

Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses

Birger Hörnfeldt

Hörnfeldt, B. 2004. Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. – *Oikos* 107: 376–392.

Cyclic vole populations, defined as showing fairly regular 3–4 yr density fluctuations but with variable amplitudes, were monitored in boreal Sweden in spring and fall 1971–2002, starting in fall 1971. Voles were snap-trapped on permanent sampling plots at the landscape level within a 100 by 100 km study area north of Umeå. The predominating species trapped were *Clethrionomys glareolus*, *C. rufocanus* and *Microtus agrestis*. In addition to the 3–4 yr cycles, there was a long-term decrease in numbers and amplitude of the fluctuations, which was especially conspicuous in *C. rufocanus*. In this latter species there was a persistent decline of both spring and fall densities, apparently bringing the population close to extinction in the area. However, the decline of spring densities from the 1970s to the 1980s and onwards was also evident in *C. glareolus* and *M. agrestis*. The declines in numbers and amplitude were largely linked to an increased frequency and/or accentuation of winter declines, which more or less neutralized or even overrode the density increase during the reproductive season in the previous summer, especially so in the second year of the cycles. Thereby the gradual two-large-step build-up of high spring densities, very much founding the base for the very large peak densities and amplitudes in the 1970s, was successively replaced by a one-smaller-step build-up of more modest spring densities, leading to lower peak densities and amplitudes in the 1980s, 1990s and early 2000s. Understanding the causes of the increased frequency and/or severeness of winter declines appears critical to understanding the observed long-term changes in numbers. However, the underlying causes of the increase of winter declines and the decrease of densities and amplitudes are unknown, but some hypotheses are presented and discussed here. Also, some implications from the decreased vole abundance for reproduction and densities of predators on the voles, and on predators' alternative prey species, are briefly discussed.

B. Hörnfeldt, Dept of Ecology and Environmental Science, Umeå Univ., SE-90187 Umeå, Sweden (birger.hornfeldt@eg.umu.se).

Classically, much of the research on vole population dynamics, especially in Fennoscandia, has focused on the short-term cyclicality and its possible causes (reviewed by Stenseth 1999). Additionally, in Fennoscandia, there has been a parallel focus on the close link between vole population cycles on one hand and reproduction and population dynamics of predators, as well as their alternative prey, on the other hand (Siivonen 1948, Hagen 1952, 1969, Englund 1970, Hörnfeldt 1978, Angelstam et al. 1985, Hörnfeldt et al. 1986, 1990,

Danell and Hörnfeldt 1987, Korpimäki 1987, 1994, Steen et al. 1988, Lindström 1989, Korpimäki and Hakkarainen 1991, Korpimäki and Norrdahl 1991, Small et al. 1993, Lindström et al. 1994, Angerbjörn et al. 1995, Laaksonen et al. 2002; but see Lindén 1988, Lindström et al. 1996).

Mainly because of the central role of voles to predator reproduction and population dynamics, monitoring of small mammal populations became part of the National Environmental Monitoring Programme (NEMP) in

Accepted 27 April 2004

Copyright © OIKOS 2004
ISSN 0030-1299

Sweden in the late 1970s (Anonymous 1985). One of the prime purposes of this vole monitoring is to detect deviations from “normal” density variations that could be “early warnings” of environmental disturbances. The adoption of vole monitoring into the NEMP has been of crucial importance for maintaining and building up two of the world’s longest, geographically most extensive and spatially most replicated records of vole population dynamics in Sweden, near Umeå in northern Sweden (1971-) and in the Grimsö area in southern central Sweden (1973-; Hörnfeldt 1994, 2004, Lindström and Hörnfeldt 1994). Additionally, some other important time series available for comparison are located in northern Finland in Kilpisjärvi (1949-) and Pallasjärvi (1970-) and in northern Norway in Finnmark (1977-; Hansen et al. 1999, Henttonen 2000, Ekerholm et al. 2001).

Long-term records of vole abundance are comparatively rare but are undoubtedly a prerequisite for detecting any long-term changes in dynamics. Indeed, during the last two decades deviations from previous density patterns have been reported from various localities in Fennoscandia. The deviations include prolongation of cyclic peaks and interspecific desynchronization of cyclic declines (Henttonen et al. 1987), temporal compression of cyclic peaks and interspecific synchronization of cyclic declines (Hörnfeldt 1986, 1991, 1994, 1995), increased seasonal variation (Hörnfeldt 1986, 1991, 1994, 1998, Lindström and Hörnfeldt 1994, Henttonen 2000, Ekerholm et al. 2001), decreased amplitudes (Hörnfeldt 1991, 1994, 1995) and long-term declines in density (Hörnfeldt 1989, 1991, 1994, 1995, 1998, Hansson and Henttonen 1995, Hanski and Henttonen 1996, Hansen et al. 1999, Hansson 1999, Henttonen 2000).

In his review, Stenseth (1999) expressed some weak scepticism of the validity of the claimed changes to the Fennoscandian vole cycles. Thus, the purpose of the present paper is to focus on long-term changes of vole population dynamics in boreal Sweden, but not on the cyclicity per se, although density changes will be analyzed with reference to the cycles. This is carried out using a detailed, updated and easily interpretable analysis of the currently geographically most extensive, landscape-based, long-term record of Fennoscandian vole populations; that from the Umeå area. I show that there has been a persistent and dramatic decline in density and amplitude for *Clethrionomys rufocanus* from the early 1970s to 2000s, and also a decline in spring density and amplitude for *C. glareolus* and *Microtus agrestis*, and that the important feature of the decline of all species has been a clear decrease in wintering success. In addition, hypotheses on the causes of the long-term decline in vole numbers are presented and discussed, as are implications of the vole decline for predator reproduction and their populations.

Material and methods

Long-term monitoring of cyclic vole populations was carried out in 1971–2002 close to Umeå, northern Sweden (approximately 64°N, 20°E; Fig. 1 in Hörnfeldt 1994). This area is situated within the middle boreal zone (Ahti et al. 1968) and is characterized by high seasonal variation (Hörnfeldt 1994). The monitoring started as a research project focused on the vole cycles with the practical purpose of forecasting damage risk to forest seedlings caused by bark-eating voles. Since 1979 the vole monitoring has been part of the NEMP (Introduction) run by the Swedish Environmental Protection Agency (Hörnfeldt 2004).

Abundance of voles was monitored by snap-trapping twice a year, in spring (late May) and fall (late September), starting in fall 1971. Voles were trapped on 58 out of 64 permanent 1-ha sampling plots. The plots were regularly distributed within the 100 × 100 km study area, according to the Swedish National Grid; the excluded plots were untrappable as they were located in wetland habitats etc. The trapping effort per sampling period (spring and fall) was normally 150 trap-nights per 1-ha plot. On average, the total trapping effort per period was about 8 475 trap-nights (range: 7 950–8 565), giving a total of approx. 534 000 trap-nights for the study period. For further details on sampling design and trapping, see Hörnfeldt (1978, 1994) or Hörnfeldt et al. (1986, 1990).

The study comprised nine vole cycles; the latest one ended in spring 2003 (Hörnfeldt 2004). Cycles are here defined as fairly regular (3–4 yr) density fluctuations, but with variable amplitudes (Hörnfeldt 1994). In all, 12 128 *C. glareolus*, 2 174 *C. rufocanus* and 1 971 *M. agrestis* were trapped, together making up >91% of all small mammals trapped. Additional species trapped were *Sorex araneus* (966), *S. caecutiens* (113), *S. minutus* (155), *S. minutissimus* (1), *Neomys fodiens* (24), *Myopus schisticolor* (191), *Arvicola terrestris* (3), *Apodemus flavicollis* (21), *Mus musculus* (1) and *Mustela nivalis* (2).

I used number of voles trapped per 100 trap-nights per species and sampling period as indices of vole density (termed density). Time series are illustrated “traditionally” with spring and fall data combined, but also separately for spring and fall, to illuminate and pinpoint long-term density changes more clearly. I also calculated indices of rate of change in numbers (termed rate of change) per species in summer (from spring to fall), winter (from fall to spring) and annually (from spring to spring and from fall to fall), using the formula: $(N_t/N_{t-1})^{(1/N_{\text{No. days}})}$, where N_{t-1} , N_t , and $N_{\text{No. days}}$ represent the consecutive trapping indices and the time lapse in days between sampling periods. To avoid infinite rates of increase or decrease when no voles were trapped, I replaced 0-indices with 0.01; the index obtained if one

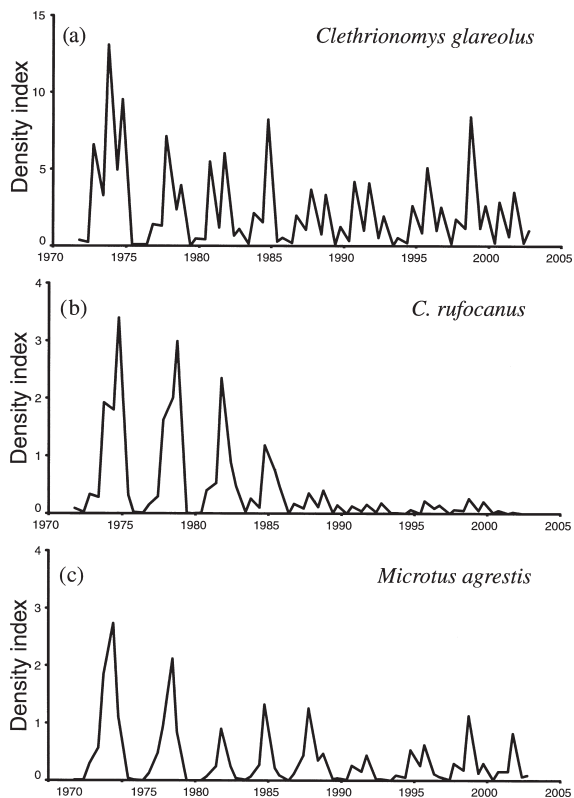


Fig. 1. Trapping indices for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis* in spring and fall from fall 1971 to fall 2002.

specimen is trapped at the present trapping efforts. As a landscape colonization index, I calculated the proportion (%) of sampling plots per species and sampling period where ≥ 1 specimen was trapped.

