Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation

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Mechanisms generating the well-known 3–5 year cyclic fluctuations in densities of northern small rodents (voles and lemmings) have remained an ecological puzzle for decades. The hypothesis that these fluctuations are caused by delayed density-dependent impacts of predators was tested by replicated field experimentation in western Finland. We reduced densities of all main mammalian and avian predators through a 3 year vole cycle and compared vole abundances between four reduction and four control areas (each 2.5–3 km²). The reduction of predator densities increased the autumn density of voles fourfold in the low phase, accelerated the increase twofold, increased the autumn density of voles twofold in the peak phase, and retarded the initiation of decline of the vole cycle. Extrapolating these experimental results to their expected long-term dynamic effects through a demographic model produces changes from regular multiannual cycles to annual fluctuations with declining densities of specialist predators. This supports the findings of the field experiment and is in agreement with the predation hypothesis. We conclude that predators may indeed generate the cyclic population fluctuations of voles observed in northern Europe.

Keywords: population cycle; predator reduction experiment; demographic model; predator–prey interactions

1. INTRODUCTION

Voies and lemmings show short-period cycles of 3–5 years in northern Europe and the arctic tundra, snowshoe hares (*Lepus americanus*) undergo 9–10 year cycles in densities in the boreal forests of North America, and red grouse (*Lagopus lagopus scoticus*) exhibit 4–8 year cycles on moors of northern England and Scotland (Hansson & Henttonen 1988; Keith 1990; Hudson 1992; Stenseth & Ims 1993; Norrdahl 1995; Stenseth *et al.* 1996; Stenseth 1999). On the basis of much recent empirical and theoretical work, such well-known herbivore cycles may be due to delayed density-dependent impacts of predators (Hanski *et al.* 1991, 1993; Korpimäki *et al.* 1991; Norrdahl & Korpimäki 1995; Turchin & Hanski 1997; Korpimäki & Norrdahl 1998), parasites (Hudson *et al.* 1998), food supply (Agrell *et al.* 1995; Turchin & Batzli 2001), or their interactions (Krebs *et al.* 1995; Stenseth 1995; Stenseth *et al.* 1997; Hansson 1999). During the past 75 years of research, however, none of these hypotheses has been adequately tested for voles and lemmings (Stenseth & Ims 1993; Batzli 1996; Korpimäki & Krebs 1996; Boonstra *et al.* 1998; Stenseth 1999; Hanski *et al.* 2001; Lindström *et al.* 2001), the critical test being a controlled manipulation, transforming cyclic populations to non-cyclic, or vice versa. Here, we demonstrate through large-scale experimental predator–density manipulations, combined with the analysis of a theoretical model, that we can transform a vole population exhibiting multiannual population cycles to a population exhibiting only annual fluctuations.

2. MATERIAL AND METHODS

(a) Predator reduction experiment

The study area in Kauhava and Lapua, western Finland (63° N, 23° E), consists mainly of agricultural fields where small mustelids (the least weasel (*Mustela nivalis*) and the stoat (*M. erminea*)) and birds of prey (the Eurasian kestrel (*Falco tinnunculus*), the short-eared owl (*Asio flammeus*), the long-eared owl (*A. otus*) and Tengmalm's owl (*Aegolius funereus*)) are the main predators of voles (field vole (*Microtus agrestis*), sibling vole (*M. rossiaemeridionalis*), bank vole (*Clethrionomys glareolus*) and water vole (*Arvicola terrestris*)) (Korpimäki *et al.* 1991; Korpimäki & Norrdahl 1991b; Korpimäki 1993; Norrdahl & Korpimäki 1995). The two *Microtus* voles are the main prey of the above predators, whereas bank and water voles are alternative prey items (Korpimäki *et al.* 1991; Korpimäki & Norrdahl 1991b). Multiannual cyclic fluctuations are most evident in *Microtus* voles (figure 1); therefore, we focused on the dynamical effects of predation on *Microtus* voles.

