Why are some microtine populations cyclic while others are not?

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Mark-recapture, radiotelemetry, and behavioural tests were used to determine whether mechanisms suggested to cause cyclic patterns in microtine rodents are present in a noncyclic *Microtus agrestis* (Linnaeus, 1761) population studied in southern Sweden. Several of the factors suggested to cause cyclicity occur also in our noncyclic population, e.g. between-year differences in individual quality and variations in food conditions. The population was found to have a high potential for fluctuating in numbers, and peak densities varied greatly between years. Intense predation, especially during winter, by various generalist predators resulted in low densities in spring and early summer every year. This probably prevented between-year cyclic patterns. Predation by specialist predators whose numbers are closely related to the abundance of their prey, might promote cyclicity in some microtine populations.

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Introduction

Microtine rodents have a high potential to fluctuate in numbers and have therefore been classical study objects in population ecology. A wide variety of fluctuation patterns occur. Some microtine populations show conspicuous cyclic fluctuations, with peak densities occurring every third or fourth year, while others fluctuate annually with low densities in spring and early summer and peak densities during some part of the breeding season (e.g. Krebs and Myers 1974, Taitt and Krebs 1985). Several hypotheses have been proposed to explain the cyclicity in microtines (for a review see Taitt and Krebs 1985), but in spite of the large amount of research conducted little is known about the underlying factors.

The field vole, *Microtus agrestis* (Linnaeus, 1761) is a grass-eating microtine that occurs over most of the Palearctic region. In northern Fennoscandia populations are typically cyclic whereas in southern Sweden they are noncyclic (Hansson and Henttonen 1985). Why does this species' population dynamics differ between the south and north? We addressed this question by setting out to determine whether the mechanisms suggested to cause a cyclic patern were present in our noncyclic population.

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Study area and methods

The population dynamics and behaviour of the field vole have been investigated in the Revinge area in southern Sweden since November 1983. The study area is a homogenous abandoned field on peat soil dominated by graminids (predominantly *Deschampsia caespitosa, Elytrigia repens* and *Phleum pratense*), *Urtica dioica, Anthriscus sylvestris*, and *Cirsium arvense*. From November 1983 to October 1985, population dynamics was studied by live-trapping in three grids, (ca. 0.5 ha each, separated by 30 m) with 7 m between trap stations. Two multiple-capture 'Ugglan' traps were used at each station. Trapping was conducted on each grid at 3-week intervals, with each trapping period lasting 5 days. To evaluate the effect of predation, all avian and mammalian predators except the weasel, *Mustela nivalis* Linnaeus, 1766, were excluded from the central grid by a net. In 1986 and in 1988 trapping was conducted only in the central grid, with the net removed. The traps were prebaited with crushed oats 1 – 2 days before beginning a trapping session. Captured animals were marked individually by toe-clipping and each time a vole was captured its body weight, sex, reproductive status, and site of capture were recorded.

When examining spacing patterns, movements and social organization, capture-recapture data were complemented by radio-tracking. We used collared transmitters weighing ca. 1.9 g, i.e. 5 – 8% of the voles' body mass. Batteries lasted for 7 – 14 days. Locations were recorded every hour around the clock. About 60 individual animals were tracked.

Encounter tests were carried out to examine aggressive behaviour. Animals taken from the grids were tested indoors in a metalic arena with a glass front ($150 \times 75 \times 50$ cm). The arena was covered with sawdust and was throughly cleaned before each test. Animals of the same sex were tested in pairs. Voles were allowed to acclimatize for 10 min. in different parts of the arena, separated by a partition. The partition was then removed and the animals were observed for 20 min. Three main categories of behaviours were recorded: aggressive behaviour (attack, counterattack, chase, boxing and wrestling), contact behaviours (approach, sniffing, grooming, and sitting together), and avoidance behaviour (escape, jump, vocalizing, and sitting; modified from Colvin 1973; Cranford and Derting 1983). Each animal was used only once, and tests were conducted during both the nonbreeding and breeding season.