It should be noted that statistical testing was only carried out for the average values based on all sampling plots ($n=58$), and that 2-tailed p -values were applied. Therefore the testing should be regarded as very conservative.

Results

Density variations

For all voles the 3–4 yr cycles (sensu Hörnfeldt 1994) were accompanied by a long-term decline in density from the 1970s through the 1980s, 1990s and early 2000s (Fig. 1). In *C. glareolus* and *M. agrestis* nine cycles (I–IX) were evident (Fig. 1–3a, c), but cycle IX (starting in 2000) and cycle VI were not evident, or questionable as examples of typical cycles, in the time series of *C. rufocanus* (Fig. 1–3b). The density decline was most dramatic in *C. rufocanus* (Fig. 1b) and evident for both spring and fall densities (Fig. 2–3b; $r = -0.440$,

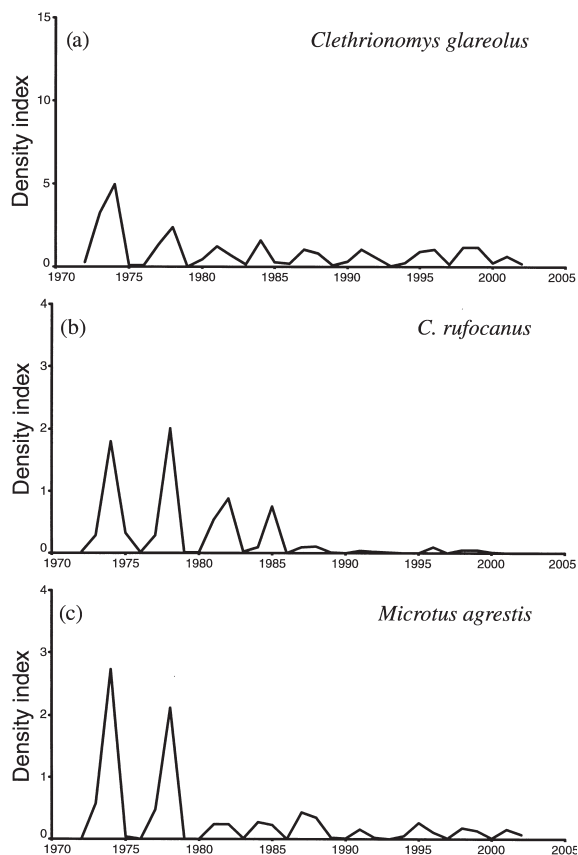


Fig. 2. Trapping indices for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis* in spring 1972–2002.

$p=0.013$ and $r = -0.483$, $p=0.005$). In addition, the decline of spring densities was also evident for *C. glareolus* (Fig. 2a; $r = -0.355$, $p=0.050$) and *M. agrestis* (Fig. 2c; $r = -0.370$, $p=0.040$). Focusing on spring densities late in the cycles only, i.e. in third springs relative to the increase phase in the 1st year (below), revealed an even stronger relationship for the decline in *C. glareolus* ($r = -0.707$, $p=0.033$), *C. rufocanus* ($r = -0.884$, $p=0.002$) as well as *M. agrestis* ($r = -0.776$, $p=0.014$). Thus, with respect to the spring situation, which is of crucial importance for predator reproduction (below), the picture was uniform with a major decline for all species from the very high densities in the 1970s to the markedly lower ones in the early 1980s, after which the decline proceeded even further up to the early 2000s (Fig. 2a–c). In contrast to the spring densities, fall densities of *C. glareolus* and *M. agrestis* did not show a clear-cut, uninterrupted, decline (Fig. 3a, c; $r = -0.253$, $p=0.163$ and $r = -0.141$, $p=0.442$).

As a contrasting example of density variation on single sampling plots, time series for overall, spring and fall densities of *C. rufocanus* is shown in Fig. 4a–c

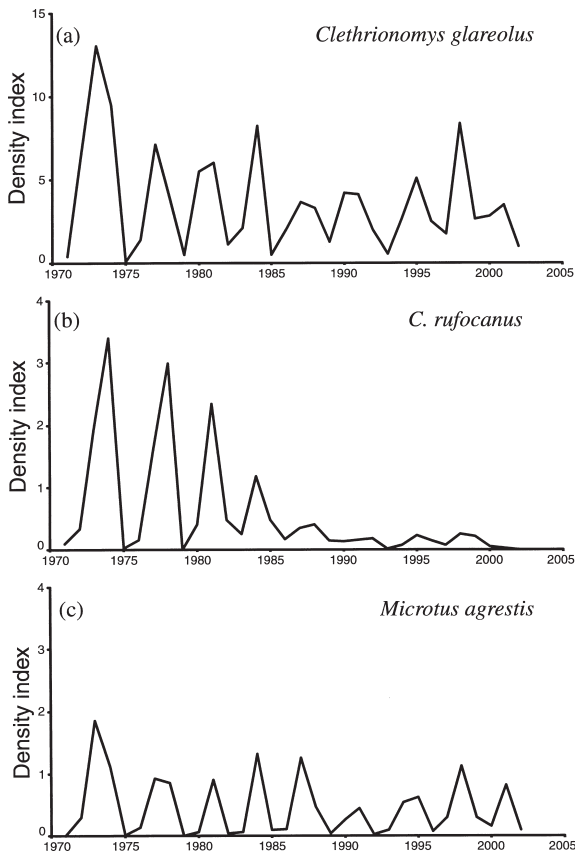


Fig. 3. Trapping indices for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis* in fall 1971–2002.

for the outstanding Ekträskkludden locality, characterized by preferred habitat (Hörnfeldt et al. unpubl.). Interestingly, the decline at Ekträskkludden was not as gradual as for the whole study area (Fig. 1b). It mainly occurred as a major shift from higher to lower densities in the mid 1980s (Fig. 4a, c), although spring densities revealed a decline in three fairly distinct steps from the 1970s, up to mid 1980s, late 1990s and onwards (Fig. 4b).

Landscape colonization rates

The decline of *C. rufocanus* and *M. agrestis* very much ran parallel with a decrease in the proportion of the landscape colonized by the voles at cyclic peak densities, in spring as well as fall (Fig. 5b, c, 6b, c). In contrast, maximum landscape colonization rate per cycle changed much less for *C. glareolus* in spring and, especially, fall (Fig. 5a, 6a). Note, however, the marked decrease in spring from cycle VIII to IX for *C. glareolus* (Fig. 5a). Also, note the gradual elevation of minimum colonization rates per cycle in fall from the 1970s to the 1980s

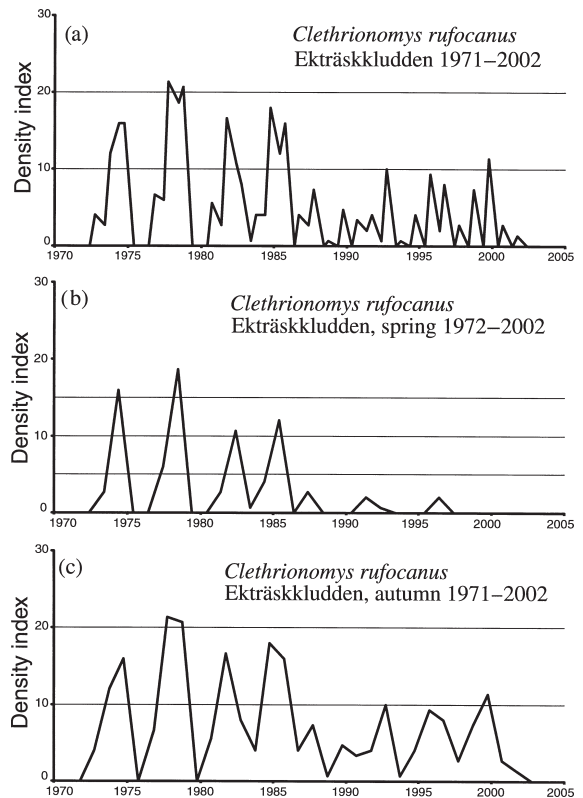


Fig. 4. Trapping indices for *C. rufocanus* at the core locality Ekträskkludden in (a) spring and fall (b) spring and (c) fall, from fall 1971 to fall 2002.

and onwards, which was very obvious in *C. glareolus* but was also seen in *C. rufocanus* (in 1980s) and *M. agrestis* (Fig. 6a–c).

Amplitudes of cycles

The average amplitude, based on combined spring and fall data, was >100-fold and of a similar size in all species (Table 1a). The decrease in densities (Fig. 1–3) was also seen as a decrease in amplitude of the cycles of all voles from the 1970s to late 1990s and early 2000s (Table 1). As expected from patterns of long-term density changes, the most heavy and gradual dampening of amplitude was found in *C. rufocanus*, especially for overall and spring data (Table 1a, b). However, also note the marked decrease in amplitude of *C. glareolus* during the latest cycle, IX, as seen for overall and spring data (Table 1a, b). The decrease in amplitude tended to be weakest for *M. agrestis* (Table 1a, b). The decrease in amplitude is less obvious for fall data (Table 1c), but fall data revealed a fairly similar-sized amplitude among species in the late 1990s and early 2000s (Table 1c).

