped sharply for all density treatments.

#### Survival rates

For juveniles and subadults there were no statistically significant effects of population density on survival rates during any of the individual trapping sessions, nor overall (repeated-measures ANOVA; juveniles:  $F_{2,6} = 0.04$ ,  $P = 0.958$ ; subadults:  $F_{2,6} = 1.34$ ,  $P = 0.329$ ). For adult voles, significant effects of density on survival rates began to appear in autumn and winter 1991–1992,  $\approx 16$  mo after the density manipulation began (Fig. 5). During this period, survival

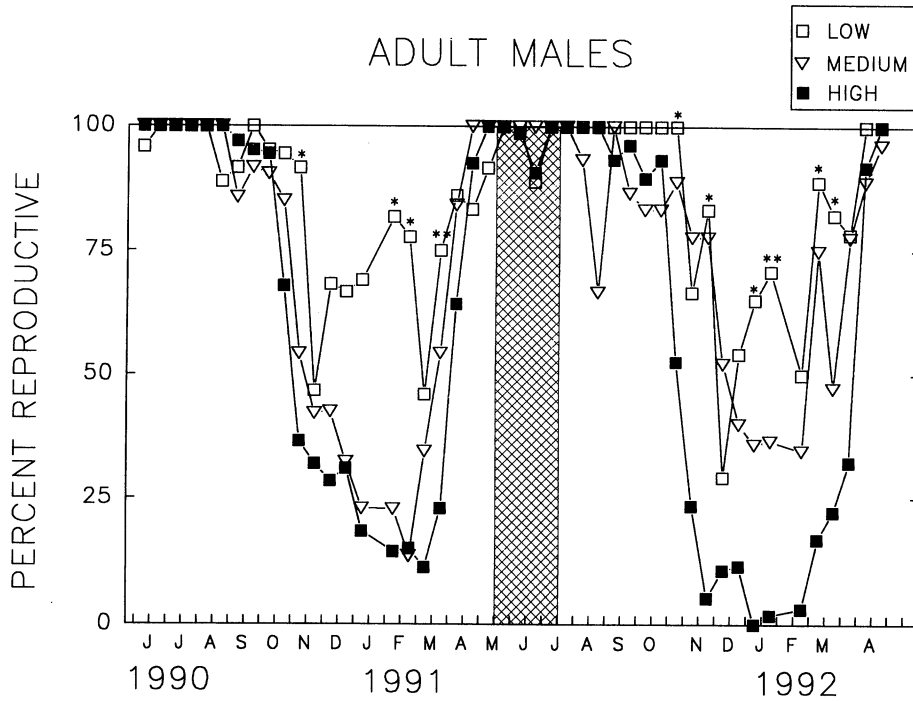


FIG. 3. Percentage of adult vole males in breeding condition, as indicated by position of the testes (scrotal or abdominal). Values are means for the three replicates of each density level. For the entire study, repeated-measures ANOVA showed statistically significant effects of density ( $F_{2,6} = 8.49, P = 0.018$ ), time ( $F_{45, 270} = 19.35, P < 0.0001$ ) and density  $\times$  time ( $F_{90, 270} = 2.23, P < 0.0001$ ). For individual trapping sessions, statistically significant effects of density on proportion reproductive (angular transformed) are indicated by \* =  $P < 0.05$ , \*\* =  $P < 0.01$ . Shading indicates the drought period. Sampling every 2nd wk gives some months three samples.