We used four manipulation–control pairs of agricultural fields (each 2.5–3 km²) for the predator reduction experiment. All experimental areas were within 180 km² (12 km × 15 km). Each manipulation–control pair was as similar as possible with respect to habitats inside and surrounding the area. For example, the proportion of forest varied from 15 to 23% in both manipulation and control areas. As the distance between all manipulation and control areas was at least 5 km (median of 6 km, range of 5–14 km), small mustelids and breeding avian predators did not disperse from control to manipulation areas during the yearly experimental periods of six to seven summer months (Norrdahl & Korpimäki 1996; Korpimäki & Norrdahl 1998). However, predators were free to move in and out of experimental areas. We reduced densities of predators over a 3 year period (1997–1999) when vole populations went through a

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Figure 1. Long-term population fluctuations of *Microtus* voles at two sites (Ruotsala, triangles; Alajoki, circles) of the study area in spring (filled symbols) and autumn (open symbols) from 1973 to 2000. The arrows denote the onset and end of the predator reduction experiment.

3 year cycle (figure 1). In the preceding year (1996), densities of vole populations were moderate and declined to low numbers towards the spring of 1997.

We removed stoats and least weasels by live-trapping from April/May to October each year (Korpimäki *et al.* 1994; Korpimäki & Norrdahl 1998). In mid-May 1997, we distributed 50–65 least weasel traps and 20–30 stoat traps evenly in one manipulation area for 5 days and checked the traps once a day. In the following week, the traps were transferred to the next manipulation area. A trapping session in all four manipulation areas took about one month, after which identical live-trapping sessions were repeated in mid-June to mid-July, and again in August, September and October. In 1998 and 1999, the trapping followed the same protocol except that trapping was started in early April and performed six times in a year from April to June and August to October. The total number of small mustelids removed from each of the four manipulation areas was 11 (five in 1997, two in 1998, and four in 1999), 15 (two in 1997, one in 1998, and 12 in 1999), 23 (10 in 1997, three in 1998, and 10 in 1999), and 32 (11 in 1997, six in 1998, and 15 in 1999) during the 3 years. Trapped mustelids were transferred and released at least 30 km from our study sites. Stoats were trapped and transferred with the permission of the Finnish Ministry of Agriculture and Forestry, and least weasels with the permission of the Finnish Ministry of Environment.

In each spring of 1997–1999, before the breeding season of avian predators, we removed all stick-nests, natural cavities and nest-boxes from the reduction areas (Norrdahl & Korpimäki 1996; Korpimäki & Norrdahl 1998). This procedure significantly reduced the number of breeding territories of main vole-eating avian predators in the manipulation areas relative to the control areas (figure 2a).

Spring (from late February to March, before predator reduction) and autumn (from late November to December, after predator reduction) density indices of mammalian predators were obtained by snow-tracking soon after a snowfall, so that tracks made by animals only during the previous one or two nights were visible. Six lines per area, each *ca.* 1 km, were skied. Identification of small mustelids was based on track dimensions (Korpimäki *et al.* 1991). No obvious differences in the initial density of small mustelids could be detected between the reduction and control areas in the spring of 1997 (mean $\pm$ s.e.: 0.36 ± 0.16 and 0.43 ± 0.15 tracks km^{-1} , respectively; $t_6 = 0.31$; two-tailed $p = 0.77$) but the density of small mustelids did differ,

Figure 2. The density estimates of (a) avian predators and (b) small mustelids in reduction (hatched bars) and control (open bars) areas (the number of areas studied given above bars) during 1997 to 1999. For densities of avian predators (a), the bars give the mean ($\pm$ s.e.) pooled number of nests and breeding territories of vole-eating birds of prey (Eurasian kestrels, Tengmalm's owls, short-eared owls, long-eared owls and common buzzards (*Buteo buteo*)). Two-way ANOVA indicated that the effects of treatment and study year on breeding densities of avian predators were significant (treatment: $F_{1,18} = 8.53$, $p = 0.009$; year: $F_{2,18} = 5.16$, $p = 0.017$; treatment $\times$ year: $F_{2,18} = 0.32$, $p = 0.73$). For density indices of small mustelids (b), the bars give the mean ($\pm$ s.e.) number of individuals crossing track-lines km^{-1} in spring (s) and autumn (a) from 1997 to 1999. See table 2 for statistical test.