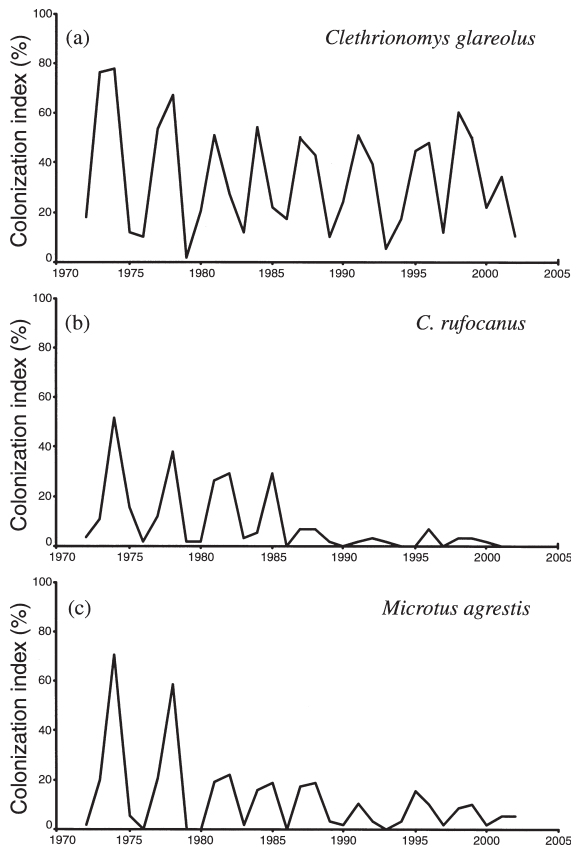


Fig. 5. Landscape colonization indices (proportion out of 58 sampling plots with ≥ 1 individual trapped) in spring 1972–2002 for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis*.

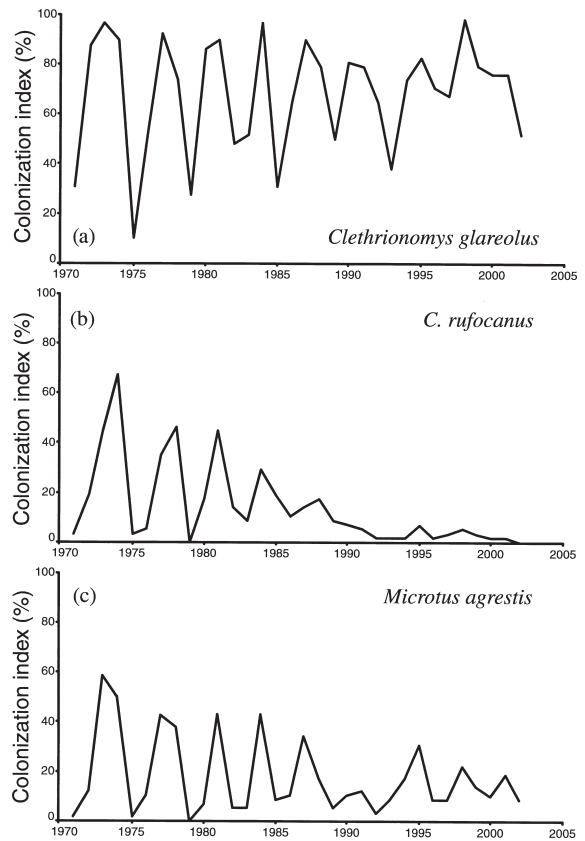


Fig. 6. Landscape colonization indices (proportion out of 58 sampling plots with ≥ 1 individual trapped) in fall 1971–2002 for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis*.

Trends of rate of change in winter

Variation in rate of change in numbers in winter (from fall to spring) showed a clear cyclical-linked pattern

throughout the study period for *C. glareolus* and *M. agrestis*, while for *C. rufocanus* the pattern became obscured in the 1990s (Fig. 7a–c). In general, wintering

Table 1. The amplitude (n_{\max}/n_{\min}) of successive vole cycles¹.

	Cycle starting with initial summer increase in									
	1972	1976	1979/80 ²	1983	1986	1989/90 ³	1993/94 ⁴	1997	2000	Mean
a) overall data										
<i>C. glareolus</i>	145	357	301	59	46	84	102	56	21	130
<i>C. rufocanus</i>	340	299 ⁵	234	118 ⁵	40 ⁵	18 ⁵	22 ⁵	25 ⁵	5 ⁵	122
<i>M. agrestis</i>	273 ⁵	211 ⁵	90 ⁵	132 ⁵	126 ⁵	44 ⁵	62 ⁵	113	82	126
b) spring data										
<i>C. glareolus</i>	55	118	60	11	13	20	20	8	4	34
<i>C. rufocanus</i>	179	200	88	75 ⁵	11 ⁵	4 ⁵	9 ⁵	5 ⁵	1 ⁵	64
<i>M. agrestis</i>	273 ⁵	211 ⁵	24 ⁵	27 ⁵	43 ⁵	16 ⁵	26 ⁵	18	15 ⁵	73
c) fall data										
<i>C. glareolus</i>	145	5	13	16	2	3	9	5	3	22
<i>C. rufocanus</i>	170	299 ⁵	6	5	2	18	3	4	5 ⁵	57
<i>M. agrestis</i>	185	93 ⁵	23	22	32	22	9	4	4	44

¹ A cycle is defined as the period starting and ending, respectively, in spring of years with subsequent cycles' initial summer increase (Fig. 1, 8a–c).

² 1979 refers to *C. glareolus*, 1980 to the other species.

³ 1990 refers to *M. agrestis*, 1989 to the other species.

⁴ 1994 refers to *C. rufocanus*, 1993 to the other species.

⁵ To avoid yielding an infinite amplitude, 0 was replaced with 0.01 for n_{\min} .

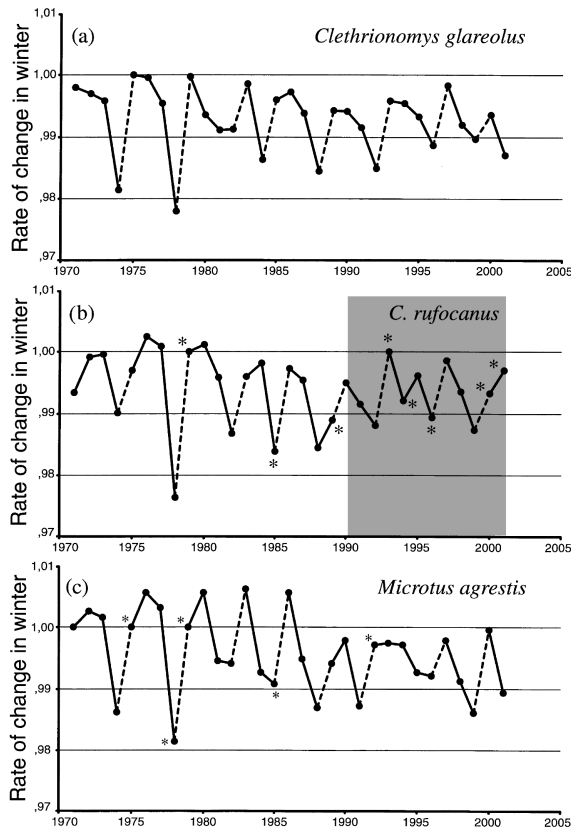


Fig. 7. Rate of change in numbers in winter 1971/72–2001/02 (according to trapping indices in fall and spring) for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis*. The horizontal 1.00-lines denote stability in numbers. Broken lines indicate the major shifts in rate of change (from low to high(er) values) at the transition between successive cycles. Asterisks denote that the value 0 was replaced with 0.01 for one or both of the trapping indices before rate of change was calculated. Shaded area for (b) *C. rufocanus* denotes period with uncertainty in data due to consistently low trapping indices (compare Fig. 1).

success, expressed as rate of change in numbers in winter, decreased from the 1970s to the 1980s and onwards for all species (Fig. 7a–c). In the mid 1980s this first changed the fairly smooth overall density curve of *C. rufocanus* (Fig. 1b) into the saw-toothed curve type characteristic of *C. glareolus* (Fig. 1a), when stability or

increase of numbers in pre-peak winters turned into recurrent winter declines (Fig. 7b). The corresponding change from smooth to saw-toothed density curve for *M. agrestis* appeared somewhat later in the late 1980s (Fig. 1c). However, the change in wintering success appears most extreme for *M. agrestis*, as cycles I–II showed increasing numbers in two pre-peak winters, cycles III–V showed increasing numbers in one winter, while in cycles VI–IX no pre-peak winter showed increasing numbers (Fig. 7c). In contrast to the other species, *C. glareolus* never increased but sometimes remained stable over winter in the 1970s (Fig. 7a), but from the 1980s and onwards always declined in winter and also frequently tended to decline deeper than before (Fig. 1a, 7a). The value of rate of change in the second winter of cycles either decreased or tended to do so for all species during the study period (Fig. 7; *M. agrestis*: $r = -0.822$, $p = 0.007$, *C. rufocanus*: $r = -0.719$, $p = 0.029$, and *C. glareolus*: $r = -0.542$, $p = 0.132$). The same applied for rate of change during the third winter of cycles (*M. agrestis*: $r = -0.744$, $p = 0.034$, *C. rufocanus*: $r = -0.583$, $p = 0.129$, and *C. glareolus*: $r = -0.736$, $p = 0.059$).

The delayed density dependence (DDD) of rate of change in winter 1971/72–1987/88 on density in previous spring (Table 2; Hörnfeldt 1994) also predominated in 1988/89–2001/02, although the relationship for *C. glareolus* and *C. rufocanus* seemed weaker (Table 2). For *C. rufocanus* there was also a significant correlation with current density in fall.