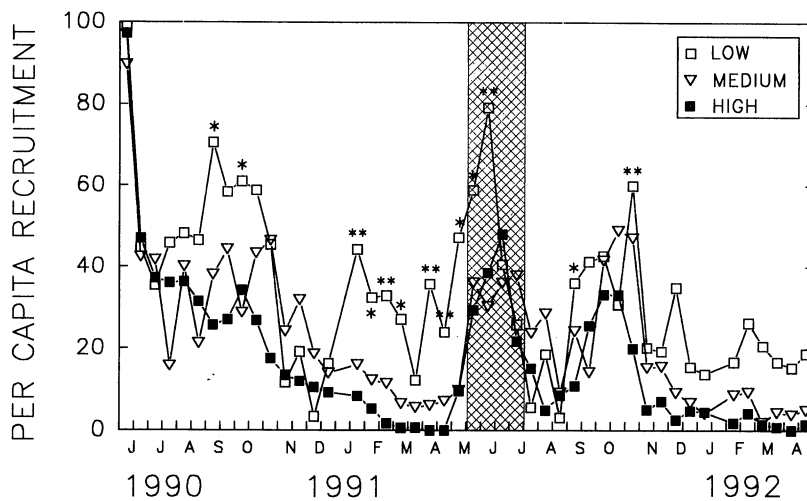


FIG. 4. Per capita recruitment by vole density treatment. Values are means for the three replicates of each density level. For the entire study, repeated-measures ANOVA showed a marginally significant effect of density ( $F_{2,6} = 4.40, P = 0.067$ ), and highly significant effects of time ( $F_{45, 270} = 16.26, P < 0.0001$ ) and density  $\times$  time ( $F_{90, 270} = 1.58, P = 0.003$ ). For individual trapping sessions, statistically significant effects of density on per capita recruitment are indicated by \* =  $P < 0.05$ , \*\* =  $P < 0.01$ . Shading indicates the drought period. Sampling every 2nd wk gives some months three samples.

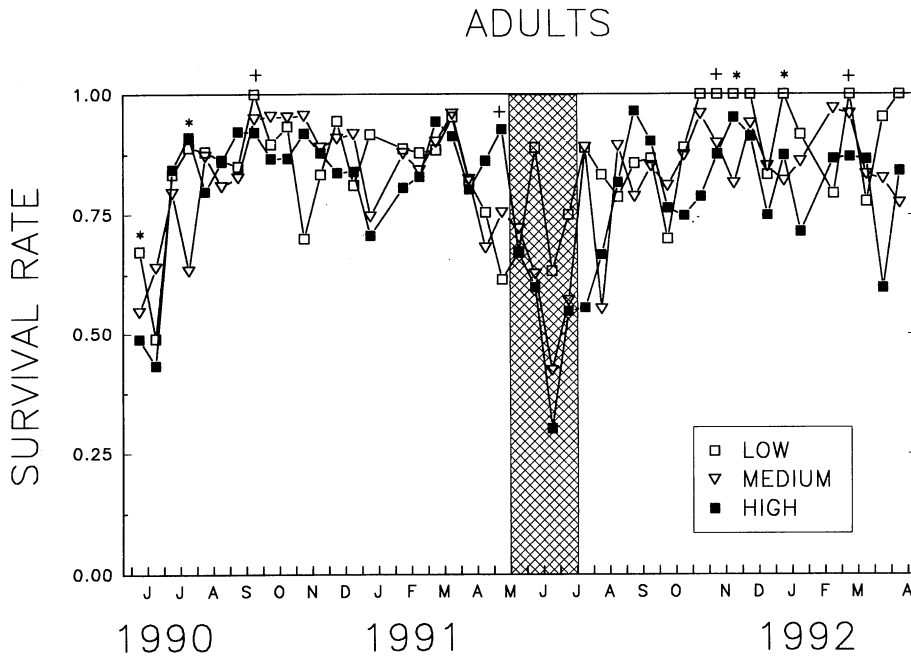


FIG. 5. Survival rates (instantaneous survival rate per 14 d) for adult voles in the density treatments. Values are means for the three replicates of each density level. See text for overall statistical results. For individual trapping sessions, statistically significant effects of density on survival rates are indicated by † =  $P < 0.10$ , \* =  $P < 0.05$ , \*\* =  $P < 0.01$ . Shading indicates the drought period. Sampling every 2nd wk gives some months three samples.