as expected, between the reduction and control areas in each autumn of the experiment (figure 2b). Because of suddenly changing weather, we were not able to ski snow-track lines in three reduction and two control areas in the autumn of 1997, in one reduction and control area in the spring of 1998, and in one reduction area in the spring of 1999. However, the number of small mustelids present in each study area was estimated by intensive one-day censuses and mapping of snow-tracks (for methods, see Korpimäki & Norrdahl 1998) in late December 1997 to January 1998. Yet again, the density (individuals km^{-2})

Figure 3. The density index (measured as the mean number of individuals captured per trap line per area) of *Microtus* voles from April to October (A, April; J, June; A, August; O, October) in predator reduction (solid line and filled circles, mean ($\pm$ s.e.) of four areas) and control areas (dashed line and open circles, mean ($\pm$ s.e.) of four areas) during 1997 to 1999.

of small mustelids was significantly lower in reduction than in control areas (mean $\pm$ s.e.: 0.50 ± 0.17 versus 1.83 ± 0.42 , $t_6 = 2.95$; two-tailed $p = 0.03$).

To quantify long-term vole abundance in the study area (figure 1), we conducted snap-trappings in early May and in mid-September at two sites (Ruotsala and Alajoki) separated by ca. 14 km during 1977–2000. We sampled the main habitat types (a cultivated field, an abandoned field, a spruce forest and a pine forest) in both sites by using four-day trapping sessions (Korpimäki & Norrdahl 1991a,b). The density index derived from the trapping results was the pooled number of *Microtus* voles trapped per 100 trap nights.

To estimate vole abundance in the eight experimental areas, a random subset of eight ditch lines and two forest lines were chosen for each trapping session from numbered ditches in agricultural fields and from numbered forest plots (i.e. the short line method; Korpimäki *et al.* 1994; Korpimäki & Norrdahl 1998). Because one ditch or forest plot was only used once per year, possible impacts of snap-trapping on vole populations remained negligible and was also similar in the reduction and control areas. Ten Finnish metal mouse snap-traps (suitable for *Microtus* and bank voles) and one Finnish metal rat snap-trap (suitable also for water voles (Korpimäki *et al.* 1991)) were set 10 m apart for two days in each selected line and were checked once a day. Snap-trapping was performed simultaneously in each manipulation–control area pair from late March to early April (before manipulation), and again in late June, August and October each year in 1997–1999. Vole abundances did not differ between reduction and control areas at the onset of the experiment in April 1997 (figure 3; one-way ANOVA: $F_{1,6} = 0.1$; $p = 0.82$).

The generalized linear models procedure of SAS statistical software (v. 6.12) was used for repeated-measures ANOVA on *Microtus* vole abundances, with year and trapping time within year as repeated factors (von Ende 1993). Small-mustelid abundances were analysed using repeated-measures ANOVA in the MIXED procedure of SAS, as its maximum likelihood method may deal with missing observations in snow-tracking data. All p -values are given for two-tailed tests.

(b) Model for voles and their predators

In order to extrapolate our experimental findings from the one-vole cycle to the long-term dynamic effects of predation, we