Trends of rate of change in summer

Variation in rate of change in numbers in summer (from spring to fall) showed a clear cyclical-linked pattern throughout the study period for *C. glareolus* and *M. agrestis*, while for *C. rufocanus* that pattern very much disappeared in the 1990s (Fig. 8a–c). In contrast to the deteriorating situation in winter (Fig. 7c), in summer *M. agrestis* showed a pattern that was more or less opposite with respect to the long-term change of values for rate of change (Fig. 8c). Especially late in the cycles, there was a clear elevation of the values from the latter part of the 1980s (cycle V) and onwards. Up to

Table 2. Correlation coefficients of rate of change in winter against density in current fall and previous spring for early and later parts of the study period. Significant coefficients are marked with *, ** and *** for p -values ≤ 0.05 , ≤ 0.01 and ≤ 0.001 , respectively.

	1971/72–1987/88		1988/89–2001/02	
	Density in			
	Current fall (n = 17)	Previous spring (n = 16)	Current fall (n = 14)	Previous spring (n = 14)
<i>C. glareolus</i>	-0.425	-0.713**	-0.114	-0.543*
<i>C. rufocanus</i>	-0.412	-0.838***	-0.684**	-0.689**
<i>M. agrestis</i>	-0.374	-0.753***	-0.404	-0.769***

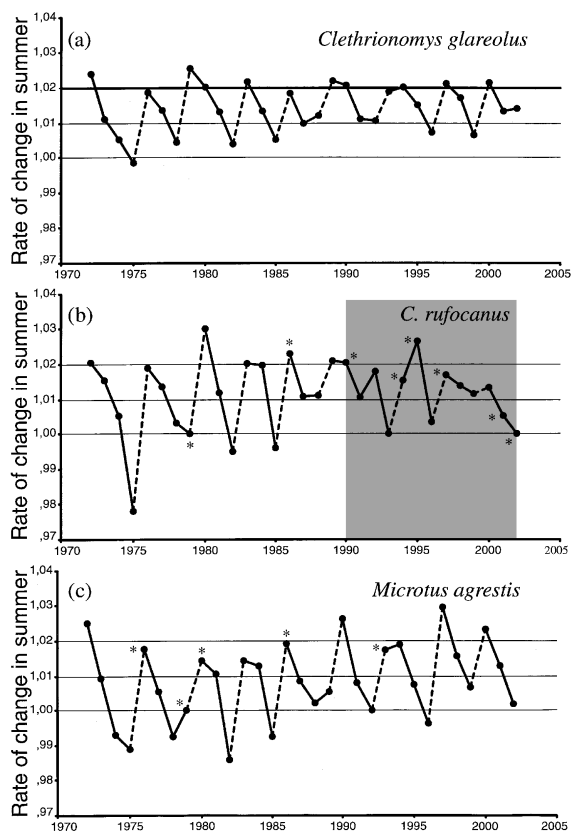


Fig. 8. Rate of change in numbers in summer 1972–2002 (according to trapping indices in spring and fall) for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis*. The horizontal 1,00-lines denote stability in numbers. Broken lines indicate the major shifts in rate of change (from low to high(er) values) at the transition between successive cycles. Asterisks denote that the value 0 was replaced with 0.01 for one or both of the trapping indices before rate of change was calculated. Shaded area for (b) *C. rufocanus* denotes period with uncertainty in data due to consistently low trapping indices (compare Fig. 1).

the mid 1980s (cycle IV) *M. agrestis* regularly decreased late in the cycles but only rarely afterwards. There appeared to be a similar, but less clear-cut, situation in *C. rufocanus* (Fig. 8b) and *C. glareolus* (Fig. 8a).

To illuminate this further, I also calculated the ratio of rate of change in summer to that in previous winter. In

M. agrestis, this ratio increased gradually with time in the first ($r=0.708$, $p=0.033$), second ($r=0.749$, $p=0.020$) and third years of cycles ($r=0.926$, $p=0.000$). In *C. glareolus* the ratio did not increase with time in the same way as in *M. agrestis* in the first ($r=0.232$, $p=0.549$) and second ($r=0.514$, $p=0.157$), but it did in the third years of cycles ($r=0.697$, $p=0.037$). In *C. rufocanus* the ratio showed no gradual increase with time in neither first ($r=-0.112$, $p=0.775$), second ($r=0.261$, $p=0.497$) nor third years of cycles ($r=0.412$, $p=0.270$).

The DDD of rate of change in summer 1972–1988 on density in previous fall (Table 3, Hörnfeldt 1994) also appeared to predominate in 1989–2002 for *C. glareolus* and *M. agrestis*, but for *C. glareolus* there was also a significant correlation with current density in spring. In contrast, for *C. rufocanus* there was no indication of any density dependence at all (Table 3).

Annual trends of rate of change

Annual rates of change based on successive spring densities (Fig. 9) show the integrated result of rate of change in the main reproductive season in summer and subsequent, essentially non-reproductive, season in winter. Thus, the measure usually integrates rate of increase in summer (Fig. 8) and additional marginal rate of increase, maintenance or rate of decrease in numbers in winter (Fig. 7). Correspondingly, rates based on fall densities (Fig. 10) show the integrated result of rate of change in winter (Fig. 7) and subsequent summer (Fig. 8). Both these measures showed a clear cyclical-linked pattern for *C. glareolus* and *M. agrestis* throughout the study, while this pattern became disrupted for *C. rufocanus* from the 1990s (cycle VI) and onwards (Fig. 9). In general, for all species and irrespective of whether based on spring or fall data, annual rates of change within cycles tended to fluctuate less strongly as time proceeded (Fig. 9, 10).

It is clear that annual values for rate of change early (1st yr) in cycles gradually decreased through the years for *C. glareolus*, *C. rufocanus* as well as *M. agrestis*, in spring (Fig. 9a–c: $r=-0.794$, $p=0.011$; $r=-0.762$, $p=0.017$ and $r=-0.730$, $p=0.026$, respectively) as well

Table 3. Correlation coefficients of rate of change in summer against density in current spring and previous fall for early and later parts of the study period. Significant coefficients are marked with *, ** and *** for p -values ≤ 0.05 , ≤ 0.01 and ≤ 0.001 , respectively.

	1972–1988		1989–2002	
	Density in			
	Current spring (n = 17)	Previous fall (n = 17)	Current spring (n = 14)	Previous fall (n = 14)
<i>C. glareolus</i>	-0.398	-0.770***	-0.739**	-0.791***
<i>C. rufocanus</i>	-0.411	-0.867***	-0.284	0.154
<i>M. agrestis</i>	-0.444	-0.831***	-0.362	-0.692***

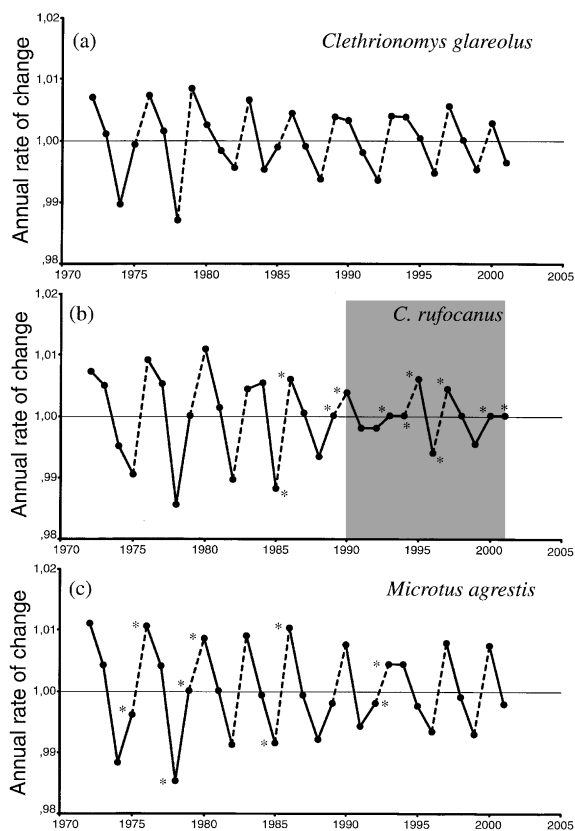


Fig. 9. Annual rate of change in numbers in spring 1972–2002 (according to trapping indices in subsequent springs) for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis*. The horizontal 1,00-lines denote stability in numbers. Broken lines indicate the major shifts in rate of change (from low to high(er) values) at the transition between successive cycles. Asterisks denote that the value 0 was replaced with 0.01 for one or both of the trapping indices before rate of change was calculated. Shaded area for (b) *C. rufocanus* denotes period with uncertainty in data due to consistently low trapping indices (compare Fig. 1).

as fall, although the fall situation was somewhat obscured in *C. rufocanus* (Fig. 10a–c: $r = -0.860$, $p = 0.003$; $r = -0.559$, $p = 0.117$ and $r = -0.780$, $p = 0.013$, respectively). For *M. agrestis*, the gradual build-up of high spring densities (Fig. 2c) by population growth during two years in the 1970s, from the 1980s (cycle III) was replaced by one year of population growth, first followed by one year of relative stability in numbers and from the 1990s (cycle VI) was frequently followed by one year of population decline (Fig. 9c). The situation was very similar for *C. rufocanus*, but the change from two to essentially one year of population growth occurred somewhat later, in the late 1980s from cycle V (Fig. 9b), leading to a less severe decline in spring densities in the early 1980s than for *M. agrestis* (Fig. 2b, c). In *C. glareolus*, two years of population growth became less frequent and the first years' popula-