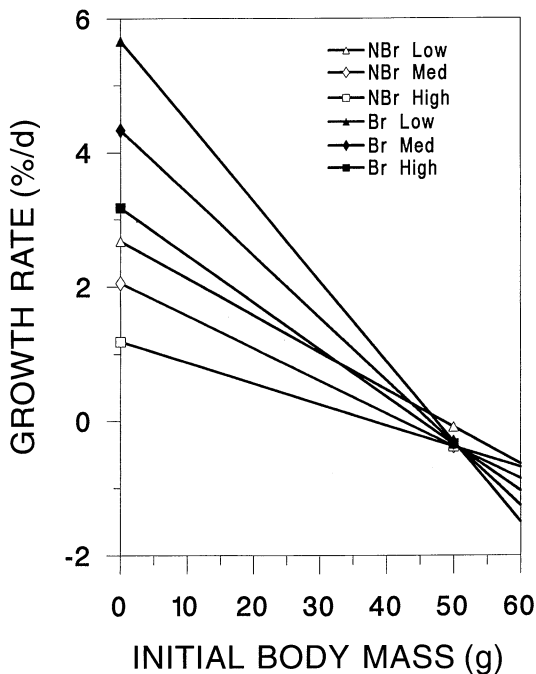


FIG. 6. Growth rates (percentage mass growth per day) for individual voles as a function of body mass, density treatment, and breeding season. Shown are least-squares regression lines describing the relationship between growth rate (calculated between every 2nd wk trapping sessions) and initial mass for the three density treatments and both nonbreeding (NBr) and breeding (Br) seasons.

rates were always highest in low-density enclosures, and usually lowest in high-density enclosures. Over the course of the study the effect of density on survival rates of adults was marginally significant (repeated-measures ANOVA,  $F_{2,6} = 4.23$ ,  $P = 0.071$ ).

Survival rates varied significantly over time ( $F_{43, 258} = 5.93$ ,  $P < 0.0001$ ), being higher during nonbreeding seasons (November–April) than during breeding seasons (May–October). Survival rates of adults declined during the 1991 drought, with voles in high-density treatments appearing to be most strongly affected, and those in low-density treatments least affected (Fig. 5). However the effect of density on survival was not statistically significant during that period.

#### Individual growth rates and body mass

Vole growth rates varied consistently with body size, season and density (Fig. 6). Regardless of season or density, growth rates (percentage mass growth per day) declined as body mass increased, converging on zero growth at  $\approx 45$ – $50$  g (Fig. 6). Because of the convergence in growth rates with increasing body mass, growth rates of adults ( $> 30$  g) were not significantly affected by density. Density had a significant effect on growth rates of individuals  $< 30$  g during the nonbreeding season (i.e., juveniles and subadults; repeated-measures ANOVA,  $F_{2,6} = 6.63$ ,  $P = 0.030$ ), and a marginally significant effect during the breeding season ( $F_{2,6} = 3.94$ ,  $P = 0.081$ ). In both the breeding and non-