Results and discussion

Population dynamics

In late autumn 1983, when the study started, vole density was high (Fig. 1). The voles continued to reproduce into November, and numbers peaked in December. A marked decline occurred during the nonbreeding period (December – March), and vole numbers decreased further during the early part of the subsequent breeding period. In July 1984 there was a rapid increase until the annual peak was reached. During the remaining part of the breeding period there was a continuous decline in density. This decrease continued until May 1985. Population density then increased rapidly and peaked in August. The peak density in 1985 was in between that of the first and second years. The pattern of change during 1983 1985 agreed with the pattern observed in this area previously (Hansson 1971, Myllymäki *et al.* 1977, Erlinge *et al.* 1983). Thus, the dynamics of this vole population was characterized by considerable between-year variation in peak densities, but densities were low in spring and early summer every year. The between-year pattern was noncyclic.

Behavioural polymorphism hypothesis

Some hypotheses consider factors within the rodent population to be the driving force causing cyclic patterns do develop. The behavioural polymorphism hypothesis assumes that
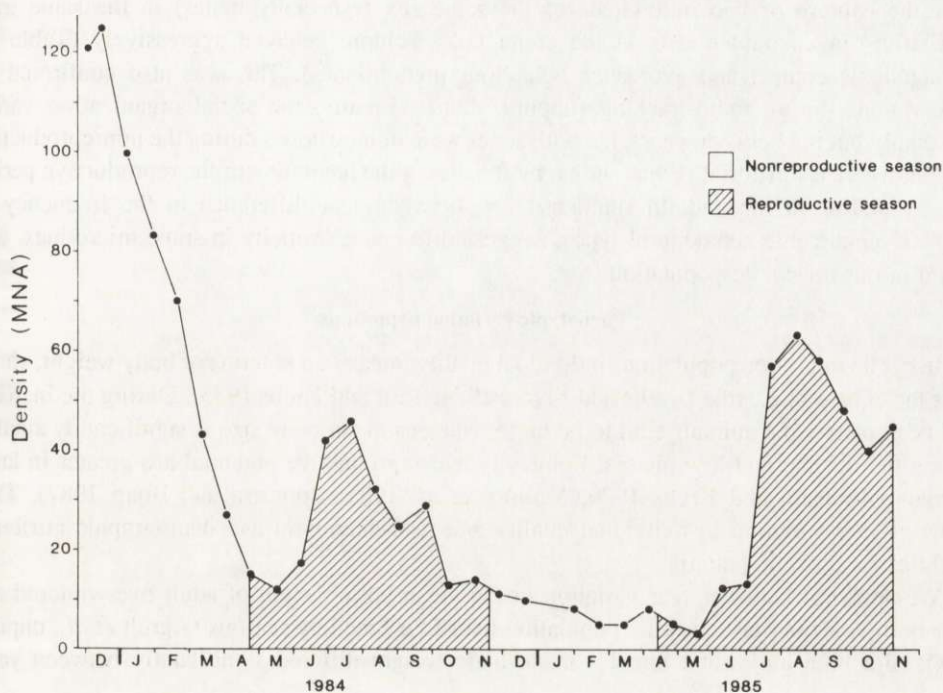
Fig. 1. Changes in field vole numbers in the unmanipulated grid from December 1983 to November 1985. The figures are minimum number of animals known to be alive (MNA).

different behavioural genotypes (amicable and aggressive individuals) are selected for and predominate during different phases of a cycle, creating the cyclicity (Chitty 1967, Krebs 1978, 1985). We looked for between-year differences in aggressive behaviour by recording signs of wounds in captured animals during the breeding seasons. There were no significant differences between years; signs of wounds were found on 4 males of 109 in 1984 and 10 of 136 males in 1985; $\chi^2 = 1.36$, $p > 0.10$; for females the corresponding figures are 4 of 176 in 1984 and 3 of 121 in 1985; $\chi^2 = 0.0013$, $p > 0.10$. Generally, signs of fighting were mainly observed

Table 1. Average number of recorded behaviour $(\bar{x} + SD)$ during dyadic encounter tests (breeding season). Statistical test: Kruskal-Wallis.

