Delayed density-dependence in a small-rorden population

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SUMMARY

The role of delayed density-dependent processes in the dynamics of animal populations poses a problem for ecologists; although generally assumed important in populations that show cyclic or chaotic fluctuations, little experimental evidence for such processes exist. Through manipulation of vole densities within enclosed areas it was shown that reproduction, recruitment, and body growth rate in introduced populations were negatively affected by high previous density. In addition, female movement patterns shifted, and territoriality as well as home-range size was increased after high density. The observed changes in female spacing-behaviour suggested that negative effects of previous density were partly mediated by social interactions, and agreed with the finding that smaller (less competitive) females were the ones suffering most from increased competition. Contrary to expectations from recent work, predation could be excluded as the cause of delayed density-dependence in this study. Instead, chemical analyses of a dominating food plant suggested that herbivory at high vole-density had delayed negative effects on food quality.

1. INTRODUCTION

Density-dependent processes are necessary for the long term persistence of populations (Hassell 1986). However, the extent to which these processes are involved in shaping the dynamics of fluctuating animal populations, e.g. small rodents and insects (Elton 1942; Andrewartha & Birth 1954), is unknown. A strong influence of direct density-dependent regulation is assumed to result in stable populations, whereas delayed density-effects are predicted to cause fluctuations in numbers (May 1976). In small rodents elevated densities were recently shown to have direct effects on demography (Ostfeld et al. 1993; Ostfeld & Canham 1995). However, most hypotheses aimed at explaining regular density fluctuations (i.e. cyclicity) in microtine rodents (Krebs & Myers 1974; Taitt & Krebs 1985), as well as theoretical models simulating such fluctuations (May 1976; Stenseth 1986; Akçakaya 1992; Hanski et al. 1993), are based on delayed density-dependent processes. Population growth is then predicted to depend on previous densities, through delayed effects on, for example, reproduction and/or survival (Taitt & Krebs 1985; Stenseth 1986; Akçakaya 1992; Hanski et al. 1993). Demographic analyses of fluctuating populations support this view (Hansson 1971; Hornfelt 1994), but experimental evidence for the existence of delayed density-dependence has for long been lacking. However, Ostfeld & Canham (1995) were able to demonstrate that delayed density-dependent effects on adult survival existed in experimental populations of Microtus pennsylvanicus.

We here present a study on the field vole (Microtus agrestis), a small microtine rodent showing both regular and irregular population fluctuations (Hansson 1971; Agrell et al. 1992; Hornfelt 1994). The aim of the study was to examine delayed effects of high density through manipulations of enclosed vole populations. To avoid the influence of direct density effects we used two different sets of voles for each replicate (enclosure): a pre-experimental population kept at either high or low density and a succeeding experimental population which was consequently exposed to the effects of previous densities. By monitoring demography as well as female spacing-behaviour in the experimental populations we hoped to determine: (i) whether high previous density affects population growth; (ii) whether voles respond behaviourally to high previous density; and (iii) whether negative effects of high density are equally distributed among the individuals.

The study focused on the response of females as they determine reproductive output and are more likely to be affected by changes in the food resource than are males (Ostfeld 1985).

2. METHODS

The study was performed in southern Scandinavia (55° 42' N, 13° 25' E) during the reproductive seasons of 1992 and 1993. Each year field vole densities were manipulated in four adjacent 0.1 ha enclosures (see figure 1). High and low density was simulated during a pre-experimental period of two months in early/mid
reproductive season (treatments of enclosures were reversed between years). High density was obtained by releasing animals trapped in two open trapping grids situated 3 km away from the experimental area, whereas in low-density enclosures animal numbers were reduced by removal trapping. During both treatments sex ratio of the pre-experimental populations was kept around 1:1, with a composition of individuals similar to that in open populations. Although densities in high density enclosures occasionally exceeded 400 individuals per ha, the average field vole density over the 8 week pre-experimental period (325 and 44 individuals per ha in high and low density enclosures, respectively) was within the ranges of what has previously been observed in the experimental area (Agrell et al. 1992). At the end of the pre-experimental period all voles were trapped and removed from the enclosures (see figure 1). Trapping was continued until release of the experimental populations to ensure that no pre-experimental individuals remained.

Experimental voles were introduced 12–14 days after removing the pre-experimental populations. The experimental populations consisted of ten laboratory raised, sexually mature individuals: six females (> 20 g) and four males (with scrotal testes). Age and release body mass of the individuals were similar for all enclosures (p > 0.5 in all cases). All voles were individually marked with microchips, and all females were fitted with radiotransmitters. The voles were allowed to establish for one week. Individuals confirmed dead or missing for ten days were replaced to retain initial adult densities (about 40% of all replacements occurred during the first week). Total number of individuals replaced were similar in low density (LD) treated enclosures and high density (HD) treated ones (females: LD = 5.0 ± 3.3 and HD = 4.8 ± 3.1; males: LD = 4.0 ± 2.0 and HD = 4.2 ± 1.2 individuals per enclosure). By keeping experimental populations at similar adult densities (see figure 1) direct density effects (Ostfeld et al. 1993), which presumably caused high density populations to decrease during the pre-experimental period, were controlled for.