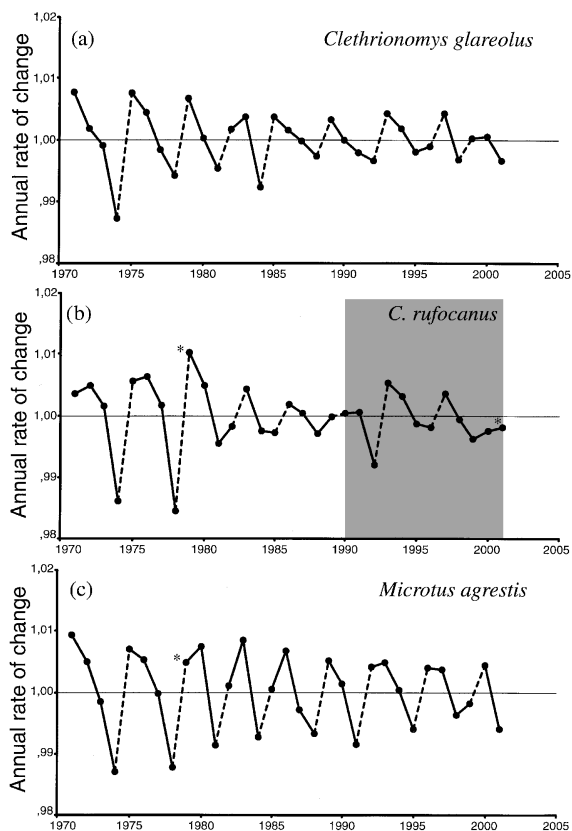


Fig. 10. Annual rate of change in numbers in fall 1971–2002 (according to trapping indices in subsequent falls) for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis*. The horizontal 1,00-lines denote stability in numbers. Broken lines indicate the major shifts in rate of change (from low to high(er) values) at the transition between successive cycles. Asterisks denote that the value 0 was replaced with 0.01 for one or both of the trapping indices before rate of change was calculated. Shaded area for (b) *C. rufocanus* denotes period with uncertainty in data due to consistently low trapping indices (compare Fig. 1).

tion growth values became reduced from cycle IV and onwards; note especially the low value of cycle IX (Fig. 9a). Also, note the weak rate of change values in fall for all species in cycle IX (Fig. 10a–c).

Loss of stepwise density increase

The magnitude of spring density change during the first years of cycles decreased gradually from the 1970s and onwards for *C. rufocanus* ($r = -0.718$, $p = 0.029$) and *M. agrestis* ($r = -0.815$, $p = 0.007$, Fig. 11b–c). Spring density change decreased even more markedly during the second years of cycles (Fig. 12b–c; *C. rufocanus*: $r = -0.833$, $p = 0.005$ and *M. agrestis*: $r = -0.737$, $p = 0.024$). At this second-year stage of cycles, summer increases were more or less neutralized

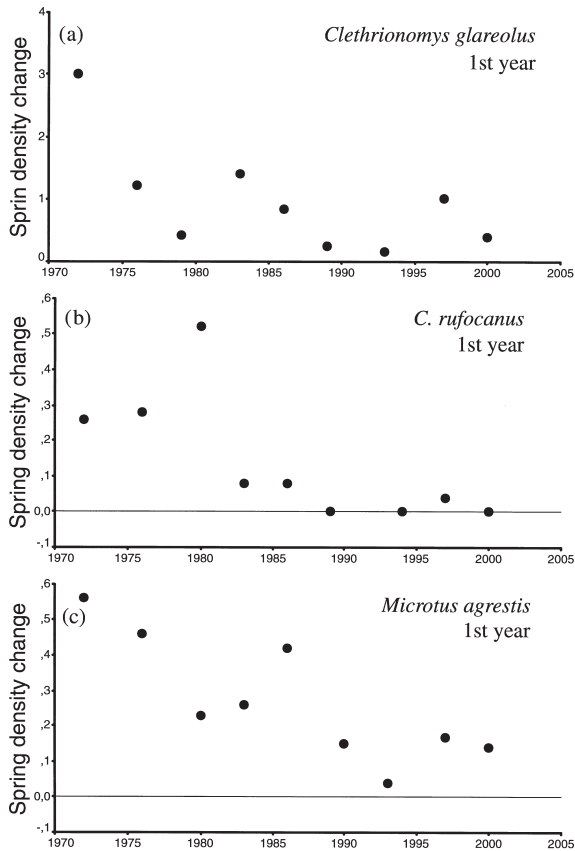


Fig. 11. Change in spring density during the first year of cycle I–IX (Fig. 8a–c) according to trapping indices in spring in 1972–2001 for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis*.

or even overridden by subsequent winter declines from the 1980s and onwards. Although these changes were less marked for *C. glareolus*, the tendency was similar in the first and second years also for this species (Fig. 11a; $r = -0.654$, $p = 0.056$ and Fig. 12a; $r = -0.516$, $p = 0.155$). In essence, the gradual two-large-step build-up of relatively large spring densities in the 1970s was successively replaced by a one-smaller-step build-up of the successively smaller spring densities from the 1980s and onwards (Fig. 2a–c, 11, 12).

Increase, peak, decline and low population phases

The increase phase (first year of cycle) with the major shift in rate of change in summer, from low to high(er) values at the transition between cycles (Fig. 8a–c), occurred simultaneously in all species in cycle I (1972), II (1976), IV (1983), V (1986), VIII (1997) and IX (2000). In cycle III the increase occurred earlier in *C. glareolus* (1979) than in the other species (1980), in cycle VI it was earlier in *C. glareolus* and *C. rufocanus* (1989) than

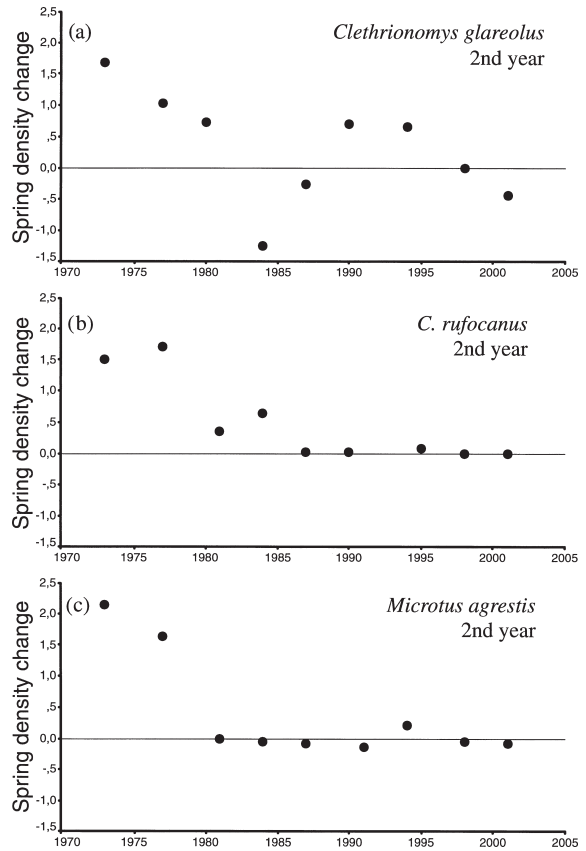


Fig. 12. Change in spring density during the second year of cycle I–IX (Fig. 8a–c) according to trapping indices in spring 1973–2002 for (a) *Clethrionomys glareolus*, (b) *C. rufocanus* and (c) *Microtus agrestis*.

in *M. agrestis* (1990), and in cycle VII the increase was earlier in *C. glareolus* and *M. agrestis* (1993) than *C. rufocanus* (1994) (Fig. 8a–c).

In the 1970s peak densities were first reached in *C. glareolus* (fall 1973, 1977), then in *M. agrestis* (spring 1974, 1978), and finally in *C. rufocanus* (fall 1974, 1978) (Fig. 1a–c). In the 1980s and onwards peaks were constantly reached in fall and were normally simultaneous for all species, i.e. in 1981, 1984, 1987 (1988 in *C. rufocanus*), 1995, 1998, and 2001 (in *C. glareolus* and *M. agrestis*). In cycle VI *C. glareolus* peaked first (1990), followed by *M. agrestis* (1991) and *C. rufocanus* (1992) (Fig. 1a–c).

The cyclic declines in numbers were asynchronous in the 1970s, starting first in *C. glareolus*, which showed stepwise and slow declines, then in *M. agrestis* which showed persistent declines of intermediate speed, and finally in *C. rufocanus* which showed persistent and rapid declines. In contrast to the asynchronous declines in the 1970s, the declines in the 1980s and onwards usually started and ended simultaneously, and were slow and synchronous among species (Fig. 1a–c). According

to the terminology of Chitty (1955) and Krebs and Myers (1974), the *C. glareolus* declines were of H-type and normally, except perhaps for the decline in cycle VI, ranged from one winter through to the next, and included a characteristic summer increase inbetween (Fig. 1a, 7a, 8a). Declines of *M. agrestis* were consistently of the G-type up to the mid 1980s (cycle IV), mainly ranging from one summer through the subsequent winter (1970s), or from one winter through to the next (1980s; cycle III–IV), so these declines regularly included summer declines (Fig. 1c, 7c, 8c). As summer declines of *M. agrestis* became more rare after the mid 1980s (cycle IV), the only G-type decline was found in cycle VII, whereas H-type declines occurred in cycles V, VIII and IX, with an intermediate decline of the G- and H-type in cycle VI (Fig. 1c, 7c, 8c). Declines of *C. rufocanus* were of M-type, mainly extending over one winter, in the 1970s, and were of G-type in the early 1980s (cycle III–IV), ranging from one winter through to the next, of M-type in cycle V and possibly cycle VI, but of H-type in cycle VII–VIII (Fig. 1b, 7b, 8b). Relative to the start (first summer) of different cycles (Fig. 8a–c), declines of *M. agrestis* in the 1980s and onwards, except in cycle VII, started about half a year earlier than in the 1970s (Fig. 1c). Declines of *C. rufocanus* also frequently started earlier (by about one year) in the 1980s and later on (Fig. 1b). In contrast, declines of *C. glareolus* usually started at a rather constant stage, except in cycle III and VII (one year later, Fig. 1a).