Sex	n	Aggressive behaviours	Contact behaviours	Avoidance behaviours	Sign.
Males	19	$1.21 \pm 3.42*$	4.63 ± 4.72	2.68 ± 4.68	$p = 0.011$
Females	15	0.33 ± 0.72	5.87 ± 6.01	2.87 ± 3.54	$p = 0.001$

* One male showed aggressive behaviours 15 times during his test. For the other males the number of aggressive behaviours ranged from 0 to 2.

after the capture of two individuals of the same sex (especially males) in the same trap. Similarly, in encounter tests in the arena voles seldom behaved aggressively (Table 1). Nonagonistic contact and avoidance behaviour predominated. This was also confirmed by observations during radio-tracking (unpubl. data). Finally, the social organization varied seasonally but not between years, i.e. both sexes were nonterritorial during the nonreproductive season, whereas territoriality was shown by females at the beginning of the reproductive period and by males at the end. In summary; no between-year difference in the frequency of aggressive/amicable behavioural types, suggested to cause cyclicity in some microtines, was found in our noncyclic population.

Phenotypic variation hypothesis

In cyclic microtine populations individual quality, measured in terms of body weight, varies over the course of a cycle (Krebs and Myers 1974, Taitt and Krebs 1985). During the increase and peak phases the animals tend to be large, whereas mean body size is significantly smaller during the decline and low phases. Longevity and reproductive potential are greater in large animals (Boonstra and Krebs 1979, Mallory *et al.* 1981, Boonstra and Boag 1987). Thus between-year variation in individual quality and its behavioural and demographic attributes might cause a cyclic pattern.

We analysed between-year variation in the mean body weight of adult overwintered and year-born voles in our noncyclic population over four breeding seasons (Agrell *et al.*, unpubl. data). For both males and females mean body weight differed significantly between years
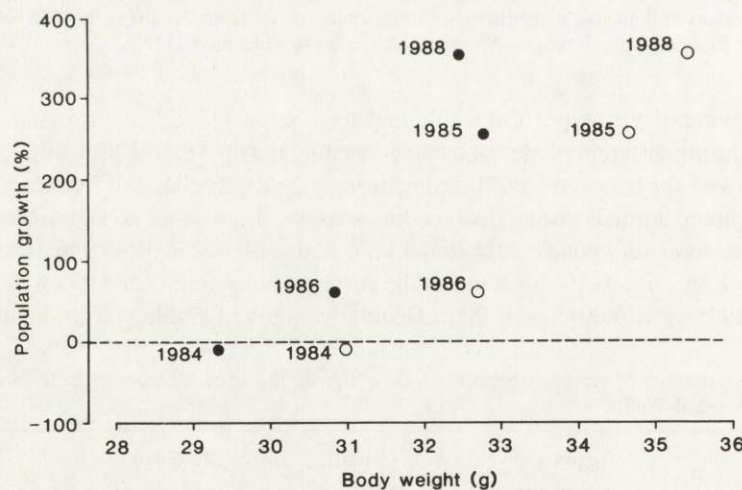

Fig. 2. The relationship between mean adult body weight of female ● and male ○ field voles and population growth during the reproductive seasons of four years. Population growth was calculated as the proportional change in density from mid – April to mid – August. Differences in body weight between years, ANOVA, males: n = 194, F = 6.00, p = 0.001; females: n = 216, F = 3.54, p < 0.05.

(Fig. 2). Also, mean body weight was positively correlated with population growth during the corresponding season. During the two years when mean body weight was low, population density decreased (1984) and only increased slightly (1986). By contrast density increased markedly over the 1985 and 1988 seasons when the mean body weight of voles was high (Fig. 2). Further, more adult survival was positively correlated with the body weight and recruitment of young was higher in years when female voles were heavier and survived longer (Agrell *et al.*, in ms). Thus, the significant between-year difference in body size observed in cyclic populations also occurred in our noncyclic population. Furthermore, mean body weight was positively related to population growth, as has been found in cyclic populations.