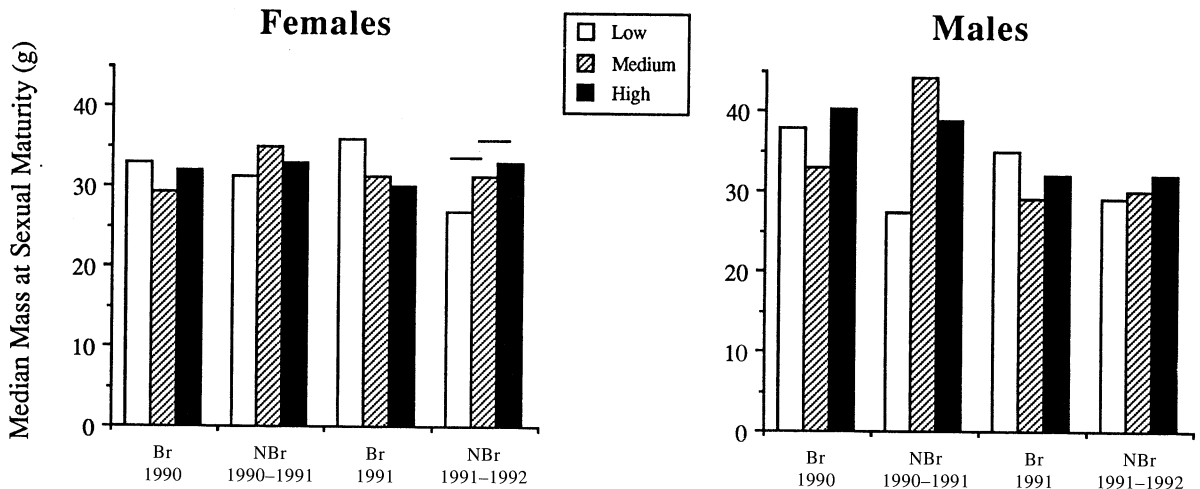


FIG. 7. Median mass at sexual maturity for vole females and males for the different density treatments and seasons. Only for females in the nonbreeding season (NBr) of 1991–1992 was there a significant effect of density (see *Results: Individual growth rates and body mass*). Horizontal lines above bars span mean values not significantly different by Tukey test.

breeding seasons the growth rates of juveniles and subadults were highest in the low-density enclosures, intermediate at medium density, and lowest in the high-density enclosures.

Although growth rates were affected by population density, density had a minimal effect on the body mass at which voles achieved sexual maturity (Fig. 7). A statistically significant effect of density was observed only for females in the 1991–1992 nonbreeding season ( $F_{2,6} = 6.02$ ,  $P = 0.037$ ). However, because individual growth rates were slower at higher densities, we infer that the age of sexual maturity increased with increasing population density.

We expected our experimental protocol (removing voles in the 20–30g mass class) to directly affect the frequency distribution of body mass in low- and medium-density treatments. The predicted effect was to increase the degree of bimodality in mass distribution by decreasing frequencies of medium-sized voles. However, during the breeding seasons of 1990 and 1991, when the majority of removals were made, all three density treatments showed similar bimodal distributions in body mass; low- and medium-density enclosures did not appear to show an underrepresentation of 20–30g voles compared to high-density enclosures (Fig. 8). In nonbreeding seasons, none of the treatments showed bimodal mass distributions. Nevertheless, we did not compare means or distributions across density treatments statistically, but only qualitatively.

There was a clear effect of population density on mass distributions in categories <20g and >30g. In both breeding and nonbreeding seasons of both years the low-density enclosures had greater proportions of juvenile voles, which reflected the higher recruitment rates in these enclosures (Fig. 4). Medium-density enclosures had the greatest frequencies of moderately large voles ( $\approx 40$ –50g), and low-density enclosures had

the highest frequencies of very large voles (>50g). Very few extremely large voles occurred in high-density enclosures, particularly during nonbreeding seasons (Fig. 8).

#### Movement distances

Movement of voles between successive captures 2–4 wk apart was strongly affected by density (Table 1). The average movement distances declined significantly from  $11.5 \pm 2.7$  m (mean  $\pm 1$  SD) at low density to  $8.6 \pm 2.0$  m at medium density and  $6.8 \pm 1.6$  m at high density (with all pairwise differences significant at  $P < 0.05$ ). Movement distances also varied significantly with age class (Table 1), in the rank order juveniles ( $8.2 \pm 2.6$  m)  $\leq$  subadults ( $8.4 \pm 2.6$  m)  $<$  adults ( $10.3 \pm 3.1$  m). However, all age classes responded similarly to the density treatments, as indicated by a statistically insignificant density  $\times$  age interaction (Table 1). Movement distances also differed between sexes, with males moving significantly farther than females (Tukey's HSD test,  $P < 0.05$ ). Movement of females appeared to be more sensitive to the density treatment (see the density  $\times$  sex interaction term, Table 1).

## DISCUSSION

### Extent of density dependence

Most demographic and behavioral processes we examined were affected by our manipulation of vole density. We found that high density caused: (1) shorter breeding seasons; (2) lower rates of recruitment; (3) slower individual growth rates to lower modal body mass; (4) older age (but generally not greater mass) at sexual maturity; (5) reduced survival rates of adults, but only after  $\approx 16$  mo had elapsed after divergence of density conditions; and (6) reduced movement dis-