The phase of very low numbers was long in the 1970s, while it was relatively shorter in the 1980s, 1990s and early 2000s (Fig. 1a–c). Also, the low phase tended to be deeper in the 1970s than afterwards (Fig. 3a–c, 6a–c), but note that *C. rufocanus* appeared to have become more or less extinct on sampling plots by the early 2000s (Fig. 2b, 3b).

Discussion

The declines in numbers (Fig. 1–3) and amplitude (Table 1), from the 1970s to the 1980s and onwards, were largely linked to an increased frequency and/or accentuation of winter declines (Fig. 7). This more or less neutralized or overrode the density increase during the reproductive season in the previous summer, especially so in the second year of the cycles. Thereby the gradual two-large-step build-up of large spring densities, very much founding the base for the very large peak densities and amplitudes in the 1970s, was successively replaced by a one-smaller-step build-up of more modest spring densities (Fig. 11–12), leading to the lower peak densities and amplitudes in the 1980s, 1990s and early 2000s (Fig. 1–3, Table 1). I postulate that understanding the causes of the increased frequency and/or severeness

of winter declines, which has clearly disturbed the stepwise population growth pattern connected with high cyclic peaks, is critical for understanding the observed long-term declines in numbers. However, the underlying causes of the increase of winter declines and the decrease of densities and amplitudes are unknown.

Other studies in Fennoscandia have also shown a decline of *C. rufocanus*, but at a later time; in northern Finland, in Pallasjärvi from the mid 1980s (Henttonen 2000), and Kilpisjärvi from the early 1990s (Hansen et al. 1999), and in the Strömsund area in northwest Sweden from the late 1980s (Hansson 1999). Even in Japan, according to fall trapping data, *C. rufocanus* seemed to have declined in a similar way as in Fennoscandia from the late 1970s up to 1992 (Saitoh and Nakatsu 1997). However, I do not know if the decline in Japan was temporary, or if it has also been persistent, as I have not seen any later data from that study. *Microtus agrestis* appeared to decline in the early 1980s in Pallasjärvi, i.e. at a similar time as in my study area, but in the late 1980s in Strömsund (Hansson and Henttonen 1995, Hanski and Henttonen 1996, Hansson 1999). Frequent and often deep winter declines have typically been observed in recent time series data also in other studies, i.e. where population densities have been monitored in both spring and fall (Lindström and Hörnfeldt 1994, Hanski and Henttonen 1996, Henttonen 2000, Ecke et al. 2001, 2003a, Ekerholm et al. 2001). The previously reported delayed density dependence (DDD) of rate of change in winter as well as summer for all species (Hörnfeldt 1991, 1994), was also observed for the latter part of the present time series, except for *C. rufocanus* in summer and that the DDD appeared somewhat weakened for *C. glareolus* and *C. rufocanus* in winter and for *M. agrestis* in summer (Tables 2–3). Also, direct density dependence (DD) not previously detected was now observed for *C. rufocanus* in winter and for *C. glareolus* in summer. In contrast to my findings for *C. glareolus*, Yoccoz et al. (2001) using a more refined analysis for the *C. glareolus* time series from Pallasjärvi did not find any evidence at all for DDD there.

It should be kept in mind that densities of cyclic voles have decreased most dramatically in *C. rufocanus*, with *M. agrestis* also showing a persistent but less severe decline, while *C. glareolus* showed the least decrease in the present study. *C. glareolus* appears to have been least affected also in other Fennoscandian studies where a decline has been observed (Hansson and Henttonen 1995, Hansson 1999, Henttonen 2000). It should also be noted that in the current study area *C. rufocanus* is close to the southeastern border of its Swedish distribution range (Siivonen 1968), which may make it more sensitive than the other species to any environmental changes that affect numbers negatively. Although my hypotheses

below on the causes of the decline in vole numbers may be more or less relevant to all species and perhaps to other areas with declining vole populations, they were formulated especially with *C. rufocanus* and the present study area in mind, because of the outstanding and early start of the decline here. Most of the hypotheses were first presented at the WWF meeting on lemmings in Finse (Hörnfeldt 1989, 1991, 1995), but have not been published adequately before now.

Destructive sampling hypothesis (DSH)

As snaptrapping is a form of destructive sampling, it has been argued that the observed decline could be an artefact limited to the sampling plots and caused by the repeated outtrapping there. Although I have not regarded it as a very likely hypothesis, in the present context we still found it worthwhile to test and, not unexpectedly, were able to refute it. Previously unsampled plots did not yield higher trapping indices than the permanent ones (Christensen and Hörnfeldt 2003).

Natural, long-term, fluctuation pattern hypothesis (NFPH)

It cannot be excluded that the decrease in vole numbers is part of a natural, very long-waved, density fluctuation pattern. However, the comparatively few long-term and quantitative data sets on population fluctuations that are available for *C. rufocanus* and other voles and lemmings are probably not long enough to “test” this hypothesis. Assuming that such a fluctuation would be symmetric and judging from the length of present time series, we would need series of at least 60–70 years to be able to trace the first signs of such patterns. It should be noted that the conclusion of Angerbjörn et al. (2001) that *Lemmus lemmus* fluctuations frequently contained extended periods of low numbers/non-cyclicity was largely based on qualitative data and hence must be treated with great caution. In this context it is interesting to note that the time series data for *Microtus* spp. in western Finland clearly appeared to be at variance with the above declines in density, showing no consistent long-term trend in the same period, although a “weakly cyclic” period was noted in the mid 1990s (Korpimäki et al. 2002, 2003b, Laaksonen et al. 2002). An initial rise in numbers from the early 1970s to the early 1990s was considered to be a possible example of inherent chaotic dynamics arising from predator–prey interactions, but the authors did not exclude that the density increase could have been a response by the voles to changes in landscape structure (Hanski et al. 1993, Hanski and Henttonen 1996). Even more striking in the time series from western Finland is the less common occurrence of

the saw-toothed density fluctuation pattern caused by frequent winter declines, that otherwise has been so typical in many other series in later years (above), but see Huitu et al. (2003).

I conclude that it is probably too early yet to refute the NFPH, although I intuitively feel it less likely to be correct. At least, it is important that the uncertainty at this point must not prevent us from seeking alternative explanations. The predominant picture emerging from Fennoscandian time series is the decrease in vole numbers (above), which may very well be an “early warning” of some environmental disturbance, perhaps of anthropogenic origin.

Habitat fragmentation hypothesis (HFH)

Land use by forestry is relatively intense in the present study area, having profound effects on temporal changes of landscape composition, e.g. by causing habitat loss and fragmentation of forests through clear-cutting (Östlund et al. 1997). Acknowledging this and the fact that *C. rufocanus* has disappeared successively from sampling plots (Fig. 5b, 6b), and in a multitude of patterns (Hörnfeldt et al. unpubl.) with one extreme case exemplified in Fig. 4a–c, makes the HFH reasonable for at least partly explaining the observed decline (Hansson 1999). Important forest habitats for reproduction of *C. rufocanus* (Christensen and Hörnfeldt, unpubl.) may have become so fragmented, that habitat patches in the landscape are no longer sufficiently large and common to permit building up densities to cyclic peaks. For similar reasons, the gradual disappearance of *M. agrestis* from the landscape (Fig. 5c, 6c), makes habitat fragmentation or habitat loss a likely candidate behind part of this decline also, however in this case due to succession of clear-cuts and abandoned farmland into forests (Hansson 1999). Although habitat fragmentation may be involved, it seems unlikely that the HFH alone could explain the observed declines, as similar but later declines have occurred elsewhere in the absence of forestry (Hanski and Henttonen 1996). However, studies related to the HFH using remote sensing data (satellite images) are in progress and seem very promising so far, as they have clearly indicated that fragmentation of older pine (*Pinus silvestris*) forests has been involved in the decline of *C. rufocanus* in the present area (Ecke et al. 2003b).

Adverse winter hypothesis (AWH)

The very striking change of overwinter dynamics, with increased frequency and severeness of winter declines in all species (Fig. 1a–c, 7a–c), suggests that this and the long-term declines of density are at least partly caused by direct or indirect effects of adverse/decreased winter

quality. My own experience is that winters in later years have been characterized by decreased stability, frequently including later establishment of snowcover, earlier snowmelt, lower snow depth, and heavily fluctuating temperatures (often around 0°C) causing recurrent thaws and freezing periods with icebark on the ground. This is also supported indirectly by a clear elevation of winter temperature since the late 1980s (Alexandersson 2002). This temperature increase has probably been partly caused by changes in the north Atlantic oscillation (NAO), bringing warmer and wetter winters to Fennoscandia. However, whether changes in the NAO in turn have been affected by global warming in some way is an open question (Hurrell 1995, Hurrell et al. 2001). NAO effects on terrestrial ecosystems have recently become a field of increasing interest (reviewed by Stenseth et al. 2002). I imagine that winter instability caused by the NAO is likely to affect voles negatively by leading to increased predation risk and actual predation because of reduced snow cover (PIH below), affecting thermoregulation and condition negatively, causing decreased availability of food and hiding places etc. when holes and cavities become filled with ice. Frequent occurrence of icebark on the ground has negatively affected reindeer (*Rangifer tarandus*) winter grazing conditions in northern Sweden since the late 1980s (Öje Danell, pers. comm.). Also, according to recent and very interesting experimental work on *M. oeconomus* in Norway, voles experienced increased mortality rates in mild winters with ice formation on the ground (Aars and Ims 2002). Although mortality causes of the voles were not studied, these results provide strong support for the AWH. However, future studies should aim to reveal whether adverse winter conditions act directly or indirectly on vole mortality rates (Aars and Ims 2002). The negative effects of deteriorating winter quality are likely to raise the level of environmental stress experienced by the voles, which in turn may trigger the occurrence of disease and thereby contribute to elevation of mortality rates (ESDH below).