Dispersal and habitat structure hypothesis

Dispersal has a profound influence on population dynamics (Lidicker 1975). When dispersal was prevented by fencing, vole numbers increased to high densities and food resources were overexploited. Thus, dispersal was considered to be a prerequisite for population regulation (Krebs *et al.* 1969, Boonstra and Krebs 1977). Immigration combined with habitat hetero-geneity has been suggested to cause cyclicity in microtines (Abramsky and Tracy 1979, Gaines *et al.* 1979, Rosenzweig and Abramsky 1980). Selective dispersal by dispersal-disposed individuals (pre-saturation dispersal) was suggested to predominate during the increase phase whereas saturation disperal by "surplus" individuals should be most important during the peak and early decline (Lidicker 1975). The role of dispersal in cyclic microtines is difficult to evaluate since it is hard to distinguish the causes of dispersal from its effects (Stenseth 1983). In addition the relationship between dispersal and density is unclear, and data obtained thus far are contradictory (for review see, e.g. Stenseth 1983).

Table 2. Correlation (Spearman rank correlation) of male and female movement distances with total density.

	n	r_s	p
Juvenile dispersal			
Males	19	0.715	< 0.001
Females	39	0.144	> 0.20
Adult dispersal			
Males	197	0.276	< 0.001
Females	316	0.317	< 0.001

We examined dispersal in our noncyclic vole population. Natal dispersal, i.e. an individual's movements from its place of birth to the place where it reproduces, predominated; 58% of the males and 23% of the females recaptured as adults had dispersed, i.e. had moved more than one home range diameter (Sandell *et al.* 1990). Female movements were not related to density, but male movement distances were negatively associated with total density (Table 2). There was no difference in mean distance moved between periods of population increase and periods of decline (Sandell *et al.* 1990). Few dispersal movements were made by adult voles (Sandell *et al.*, in press), and the distance moved between sequential trapping periods showed a strong negative correlation with density, i.e. both sexes moved shorter distances at higher densities (Table 2).

Thus, dispersal in our noncyclic population did not seem to be frequent. It occurred mainly as natal dispersal and seemed to have little influence on population dynamics. The study area
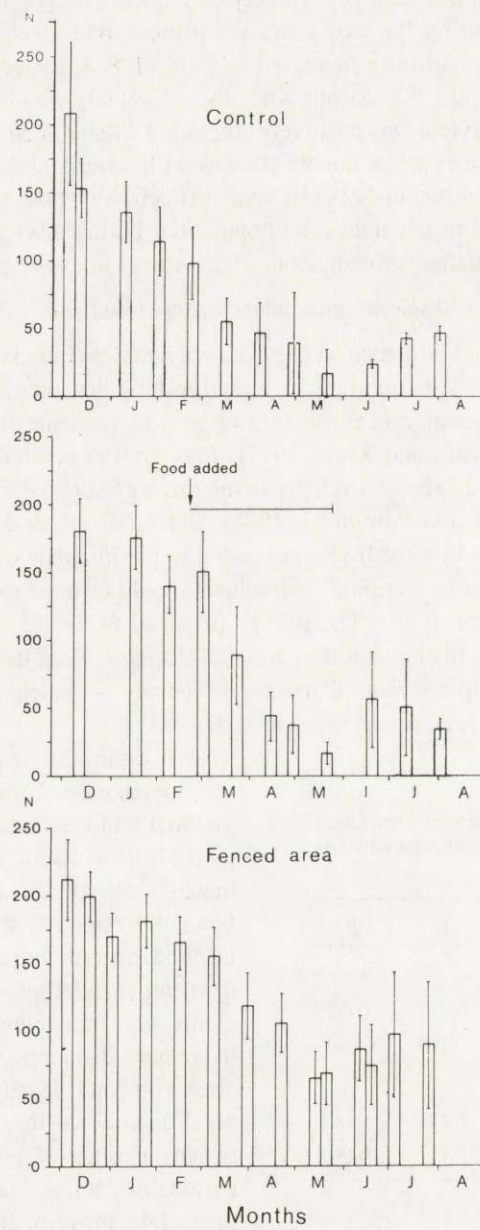
Fig. 3. Changes in field vole numbers from winter to
summer in a grid where predation on voles was prevented
by fencing and in two other grids; one control and one
where food was added. Figures are Jolly (1965) estimates
based on live-trapping data.

is part of a larger homogeneous habitat surrounded by extensive grazed fields that are sub-optimal habitats for field voles. There is, however, no barrier for dispersal. We consider the low degree of dispersal in our population to be a consequence of its population dynamics rather than a factor causing population change.