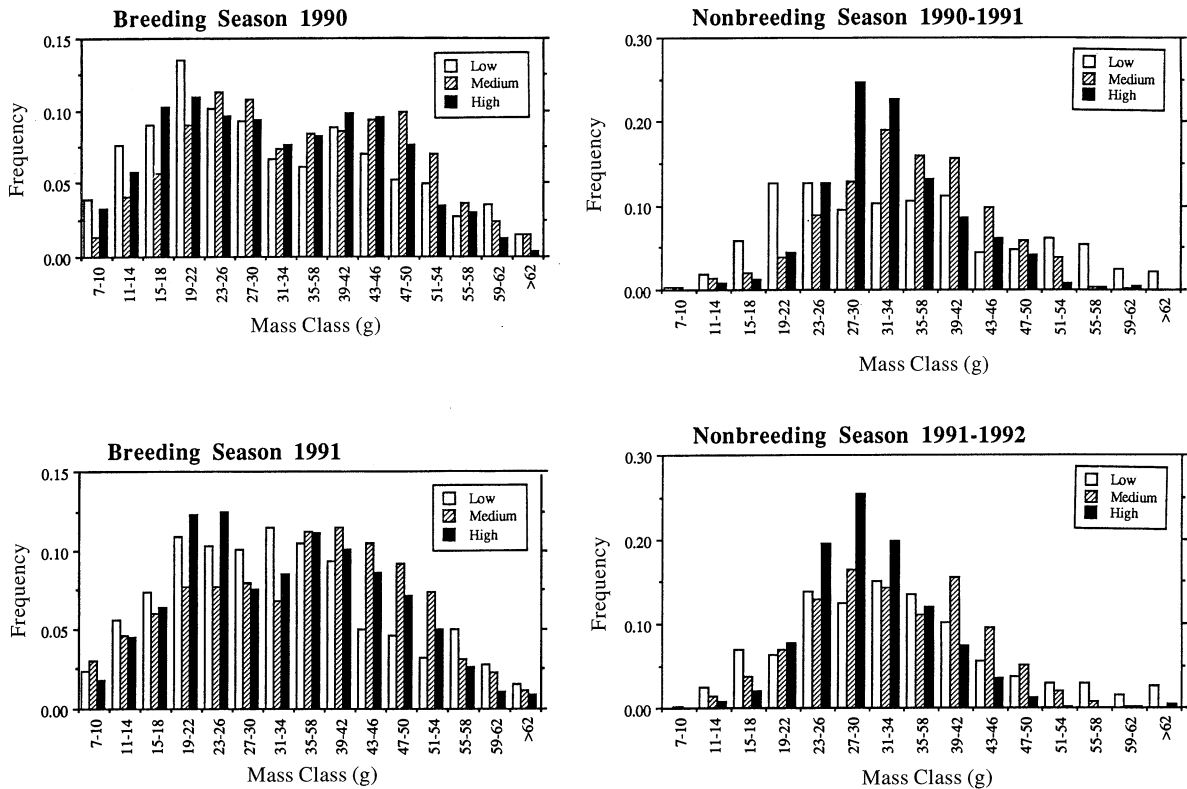


FIG. 8. Frequency distributions of body masses for voles in the three density treatments, arranged by season and year.

tances. In nearly all parameters, medium-density treatments were intermediate between high- and low-density treatments. The density treatments did *not* affect: (1) reproductive activity in the summer breeding season; (2) reproductive response to drought conditions; and (3) survival rates of juveniles and subadults.

Studies of freely fluctuating vole populations have given mixed results regarding the strength of density dependence in demographic and behavioral processes. Several studies have found shortened breeding seasons following periods of peak density (Kalela 1957, Krebs et al. 1969, Batzli and Pitelka 1971, Hansson and Hent-

tonen 1985, Bernshtein et al. 1989), but others have not (Hoffman 1958, Krebs and Myers 1974, MacLean et al. 1974). Individual growth rates were affected by the phase of the cycle (highest during increase phase, lowest during decline phase), but not density in *Microtus pennsylvanicus* (Krebs et al. 1973). Mass at sexual maturity increased with increasing density in *M. townsendii* (LeDuc and Krebs 1975), and was highest at peak density in *M. pennsylvanicus* (Keller and Krebs 1970), but was unrelated to density in several other arvicoline species (Krebs 1964, Keller and Krebs 1970).