Live trapping was carried out 2–3 days per week until the end of the reproductive season. Sex, body mass, and reproductive condition was determined for each individual trapped. Females were considered to have become reproductively active if they were observed to be pregnant and/or lactating. As pregnancies are not detectable during the first 14 days, only females examined more than 14 days after release were included in the analysis on reproductive activity. Recruited juveniles were marked with microchips at first capture. To obtain comparable estimates of body mass changes we calculated the relative body-growth rate, i.e. the residual in mass change per day from a regression, calculated separately for each sex and year, between release body mass and body-growth rate. Thus relative body growth rate is independent of body mass, sex and year. Only individuals present 14 days after release were included in this analysis.

Radiotracking data were obtained from the first 14 day period in September during which all females were established and had radiotransmitters that operated at least 80% of the time (start of the 14-day period varied from 1 to 9 September). Radiotracking data were on average obtained one month after removal of the pre-experimental populations. Females were located 2–5 times per day, and the total number of radio-fixes per individual ranged between 20 and 41 (34 ± 7.5). Movement activity was measured as the average distance moved between two radiotracking positions and home-range size was calculated as 90% harmonic mean isopleths (Dixon & Chapman 1980). We also measured the distance between individuals within an
enclosure as the average distance between the arithmetical means of the home ranges. Female home-range exclusiveness was calculated for each enclosure as a normally distributed index ranging from 0–1000 (Agrell 1995). A low value of a telemetry session indicates great overlap between home ranges, whereas a high-rank value indicates more exclusive ranges (i.e. territoriality). This index takes the observed number of individuals and their home-range sizes into account, and is based on a comparison between the observed home-range overlap to that expected from a random distribution of the same ranges (Agrell 1995). Regarding all radiotracking data the statistical analyses were performed as pairwise t-tests (two tailed), pairing LD-treated and HD-treated enclosures from the same year and with the same number of females (ranging from four to six) present during the 14 day radiotracking period.

During both years, plants' species composition, as well as height, and mass or tussock circumference of the five dominating plant species (Deschampsia caespitosa, Dactylis glomerata, Phleum pratense, Anthriscus sylvestris and Urtica dioica) was examined in ten randomly selected 1 m² squares in each enclosure. In addition, because quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed qualitative analyses on the grass D. caespitosa, an important field vole food plant (Hansson 1971) dominating the vegetation in the experimental area. Ten D. caespitosa samples were collected from each enclosure in mid-September 1993. Samples were immediately frozen at —45 °C and freeze-dried. Levels formed qualitative analyses on the grass vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed quantitative effects of high vole density on the vegetation seemed negligible (see results), we performed qualitative analyses on the grass D. caespitosa, an important field vole food plant (Hansson 1971) dominating the vegetation in the experimental area. Ten D. caespitosa samples were collected from each enclosure in mid-September 1993. Samples were immediately frozen at —45 °C and freeze-dried. Levels of protein (measured as NH₄ content) were determined by the Kjeldahl method. From ethanol extracts we estimated sugar (mono- and disaccharides) and starch content (Yemm & Willis 1954; Hansen & Möller 1982), as well as total phenolic content (Martin & Martin 1982).

3. RESULTS

High previous density significantly reduced both reproduction and recruitment (see figure 2). The proportion of females that became reproductively active was higher in LD-treated than in HD-treated enclosures (log-likelihood Chi-square test: p < 0.01). The number of recruits trapped was on average 2.7 ± 1.5 in HD treated compared with 6.0 ± 1.4 in LD treated enclosures (t-test: N = 8, t = 3.15, p < 0.05). However, the number of recruits per reproducing female was similar in the HD and LD treatments (1.75 ± 0.87 and 1.45 ± 0.41, respectively, N = 8, t = 0.63, p > 0.01). Reproducing females also showed similar pregnancy rates in the two treatment rates, producing an average of 1.33 ± 0.25 litters in LD and 1.12 ± 0.25 litters in HD treatments (t-test, N = 8, t = 0.28, p > 0.10). Due to replacements of individuals that died/disappeared some of the females were released after the start of the experimental period. The time elapsed from release until reproduction was initiated was similar in the two treatments (LD: 16.3 ± 9.5 and HD: 18.7 ± 17.2 days, N = 25, t = 0.45, p > 0.10). On average, reproducing females initiated reproduction 42 ± 15 days after removal of the pre-experimental populations.