Predation increase hypothesis (PIH)

The major decline in vole numbers in the 1980s (Fig. 1–2) followed upon the spread of sarcoptic mange (*Sarcoptes scabiei*) and the subsequent decline of the red fox (*Vulpes vulpes*) population (Danell and Hörnfeldt 1987). The decline in fox numbers ought to have caused vole numbers to rise, not to decline, due to relaxed predation on the voles by foxes (Hansson 1988). Decline phases of *C. rufocanus* and *M. agrestis* frequently started at an earlier stage of the cycles, and these voles and *C. glareolus* usually declined synchronously (although they had previously declined asynchronously) from the 1980s and onwards. Also, winter declines in

general became more frequent (Fig. 7 and above). However, other predators, such as small mustelids (*Mustela nivalis* and *M. erminea*), regarded to prey on voles more efficiently than foxes in winter (Hansson 1987, Henttonen et al. 1987), may have benefited from the fox decline in the 1980s, partly by reduced fox predation on the mustelids. This may have elevated cyclic lows of the mustelids, leading to a faster numerical response by mustelids and thereby to an increased and advanced (relative to the increase phase of vole cycles) mustelid predation on the voles (Hörnfeldt 1991). Thus, increased and advanced predation by small mustelids, especially in winter, could be an important change from the 1970s to the 1980s and onwards, that has contributed to the increased frequency and severeness of winter declines, increased synchronization of the cyclic decline phase, and to the long-term decline in density. Also, predation by small mustelids has turned out to be an important mortality factor in cyclic vole populations (Norrdahl and Korpimäki 1995), although the role of these and other specialist predators in causing the decline and generating the cycles is still debated after a period of intense experimental work on this issue (Korpimäki and Norrdahl 1998, Klemola et al. 2000, Graham and Lambin 2002, Korpimäki et al. 2002, 2003a, Lambin and Graham 2003, Oli 2003a, b). Unfortunately there are no population density data available on small mustelids for this area, but the link between decreasing fox and subsequently increasing numbers of pine marten (*Martes martes*), another mustelid, is well established in Sweden (Lindström et al. 1995). However, the decline and extinction of *M. erminea* from a coastal area in the Netherlands followed upon, and was interpreted as caused by, the arrival of *V. vulpes* into the area (Mulder 1990). Interestingly, the prolongation of a cycle in the early 1980s in Pallasjärvi, Finland, characterized by a long and asynchronous decline phase, was ascribed to a very weak and delayed numerical response by *M. nivalis* (Henttonen 1987, Henttonen et al. 1987). Oksanen et al. 2001 suggested that the change from cyclical towards seasonal dynamics in Pallasjärvi (Hanski and Henttonen 1996), and towards increased seasonality in their own study area in northern Norway, could have been partly caused by stabilizing predation of invading American mink (*Mustela vison*), a generalist predator, on voles and small mustelids.

Clethrionomys rufocanus and *M. agrestis* are less exposed to avian predators in winter than *C. glareolus*, because of the former voles' more persistent use of the sub-nivean space as a refuge (Sonerud 1986, Hörnfeldt et al. 1990, Nybo and Sonerud 1990). However, due to frequent shortening of periods with snowcover and decrease of snow depth (AWH above), predation by both mammalian (Lindström and Hörnfeldt 1994) and avian predators, like Tengmalm's owl (*Aegolius funereus*)

(Hörnfeldt et al. 1990), may have become enhanced on all voles, with all predators contributing to the more frequent and deeper winter declines of voles from the 1980s and onwards. The idea to include the combined predation by all predators when assessing the killing impact by predation on vole numbers, rather than focusing only on that by small mustelids, is supported by recent field experiments (Korpimäki and Norrdahl 1998, Korpimäki et al. 2002).

Food/shelter decrease hypothesis (FSDH)

Bilberry (*Vaccinium myrtillus*) is a staple food plant of *C. rufocanus* in winter, and is also an important food source in summer (Kalela 1957). Dense *V. myrtillus* stands are also important as a general microhabitat for *C. rufocanus* (Löfgren 1995). Therefore, any major decrease in the quantity of *V. myrtillus* is likely to be negative for *C. rufocanus*, probably by reducing survival through lack of winter food, or shelter against predators. The relevance of the FSDH is supported by recurrent outbreaks of the moth *Operophtera brumata* on *V. myrtillus* stands within the study area in 1981–82, 1985–86 and also afterwards, the latest outbreak occurring in 2002–03 (Lars Ericson, pers. comm.). The larvae defoliate, kill, and consequently decrease the abundance of bilberry plants. Having seen such outbreak areas myself, it is clear that at least locally they have the capacity to destroy *C. rufocanus* habitats, and hence add to other habitat fragmentation or habitat loss caused by forestry logging (HFH above). In later years, *V. myrtillus* leaves have also been attacked by the parasitic fungus *Valdensia heterodoxa* causing defoliation and further mortality (Strengbom et al. 2002, Lars Ericson, pers. comm.), thus adding to that caused by the *O. brumata* larvae. Both the larvae and fungus attacks are likely to be promoted by N-fertilization through increased palatability and susceptibility of the leaves to attack from these enemies (Strengbom et al. 2002, 2003, Lars Ericson, pers. comm.). In this context it is interesting to note that adverse winters (AWH above) with heavily fluctuating temperatures around 0°C have also contributed to increase mortality of *V. myrtillus*, probably owing to freezing after the plant has first become sensitized by progressive respiratory loss of cryo-protective sugars (Ögren 1996). Thus, this has added further to the mortality caused by the larvae and fungus. A general effect of the defoliation and subsequent die-off of *V. myrtillus* is that *Deschampsia flexuosa* is favoured and has been found to increase in abundance, which in turn disfavoured recovery of *V. myrtillus* (Strengbom et al. 2002, Lars Ericson, pers. comm.). Although the extent of the different kinds of *V. myrtillus* mortality has not been monitored at the landscape level, it is reasonable to assume that

large areas may have been affected, acknowledging the elevation of winter temperatures since the late 1980s (AWH above) and the increase of N-fertilization by forestry and airborne, diffuse deposition during the current study period (Lövblad et al. 1995, Östlund et al. 1997).

In line with the above negative effects on *V. myrtillus*, which could also be negative for *C. glareolus*, decline of pendulous lichens was suggested by Hansson (1999) as a possible contributing cause to the decline of *C. glareolus*.

Food-quality decrease hypothesis (FQDH)

Any decrease in the food quality of plants is also likely to be negative to the voles and, in the case of *C. rufocanus*, decrease in quality of *V. myrtillus* would be especially negative (FSDH above). Long-term changes in food quality are likely to be related to environmental pollution processes, leading to adverse effects from contamination by heavy metals or organic compounds or from deficiencies or imbalances of mineral elements.

Data from a pilot study of *C. rufocanus* specimen trapped at Ekträskkludden in 1980–97 (Fig. 4a–c) and preserved for the Environment Specimen Bank (Odsjö 1993, Odsjö et al. 1997) did not support any alarming increase of heavy metals in kidney and liver tissue (Hörnfeldt et al. unpubl.). On the other hand, a striking impression was that concentration of some essential mineral elements had changed significantly over the same period; for example Ca- and Mn-concentrations decreased, while ratios of K/Ca and P/Zn increased in both liver and kidney tissue. It is interesting to note that a decrease of Ca and Mn in moose (*Alces alces*) tissue has previously been observed in southwestern Sweden (Frank et al. 1994). Current preliminary data make FQDH a viable hypothesis with respect to the occurrence of mineral element deficiencies or imbalances, which may act as stressors interacting with disease in the voles (ESDH below), and as Zn is involved in the immune system (Fernandes et al. 1979) perhaps impair its function. As Ca is important for vole reproduction (Batzli 1986), the observed decline of Ca-concentrations in *C. rufocanus* tissues may be indicative of impaired reproduction at least in this species. Increased N-fertilization (FSDH above) may have contributed to a decrease in mineral elements in food plants by favouring plant biomass growth above ground positively while having little effect on the root system, thereby leading to dilution of a similar uptake of mineral elements into a larger green biomass (Marschner 1995, Bengt Nihlgård pers. comm.).