developed a demographically based population model for *Microtus* voles and their predators. We modelled the dynamics of *Microtus* voles, specialist predators, generalist predators and interactions between predators and prey by using a stage-structured model with discrete time-steps. (Supplementary material, including the description (electronic Appendix A) and parametrization (electronic Appendix B) of the model, and incorporation of sampling variance to model results (electronic Appendix C) is available on the Royal Society's Publications Web site.) The modelled vole specialist predator resembles small mustelids, especially least weasels, responding on a slow time-scale to changes in vole densities (Korpimäki *et al.* 1991; Oksanen & Henttonen 1996). Our generalist predators resemble avian predators (nomadic specialists (Eurasian kestrels, short-eared owls and long-eared owls) and resident generalists (Tengmalm's owls)) being able to respond rapidly to changes in vole densities (Korpimäki & Norrdahl 1991a,b; Turchin & Hanski 1997). Voles are grouped into three life-stages, namely juveniles, immature subadults and reproducing adults, whereas predators are only grouped into juveniles and adults. Voles are also assumed to exhibit direct density dependence in their demographic performances through lowered maturation with increasing density (electronic Appendix A). The length of each time-step equals 28 days (i.e. 13 time-steps yr^{-1}), which is close to the time between subsequent litters in voles during the breeding season (Nadeau 1985; Yoccoz *et al.* 1993). The numbers of voles, specialist predators and generalist predators were recorded at the end of each time-step. We considered only the female component of the population and assumed an even sex-ratio. For the model results, we recorded vole densities (females km^{-2}) with sampling variance added (electronic Appendix C) in order to analyse the otherwise deterministic simulated time-series statistically (within a time-series setting).

First, we addressed the question of whether predator reduction is able to terminate the vole cycles; and if so, how much predator reduction is needed. We mimicked the design of the predator reduction experiment by reducing the density-independent survival rate of specialist predators during six time-steps each year (electronic Appendices A and B). The removal of potential nest-sites for avian predators was modelled by reducing the number of potential settlers which lowered the density of avian predators during the settlement in spring (electronic Appendices A and B).

Second, we investigated to what extent this model can capture the statistical time-series signatures of real data by conducting statistical time-series analyses. The model was, in each case, run for a period of 200 years from which only the last 100 years were used for further time-series analyses. The prevailing cyclic period in the model results was calculated by spectral analysis (Brockwell & Davis 1991) and the amplitude was calculated as maximum density divided by minimum density of voles. Earlier autoregressive time-series analyses have revealed that fluctuating small-rodent populations are appropriately described by an order-two process including both direct and delayed annual density dependence (Stenseth *et al.* 1996; Stenseth 1999); that is, an appropriate model for studying the time-series signature of the simulated data may be given as

$$x_y = a_0 + a_1 x_{y-1} + a_2 x_{y-2} + \varepsilon_y, \quad (2.1)$$

where x_y is the log-transformed density of voles in the autumn time-step (i.e. the model time-step given by $t = 6$) in the year y , and where ε_y is the random error with a constant mean and variance (for further details see Royama (1992), Stenseth *et al.*

Table 1. Repeated-measures ANOVA table on the density indices of *Microtus* voles (primary data in figure 3), involving treatment (reduction of small mustelids and breeding avian predators or control without predator reduction) as a between-subject factor, and trapping month (April, June, August or October) and study year (1997, 1998 or 1999) as within-subject (repeated) factors. (For the within-subject effects in which the assumption of compound symmetry was only slightly violated (the Huynh–Feldt ϵ being between 0.75 and 1.00), Huynh–Feldt-adjusted significance levels are given (von Ende 1993).)

source	d.f.	mean square	<i>F</i>	<i>p</i>
treatment	1	4.25	16.41	0.007
error	6	0.26		
month	3	3.98	12.77	< 0.001
treatment $\times$ month	3	1.10	3.54	0.049
error (month)	18	0.31		
year	2	24.31	139.94	< 0.001
treatment $\times$ year	2	1.78	10.25	0.003
error (year)	12	0.17		
month $\times$ year	6	2.32	7.69	< 0.001
treatment $\times$ month $\times$ year	6	0.32	1.07	0.40
error (month $\times$ year)	36	0.30		

Table 2. ANOVA table for the effect of treatment (reduction of small mustelids or control without reduction), study year (1997, 1998 or 1999) and season (early spring or late autumn) on small mustelid abundance (see figure 2b).

source	d.f.	<i>F</i>	<i>p</i>
treatment	1,6	7.31	0.035
season	1,22	35.37	< 0.001
treatment $\times$ season	1,22	23.02	< 0.001
year	2,22	8.11	0.002
treatment $\times$ year	2,22	0.45	0.64
season $\times$ year	2,22	2.10	0.15
treatment $\times$ season $\times$ year	2,22	0.28	0.76

(1996) and Stenseth (1999)). Obtained density-dependent structures are then compared with real small-rodent data.