The effects of population density on survival rates are controversial. In their review, Krebs and Myers (1974) reported that survival rates of voles vary consistently with the phase of the cycle, but not with density per se. However, other studies of voles (e.g., Erlinge et al. 1984, Hansson 1987, Hanski et al. 1991, 1993, Korpimäki 1993) have argued that density-dependent mortality occurs in areas dominated by generalist predators, and that specialist predators cause delayed density-dependent mortality.

Suppression of movement at high density has been observed for several vole species (Abramsky and Tracy 1980, Gaines and Johnson 1982, Desy et al. 1990, Sandell et al. 1991a). However, Taitt and Krebs (1981), Taitt et al. (1981), Bondrup-Nielsen (1986) and Jones (1990) have reported that movement distances decrease

TABLE 1. Results of three-way analysis of variance for effects of Density, Age (juvenile, subadult, or adult), and Sex (male or female) on movement distances between successive vole captures on 2-wk intervals. Enclosures were used as the unit of replication, thus all individual vole movement data within a Density  $\times$  Age  $\times$  Sex grouping were averaged prior to analysis.

Source of variation	df	F	P
Model	13, 40	8.50	0.0001
Density	2, 40	35.17	0.0001
Age	2, 40	8.14	0.001
Sex	1, 40	4.42	0.042
Density $\times$ age	4, 40	1.34	0.271
Density $\times$ Sex	2, 40	3.53	0.039
Age $\times$ Sex	2, 40	3.52	0.039

with increasing food availability, but are not necessarily (or only secondarily) responsive to population density. However, these studies did not control for the effects of increasing local density in response to increased food availability. In our populations food quantity was reduced in high-density enclosures relative to medium- and low-density grids (Ostfeld 1994). Therefore, the smaller movement distances we observed in the former must have been caused by high density, and not by food availability, which would have caused the opposite effect. Our data support the conclusion of Desy et al. (1990) that movement distances in voles are primarily affected by density, and only secondarily by food availability.

Few prior population studies have manipulated vole density, and all have consisted of short-term removals. Several (Redfield et al. 1978, Boonstra and Rodd 1983, Porter and Dueser 1986) manipulated density of one sex per study plot, and therefore (intentionally) altered sex ratios as well as total density. Boonstra (1977) and Rodd and Boonstra (1984) removed adult *M. townsendii* and *M. pennsylvanicus*, respectively, during the autumn and spring preceding expected spring declines. In both studies the effects of temporary reductions in density were modest. Survival rates of adult males and females were improved in *M. townsendii* (Boonstra 1977), but generally not in *M. pennsylvanicus* (Rodd and Boonstra 1984). Reproductive condition of both female and male *M. pennsylvanicus* was largely unaffected (Rodd and Boonstra 1984). Movement distances of *M. pennsylvanicus*, but not of *M. townsendii*, increased after experimental removals (Boonstra 1977, Rodd and Boonstra 1984). Inconsistencies between these results and those of the present study are difficult to interpret due to different experimental procedures: in the prior studies adults (not subadults) were removed, removal periods were brief, and trapping grids were not enclosed.

#### *Density dependence and cycle-phase dependence*

Some of the confusion regarding the importance of density dependence in vole population dynamics exists because the focus has been predominantly on effects of the cycle phase (i.e., low, increase, peak, decline), rather than effects of density per se (Frank 1957, Krebs et al. 1973, Schaffer and Tamarin 1973, Krebs and Myers 1974, Tamarin 1983, Cockburn 1988, Hansson 1989). In our view, the focus on cycle phase has been helpful but insufficient for elucidating the mechanisms of population change for the following reasons. First, in freely fluctuating populations detecting direct effects of density is difficult or impossible because comparisons of populations at the same or different density levels are confounded by seasonal conditions and recent history. Second, a focus on the effects of cycle phase limits the applicability of resulting models to less cyclic populations (Sandell et al. 1991b). Third, the implication of the focus on cycle phase is that vole

populations respond to the direction and rate of density change rather than to current density, an assumption without supporting evidence. Animals are likely to experience directly the effects of current and recent density, but not necessarily the current rate of change in population size. Fourth, because increase and decline phases are defined based on whether or not gains exceed losses, conclusions regarding the effects of cycle phase on rates of gain and loss may be circular. Finally, if the effects of density involve substantial time lags, a demographic or behavioral response to density may be correlated with, but not caused by, the present cyclic phase.