In all enclosures where both reproducing and non-reproducing females were found (N = 7, because all females reproduced in one LD enclosure), the average body mass at release of reproducing females was greater than that of non-reproducing females (pairwise t-test: N = 14, t = 4.10, p < 0.01). However, the voles' absolute body mass seemed to be of limited importance. After pooling the data from all enclosures, reproducing females were not found to be significantly heavier than those that did not reproduce (release body mass was 26.4 ± 5.3 and 23.6 ± 5.2, respectively), neither if the analysis was performed with enclosure as the unit of study (t-test: N = 41, t = 1.63, p > 0.10). Individuals in HD treated enclosures had a lower body-growth rate than did individuals in LD-treatments (see figure 3); the average relative body-growth rate was 81 ± 53 mg day⁻¹ (mean ± s.e.) in LD-treated enclosures and -71 ± 54 mg day⁻¹ in HD-treated enclosures (t-test: N = 8, t = 4.02, p < 0.01).

Observed demographic differences between treatments were not due to differences in life span: the time elapsed from release to last time known to be alive was similar for females in LD and HD treatments (LD: 45.9 ± 15.4 days and HD: 40.3 ± 16.6; N = 42, t = 1.17, p > 0.10). In all, the numbers of females killed or noted missing in 1992 and 1993 were 14 and 15 in HD-treated, and 10 and 6 in LD-treated enclosures (χ² = 0.50, p > 0.10). The cases where predation was confirmed (43 %)
were evenly distributed between enclosures, being three in all enclosures in 1992, and one in all except one LD enclosure (where zero predation was observed) in 1993.

Previous densities also had pronounced influence on female spacing-behaviour (see table 1). In HD-treated enclosures, females had larger and more exclusive home ranges compared with females in LD treatments. Furthermore, movement patterns were different between treatments. Females in previous high-density areas showed a tendency towards increased movement activity and significantly less variation in distances moved. Finally, distances between neighbours were longer and tended to be more constant in HD treatments than in LD treatments.

Pre-experimental populations in HD-enclosures were calculated to have consumed 1—2% of the standing crop, so the potential for quantitative effects on the vegetation was low. In both years biomass of the five dominating plant species, as well as overall plant vegetation was low. In both years biomass of the five dominating plant species, as well as overall plant vegetation was low.

4. DISCUSSION

Previous densities significantly affected several demographic parameters that constitute the basis for population growth. Reproduction, both in terms of number of females reproducing and the number of recruits produced, was significantly reduced in areas where previous density had been high. However, because reproducing females in LD- and HD-treated enclosures initiated reproduction at the same time and showed similar pregnancy rates, the primary effect of previous high densities was obviously that more females refrained from reproduction. Females that did not reproduce most likely postponed reproduction due to low potential for current reproductive success (cf. Ylönen 1994). These females then instead adopted the more risky strategy of trying to survive winter and reproduce the next spring. Reproduction before and after winter seems to represent two different female strategies in this population of field voles, because overwinter survival is very low (Agrell 1995), and no females have been observed to survive winter after having reproduced during the previous summer/autumn (Nelson et al. 1991).

In addition to the differences in reproductive activity and recruitment between treatments, individual body-growth rate was significantly reduced in HD-treated enclosures compared with LD-treated ones. Overall, the demographic changes observed in HD treatments correspond to those reported to occur in open microtine populations after periods of high density (see, for example, Krebs & Myers 1974; Boonstra & Boag 1987).

Table 1. Home range characteristics, movements and nearest-neighbour distances of radio-tracked female field voles in enclosures where the previous density had been low (LD-treated) or high (HD-treated)