3. RESULTS AND DISCUSSION

The reduction of mustelid predators and breeding birds of prey increased densities of *Microtus* voles in each study year (figure 3). This is indicated by a significant effect of interaction between treatment and month, which did not change after an addition of the year into the interaction in repeated-measures ANOVA on vole abundances (table 1). The reduction of predators reversed the density decline of *Microtus* voles in the course of the summer of 1997, thereby increasing the autumn density of voles (figure 3). During the following winter (November 1997 to March 1998) without predator removal, vole densities in treatment areas decreased to the level of control areas. The reduction of predators in 1998 induced an earlier initiation of increase in vole densities, resulting in higher vole densities in reduction than control areas in the autumn of 1998. During the following winter (November 1998 to March 1999) without predator removal, vole densities in reduction areas again declined to the level of control areas. The reduction of predators in 1999 caused faster population growth and a higher peak of voles in comparison with control areas, where the decline of vole densities began in August 1999; in reduction areas vole densities continued to increase (figure 3).

That the termination of the predator reduction in two winters brought vole densities to the level of control areas

in early spring was probably due to an influx of new predators to the reduction areas. There were no obvious differences in densities of small mustelids in early spring before the initiation of predator reduction, although there were significantly fewer small mustelids in reduction than control areas in autumn, after the termination of manipulation (figure 2b; table 2). This suggests that, like avian predators (Norrdahl & Korpimäki 1996), small mustelid predators rapidly respond to small-scale changes in vole densities and bring out-of-phase patches of voles to the same density level as in the surrounding areas. Small mustelids appeared to respond numerically to increasing vole densities, because altogether there were more small mustelids in both the reduction and control areas in 1999 than in 1997 and 1998 (figure 2b; table 2).

The density reduction of all main predators increased the autumn density of *Microtus* voles fourfold in the low phase, accelerated the increase twofold, and increased the autumn density of voles twofold in the peak phase of the vole cycle (figure 3). In addition, predator reduction retarded the initiation of the decline phase of the vole cycle, and an earlier replicated predator reduction experiment with similar methods also prevented the summer decline in *Microtus* vole densities (Korpimäki & Norrdahl 1998). Previous empirical and theoretical studies from the study area have suggested that delayed density-dependent mortality—a well-known prerequisite for the population cycle—is imposed on voles by specialist predators (Korpimäki *et al.* 1991; Korpimäki & Norrdahl 1991b; Hanski *et al.* 1993; Korpimäki 1993; Norrdahl & Korpimäki 1993).