Food quality/quantity

Some reserchers have suggested that the cyclic pattern in microtines is due to external factors such as variations in food quality or quantity (Tast and Kalela 1971, but see Andersson and Jonasson 1986). We examined the relationship between reproductive performance and population dynamics and its connection with food conditions. Peak densities reached different levels and occurred at different times of the breeding season in different years (Fig. 1). The reproductive effort of females that bred the same year they were born (year-born females) was decisive for the annual pattern of dynamics whereas overwintered females played an un-important role (Nelson *et al.*, unpubl. data). During the year when densities increased, year-born females began breeding early, and their breeding frequency (proportion of pregnant and lactating females in the population) was high as was juvenile recruitment. The between-year variation in reproductive effort by year-born females was probably caused by differences in food conditions between years; a positive correlation was found between a plant-growth index for the region (agricultural statistics) and vole population growth, which in turn was influenced by juvenile recruitment (Agrell *et al.*, in ms). The results parallel observations in cyclic populations (Abramsky and Tracy 1979, Ford and Pitelka 1984, Taitt and Krebs 1981).

Predation

Theoretical models on predator-prey systems predict cyclic fluctuations in predator and prey populations due to delayed numerical responses (Lotka 1925, Volterra 1926). In such a system the number of specialist predators are largely a function of prey densities. In cyclic rodent populations predators show a delayed numerical response (Pearson 1966). Predation rate is low during the increase in vole density, but becomes high during the decline and low phase. It has been suggested that predation deepens the decline and delays the recovery (Pearson 1966, 1971).

We examined interactions between the field vole population and predators in our area (Erlinge *et al.* 1983). Predation on field voles was mainly due to generalist predators (approximately 80 per cent of the annual predation on voles). The generalist predators, however, only showed a slight numerical response to variations in vole numbers. Instead the predators reacted functionally by switching to alternate prey (primarily rabbits) when vole densities became low. Our noncyclic vole population characteristically showed a marked decline in density over winter. To experimentally determine whether this decline was due to predation we fenced the central grid, which prevented the predators (except weasels) from preying on voles within this area. Vole numbers in the fenced area showed a significantly smaller decrease over winter compared with the control grid as well as the grid where food was added in late winter (Fig. 3). The differences between the grids were due to different survival (Erlinge 1987). In the fenced area average survival time was twice as long as in the controls (males: 9.7 ± 6.6 and 5.4 ± 4.2 weeks respectively, females: 12.8 ± 8.4 and 5.7 ± 5.4

weeks, respectively, $p < 0.001$ in both sexes, Mann-Whitney U-test). As the voles moved freely in and out of the fenced area, their spacing behaviour was unaffected and could not explain the significantly lower rate of decrease in this area compared with the unfenced ones. Insetead the differences were due to a reduced predation-related mortality in the fenced grid. Further more multiannual analysis showed that predation rate in winter was density-dependent, i.e. a high proportion of the vole population was taken by predators during winters following high densities in autumn and vice versa (Erlinge *et al.* 1988). The results strongly suggest that generalist predation prevents cyclic fluctuations in this vole population by reducing vole numbers to a similar low density every spring.

In summary: several of the mechanisms suggested to cause cyclic fluctuations in microtine populations, i.e. between-year variation in individual quality and variations in food conditions, also operated in our noncyclic population. Thus the population seems to have a potential for marked between-year fluctuations. No differences in social behaviour between-years and no tendencies towards high-density dispersal could be found. Our analyses suggest that predation has a decisive influence on the pattern of population change; in systems dominated by predators specializing on voles, a cyclic pattern is promoted while in systems dominated by switching generalist predators, cyclicity is prevented.

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