<table>
<thead>
<tr>
<th></th>
<th>low previous density</th>
<th>high previous density</th>
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<tr>
<td></td>
<td>(n = 4)</td>
<td>(n = 4)</td>
</tr>
<tr>
<td>home range size (m²)</td>
<td>55.0±27.0</td>
<td>96.0±35.9</td>
</tr>
<tr>
<td>home range exclusiveness (index)</td>
<td>114±94</td>
<td>940±52</td>
</tr>
<tr>
<td>movement activity (m)</td>
<td>2.06±0.52</td>
<td>2.77±0.93</td>
</tr>
<tr>
<td>CV movement activity (%)</td>
<td>126±33</td>
<td>113±37</td>
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<tr>
<td>nearest-neighbour distance (m)</td>
<td>5.8±2.2</td>
<td>10.1±2.2</td>
</tr>
<tr>
<td>CV nearest-neighbour distance (%)</td>
<td>55.3±30.1</td>
<td>26.9±11.0</td>
</tr>
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Figure 3. Body growth rate of field voles in areas previously exposed to low (LD, broken line) or high (HD, solid line) density. Data are presented separately for the two years, because overall growth rate was higher in 1993 than in 1992.
Apart from demonstrating delayed density-dependent effects on demography, this experimental study also show that previous densities can affect spacing behaviour. In a similar study by Ostfeld & Canham (1995), voles were shown to reduce movement activity in response to high density, probably due to social effects. In this study, the females showed increased movement activity in areas where density had previously been high. These studies indicate that voles are not able to adjust their spacing behaviour to compensate for negative effects of density on the food resources until after density has decreased. After high density females occupied more exclusive ranges which further support the view that spacing behaviour was affected by previous densities through the food resource. The increased territoriality among females in HD treatments also suggested that delayed negative effects of high density may not have been evenly distributed in the population, but that spacing behaviour caused less competitive females to suffer most. This seems also to be the case because within each enclosure, reproducing females were larger than those which were not reproducing. Large field vole females are dominant over smaller ones (J. Agrell, unpublished results) and the former may consequently have gained better access to scarce resources. An alternative explanation would be that only females large enough were physiologically able to reproduce. However, reproducing females were overall not heavier than non-reproducing ones. The fact that reproductive potential was not determined by absolute, but by relative body mass, indicates the importance of competitive process.

Considerable controversy exists over the mechanisms potentially causing delayed density-dependence in small rodents, for example maternal effects (Mihok & Boonstra 1992), genetic-behavioural polymorphism (the Chitty-hypothesis, see Krebs 1978), and interactions with pathogens (Stenseth 1985), predators or food plants (reviewed by Taitt & Krebs 1985). In this study, whereas the populations were allowed to build up slowly in the study of M. pennsylvanicus, whether this may have caused different effects on the vegetation, e.g. through a less systematic use of food plants in the introduced populations, is not known.

The contrasting results may also have been caused by habitat differences. If productivity is high, and/or the food plant species are not responding to grazing by qualitative changes, delayed effects of high density are likely to be weak (cf. Ostfeld 1994). The pronounced negative effects of high density found in the present study were, however, probably not due to low productivity. The experiment was performed in an area with highly fertile peat soil, and no grazing effects on biomass could be detected. Instead, as indicated by the chemical analyses of the dominating grass species, differences in qualitative responses by the food plants are more likely to explain the variation between our study on the field vole and the study on M. pennsylvanicus (Ostfeld et al. 1993; Ostfeld & Canham 1995).

Whether the voles depended on food quality cues to adjust their behaviour is difficult to know. Voles in HD-treatments may also have used direct signs (e.g. of grazing) of previous high densities. It is, however, highly unlikely that individuals in previous high density areas falsely perceived density as high because on average, data in the present study were collected one month or more after removal of the pre-experimental populations. Voles have very sophisticated odour communication (see, for example, Ferkin & Johnston 1995) and respond immediately to the disappearance of surrounding individuals (Ostfeld 1986; J. Agrell, unpublished results).

In conclusion, the general assumption that delayed density-dependent demographic processes strongly influences fluctuating populations of small rodents has received little support by experimental evidence. However, this study shows a significantly reduced potential for population growth in areas previously exposed to high densities, including changes in reproduction, recruitment, and body-growth rate. Spacing behaviour was also influenced by previous densities, and may have caused unequal distribution of negative biomass could be detected. However, these analyses do not exclude that preferred parts of plants had been removed in HD-treatments. The idea that high density can cause delayed effects on food quality (Haukioja 1980; Batzli 1985; Edelstein-Keshet & Rausher 1989; Seldal et al. 1994; Lundberg et al. 1994) received support from the chemical analyses of the grass D. caespitosa, though. The observed differences in grass quality (increased protein- and reduced sugar-content) do not explain demographic differences between treatments per se, but indicate that food plants were qualitatively affected by previous vole densities. In contrast to our results, a corresponding study on M. pennsylvanicus demonstrated delayed density effects on adult survival rates, but not on reproduction and recruitment (Ostfeld et al. 1993; Ostfeld & Canham 1995). One difference between the two studies was that although high densities were similar, a large number of voles was simultaneously introduced to the enclosures in this study, whereas the populations were allowed to build up slowly in the study of M. pennsylvanicus.
density effects among the individuals. A strong influence of competition was indicated by relative, but not absolute body mass and seemed to determine reproduction. In contrast to expectations from recent work (Akgakaya 1992; Hanski et al. 1993; Ostfeld et al. 1993), predation could be excluded as the factor causing delayed density-dependence. In this study, the results instead supported the view that delayed effects of grazing play an important role in the regulation of herbivore populations.

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