Figure 4. The effect of simulated reduction of specialist and generalist predators on the population trajectories of voles (a–p), deduced density-dependent structure of those trajectories (q) and deduced density-dependent structure in real data (r). Dynamics with multiannual periodicity are given in red, while green is used for the dynamics without multiannual periodicity. (a–p) Years from 151 to 166 (p , prevailing period in years and a , amplitude as maximum density divided by minimum density of voles. (a) $p=4.0$, $a=15.8$; (b) $p=3.7$, $a=11.9$; (c) $p=4.4$, $a=26.5$; (d) $p=5.0$, $a=37.0$; (e) $p=1.0$, $a=5.9$; (f) $p=4.0$, $a=12.0$; (g) $p=4.0$, $a=12.5$; (h) $p=5.3$, $a=25.7$; (i) $p=1.0$, $a=5.6$; (j) $p=1.0$, $a=5.9$; (k) $p=4.6$, $a=7.7$; (l) $p=5.0$, $a=14.3$; (m) $p=1.0$, $a=5.3$; (n) $p=1.0$, $a=5.3$; (o) $p=1.0$, $a=5.7$; (p) $p=5.6$, $a=6.1$). Reduction levels per time-step ($r_s=1.00, 0.96, 0.92$ or 0.88) of specialist predators are given for columns and reduction levels ($P_{g,source}=4, 3, 2$ or 1) from the maximum density (four nests km^{-2}) in potential settlers of generalist avian predators are given for rows (see electronic Appendices A and B). Locations of estimated first-order (a_1) and second-order (a_2) autoregressive coefficients are plotted in the second-order parameter-space (see Royama 1992) for the model results (as shown in panels (a)–(p) with added sampling noise) (q) as well as for the real data (r). Any persistent population must fall within the triangle (Royama 1992); below the parabola, proper multiannual cycles arise (Stenseth *et al.* 1996; Stenseth 1999). Lengths of cyclic periods are indicated with figures within the parabola. Data for (r) are derived from autumn densities of *Microtus* voles in Ruotsala (triangle) and Alajoki (asterisk) study sites as given in figure 1 and reproduced from Stenseth (1999) including the following populations: A, the grey-sided vole (*Clethrionomys rufocanus*) in Kilpisjärvi, northern Finland; B, the grey-sided vole in Heian, Hokkaido, Japan; C, the grey-sided vole in Nagatoyo, Hokkaido, Japan; D, the collared lemming (*Dicrostonyx torquatus*) in Yamal Peninsula, northwest Siberia; E, the bank vole near Moscow, Russia; F, the Norwegian lemming (*Lemmus lemmus*) in Finse, mountains of southern Norway; G, the bank vole in Bialowieza, Poland; H, the bank vole in Wytham Woods, England; I, the field vole in Kielder forest, Scotland; J, the red-backed vole (*Clethrionomys gapperi*) in Algonquin Provincial Park, Ontario, Canada; K, the prairie vole (*Microtus ochrogaster*) in Urbana, Illinois, USA; and L, the brown lemming (*Lemmus trimucronatus*) in Point Barrow, Northern Alaska, USA. See Stenseth (1999) for further sources of the data used in (r).

mäki 1995, 1996), but also that it is not necessary to invoke delayed effects of food supply as the cause of *Microtus* vole cycles (Klemola *et al.* 2000a,b; see also Turchin & Batzli 2001). Taken together, these novel results add the crucial missing experimental support for the hypothesis that predators may generate cyclic population fluctuations of voles.

Results from our model show that increasing reduction of specialist predators changed multiannual cycles to annual fluctuations, whereas reduction of generalist predators tended to increase the period and the amplitude of these fluctuations (figure 4). As can be seen in figure 4e, a reduction of 0.04 per time-step (28 days) in the survival rate of specialists is sufficient to terminate the multiannual cycles when the density of generalists remains unchanged. However, when the numbers of potential settlers of generalist avian predators were reduced by 25, 50 or 75% (resulting in approximately similar percentage decreases in the actual densities of generalists), a reduction of 0.08, 0.12 or more, respectively, in the survival rate of specialists is required for changing the dynamic behaviour of the model (figure 4j,o,p). Statistical time-series analyses on the results from the deterministic model show that patterns closely resemble those observed in real rodent time-series data (as earlier reported in the literature; see Stenseth *et al.* 1996; Stenseth 1999) (figure 4q,r). Altogether, these theoretical results support the findings of the field experiments and are in agreement with the predation hypothesis proposed to explain the population cycles of small rodents (Hanski *et al.* 1991, 1993; Korpimäki *et al.* 1991; Norrdahl 1995; Norrdahl & Korpimäki 1995, 2002; Korpimäki & Krebs 1996; Turchin & Hanski 1997; Korpimäki & Norrdahl 1998).

4. CONCLUSIONS

Previous large-scale experimental studies on cyclic vertebrate animals have demonstrated that snowshoe hare cycles are probably driven by three trophic level interactions between food supply, hares and their predators (Krebs *et al.* 1995), whereas red grouse cycles are a probable result of a single trophic interaction between a nematode parasite and its host (Hudson *et al.* 1998). By combining the large-scale experimental work with theoretical modelling, we have been able to demonstrate, for the first time to our knowledge, that cyclic vole populations may be transformed to non-cyclic vole populations by manipulating their predator assemblage. We conclude that predators may indeed generate the cyclic population fluctuations of voles observed in northern Europe.

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