An example of potential confounding of correlation with causation is the Chitty Effect, which is the occurrence of especially heavy voles particularly during the peak of a multiannual cycle (Chitty 1952, Boonstra and Krebs 1979, reviewed by Lidicker and Ostfeld [1991], Wolff [1993]). The Chitty Effect has been interpreted as an outcome of natural selection favoring large, and ostensibly dominant, individual voles during periods of population growth and at high density (Chitty 1967, but see Chitty 1987). Under our experimental conditions, especially large voles were substantially less frequent under high- than low-density conditions (Fig. 7), suggesting that high density per se is not the cause of the Chitty Effect. Apparently, conditions favorable for both individual body growth (Fig. 6) and population growth occurred in the low-density enclosures, but our manipulation prevented population growth while allowing body growth to large size. Our data support the conclusions of Lidicker and Ostfeld (1991) and Wolff (1993) that large-bodied voles are produced during periods that are especially favorable for growth and survival (often low-density periods), and that their predominance during population peaks results from conditions preceding, not during, the peak.

#### *Stabilizing and destabilizing effects*

A critical effect of high and medium density was to reduce the length of the breeding season, and therefore the number of generations per year (Figs. 2–4; Ostfeld et al. 1993). In addition, by reducing individual growth rates while not affecting mass at sexual maturity, high- and medium-density conditions increased age at sexual maturity and therefore slowed the potential rate of population growth (Cole 1954). The effects of density on reproduction and body growth were immediate and constant through time. These two density-dependent processes should be strongly stabilizing influences on population dynamics.

However, several experimental results revealed destabilizing processes. First, population density did not affect reproductive activity during the height of the breeding season (summer), which could lead to seasonal, rapid population growth even in high-density populations. Second, the density-independent response to drought (Fig. 2; see also Ostfeld et al. 1993) could

contribute to erratic population fluctuations. Third, survival rates of juveniles and subadults were unresponsive to population density, which would act against the regulation of population growth. Fourth, the compression of movements with increasing density acts to accommodate density buildups, and therefore is not stabilizing. Spacing behavior previously has been considered a strong stabilizing force in vole population dynamics (e.g., Boonstra and Rodd 1983, Stenseth 1986). The emphasis has been on the effects of spacing behavior on population density rather than vice versa. However, if spacing behavior and social organization are highly responsive to density (Ylönen et al. 1988), then their stabilizing effects may be weak or absent in fluctuating populations (Heske and Bondrup-Nielsen 1990).

Survival rates of adults in the medium- and high-density enclosures declined significantly relative to low-density conditions beginning  $\approx 16$  mo after the densities diverged (Fig. 5). Because delayed density-dependence can cause population cycles or chaos (May 1976, Ostfeld 1992, Hanski et al. 1993, Hornfeldt 1994), factors influencing adult survival rates may be of particular importance to vole population dynamics. The causes of the delayed effect of density on adult survival are not entirely clear. High and medium vole density caused a winter-spring decrease in above-ground plant biomass relative to low density, but the effect was ephemeral (Ostfeld 1994). Plant biomass recovered and was equivalent across density treatments by autumn 1991 when the effect of density on survival became evident (Ostfeld 1994). Therefore, we do not believe the delayed density-dependent survival was due to vole-resource dynamics (see also Ostfeld et al. 1993). Although our experiment manipulated only population density directly, we recognize that resource levels, social interactions, dispersal, and possibly age structure and predation rates also may have been affected indirectly.

Populations of voles differ radically in their tendency to fluctuate through time (Henttonen et al. 1985, Taitt and Krebs 1985, Ostfeld 1988). We suggest that future research should focus on the indirect effects of differences in vole density, and on differences among populations in the strength of density dependence in demographic and behavioral features.

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