Environmental stress/disease hypothesis (ESDH)

Recently, the previously unknown Ljungan virus (LV) was isolated from *C. glareolus* in Sweden (Niklasson et al. 1999). Danish *C. glareolus* individuals brought into the laboratory showed signs of diabetes (Schoenecker et al. 2000). While being non-symptomatic at the time of trapping, the voles successively developed type 1 diabetes. By application of immunohistochemistry, the diabetes was associated with the occurrence of LV in pancreas tissue showing damaged structure (Niklasson et al. 2003a). Interestingly, Danish laboratory observations have also shown that an increased proportion of *C. glareolus* individuals developed diabetes when subjected to stress (Freimanis et al. 2003). Another intriguing observation is that *C. glareolus* individuals in northern Sweden at or close to peak population densities, and at the time of trapping, showed high blood glucose levels and also pathological results when tested for glucose tolerance (Niklasson et al. 2003b). LV has now also been isolated from *C. rufocanus*, *M. agrestis* and *Lemmus lemmus*. In fact, LV appears to cause a systemic infection in all these voles, affecting gland, muscle as well as nerve tissue, causing β -cell dysfunction and myocarditis (Niklasson et al. unpubl.). While we have observed both diseases in all these voles, the relative frequency differed among species, diabetes seemingly more common in the *Clethrionomys* species, and myocarditis more common in *Lemmus lemmus*. It must be noted here that the role of disease is indeed an unexplored field in vole and lemming population ecology (Hansson and Henttonen 1988, Hörnfeldt 1994, Stenseth 1999, Cavanagh et al. 2004). However, following the above recent findings on disease occurrence, I advance the hypothesis that increased environmental stress has increased the susceptibility of voles to disease such as diabetes and perhaps myocarditis, and that decreased stability of winters (AWH above) is such a possible stress trigger. In turn, increased occurrence of disease-related mortality may explain part of the increased frequency and severeness of winter declines and long-term declines in numbers. Deficiency or imbalance of mineral elements, as referred to above for *C. rufocanus*, may well act as an additional stress trigger and may also impair function of the immune system (FQDH above), all potentially contributing to increased susceptibility to disease.

Implications from decreased vole densities

Some implications from the annual winter declines in later years (Fig. 7) and from the long-term decline in vole abundance (Fig. 1– 2) are very clear, especially if the process continues even further towards mainly seasonal fluctuations, with even lower spring densities (Fig. 2). This will strongly affect many owls, raptors

and mammalian predators that are more or less specialized predators of small mammals, and whose reproductive success is highly dependent on vole numbers in spring (Hansson and Henttonen 1995, Hörnfeldt 1998, Henttonen 2000, Strann et al. 2002). Previous cyclical-linked variation of reproductive parameters and predator abundance should switch towards relative stability, with lower reproductive success and lower abundance.

Unfortunately, few long-term records are available from breeding grounds on abundance and reproduction of these predators in Sweden; for example, none are included in the NEMP. However, in the present study area we have a programme running since 1980 for monitoring the breeding population of *A. funereus* (Hörnfeldt et al. 1990), and at peak densities we have observed an approx. 75% decline in numbers of the breeding population in our nest-boxes. Also, it seems that rate of nest box occupancy is evening out; this has been around 10% in 2001, 2002 and 2003 (Hörnfeldt et al. unpubl.). Also, for the mountain region long-term monitoring data are available for the arctic fox (*Alopex lagopus*), which now however is only represented by a diminutive population after a long-term decline in the major part of the Scandinavian mountains, a decline which was attributed to a lack of high cyclic peak numbers of voles and lemmings since the early 1980s (Angerbjörn et al. 1995). Especially from Finland there are additional time series on different vole predators from their breeding grounds, but to my knowledge there have been no reports from these studies of any long-term predator declines associated with the current long-term decline of small rodents in Fennoscandia; but see Laaksonen et al. 2002 for a temporary decline in *A. funereus* during a period of “weakly cyclic” *Microtus* spp. populations in the mid 1990s.

It is possible that the decline in vole numbers will also have indirect effects on predators' alternative prey such as mountain hare (*Lepus timidus*) and grouse (*Tetraonidae*). The fluctuations in these latter species in these parts of Fennoscandia have been closely linked to the vole cycles by predators shifting from voles to alternative prey during declines and thereby synchronizing hare and grouse fluctuations to those of voles (Hörnfeldt 1978, Angelstam et al. 1984, Hörnfeldt et al. 1986, Lindström et al. 1987, Marcström et al. 1988, 1989). It seems reasonable to predict that predators' synchronizing and limiting effect on hare and grouse numbers will become weakened, and perhaps that alternative prey will thereby increase and start to fluctuate more independently of vole fluctuations (Hansson and Henttonen 1995).

Acknowledgements – This study has been financed by many sources, the most important ones being the Swedish Natural Science Research Council, Stiftelsen Seth M. Kempes Minne,

Långmanska kulturfonden, Olle och Signhild Engkvists Stiftelser, and the Swedish Environmental Protection Agency (via the National Environmental Monitoring Programme). T. Hipkiss kindly improved the English.

References

- Aars, J. and Ims, R. A. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. – *Ecology* 83: 3449–3456.
- Ahti, T., Hämet-Ahti, L. and Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. – *Ann. Bot. Fenn.* 5: 169–211.
- Alexandersson, H. 2002. Temperature and precipitation in Sweden 1860–2002. SMHI Meteorologi rapport 104 (in Swedish with English abstract).
- Angelstam, P., Lindström, E. and Widén, P. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. – *Oecologia* (Berlin) 62: 199–208.
- Angelstam, P., Lindström, E. and Widén, P. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia – occurrence and distribution. – *Holarct. Ecol.* 8: 285–298.
- Angerbjörn, A., Tannerfeldt, M., Bjärvall, A. et al. 1995. Dynamics of the arctic fox population in Sweden. – *Ann. Zool. Fenn.* 32: 55–68.
- Angerbjörn, A., Tannerfeldt, M. and Lundberg, H. 2001. Geographical and temporal patterns of lemming population dynamics in Fennoscandia. – *Ecography* 24: 298–308.
- Anonymous. 1985. The National Swedish Environmental Monitoring Programme (PMK). Monitor 1985. National Environmental Protection Board, Stockholm.
- Batzli, G. 1986. Nutritional ecology of the California vole: effects of food quality on reproduction. – *Ecology* 67: 406–412.
- Cavanagh, R. D., Lambin, X., Ergon, T. et al. 2004. Disease dynamics in cyclic populations of field voles (*Microtus agrestis*): cowpox virus and vole tuberculosis (*Mycobacterium microti*). – *Proc. R. Soc. Lond. B* 271: 859–867.
- Chitty, D. 1955. Adverse effects of population density upon the viability of later generations. – In: Cragg, J. B. and Pirie, N. W (eds), *The numbers of man and animals*. Edinburgh, pp. 57–67.
- Christensen, P. and Hörnfeldt, B. 2003. Long-term decline of vole populations in northern Sweden: a test of the destructive sampling hypothesis. – *J. Mammal.* 84: 1292–1299.
- Danell, K. and Hörnfeldt, B. 1987. Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. – *Oecologia* 73: 533–536.
- Ecke, F., Löfgren, O., Hörnfeldt, B. et al. 2001. Abundance and diversity of small mammals in relation to structural habitat factors. – *Ecol. Bull.* 49: 165–171.
- Ecke, F., Hörnfeldt, B., Christensen, P. et al. 2003a. Habitat selection and population dynamics of small mammals on different spatial scales in a Swedish mountain region. – In: Ecke, F., *Effects of landscape patterns on small mammal abundance*, PhD thesis. Luleå Univ. of Technology, Sweden.
- Ecke, F., Christensen, P., Hörnfeldt, B. et al. 2003b. GIS-based identification of important landscape elements for predicting the occurrence of *Clethrionomys rufocanus*. – In: Ecke, F., *Effects of landscape patterns on small mammal abundance*, PhD thesis. Luleå Univ. of Technology, Sweden.
- Ekerholm, P., Oksanen, L. and Oksanen, T. 2001. Long-term dynamics of voles and lemmings at the timberline and above the willow limit as a test of hypotheses on trophic interactions. – *Ecography* 24: 555–568.
- Englund, J. 1970. Some aspects of reproduction and mortality rates in Swedish foxes (*Vulpes vulpes*) 1961–63 and 1966–69. – *Viltrevy* 8: 1–82.
- Fernandes, G., Nair, M., Onoe, K. et al. 1979. Impairment of cell-mediated immunity functions by dietary zinc deficiency in mice. – *Proc. Natl. Acad. Sci. USA* 76: 457–461.
- Frank, A., Galgan, V. and Petersson, L. R. 1994. Secondary copper deficiency, chromium deficiency and trace element imbalance in the moose (*Alces alces* L.): effect of anthropogenic activity. – *Ambio* 23: 315–317.
- Freimanis, T., Heller, K. E., Schoenecker, B. et al. 2003. Effects of preweaning stress on the development of type 1 diabetes in bank voles (*Clethrionomys glareolus*). – *Int. J. Exp. Diabetes Res.* 4: 21–25.
- Graham, I. M. and Lambin, X. 2002. The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. – *J. Anim. Ecol.* 71: 946–956.
- Hagen, Y. 1952. Rovfuglene og viltpleien. – Gyldendal Norsk Forlag.
- Hagen, Y. 1969. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent population fluctuations. – *Fauna* 22: 73–126. (In Norwegian with English summary).
- Hansen, T. F., Stenseth, N. C., Henttonen, H. et al. 1999. Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. – *Proc. Natl. Acad. Sci. USA* 96: 986–991.
- Hanski, I. and Henttonen, H. 1996. Predation on competing rodent species: a simple explanation of complex patterns. – *J. Anim. Ecol.* 65: 220–232.
- Hanski, I., Turchin, P., Korpimäki, E. et al. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. – *Nature* 364: 232–235.
- Hansson, L. 1987. An interpretation of rodent dynamics as due to trophic interactions. – *Oikos* 50: 308–318.
- Hansson, L. 1988. Grazing impact by small rodents in a steep cyclicity gradient. – *Oikos* 51: 31–42.
- Hansson, L. 1999. Intraspecific variation in dynamics: small rodents between food and predation in changing landscapes. – *Oikos* 86: 159–169.
- Hansson, L. and Henttonen, H. 1988. Rodent dynamics as community processes. – *Trends Ecol. Evol.* 3: 195–200.
- Hansson, L. and Henttonen, H. 1995. General changes in rodent dynamics and possible disappearance of lemmings. – *WWF meeting on lemmings, Finse, Norway*, pp. 18–19.
- Henttonen, H. 1987. The impact of spacing behavior in microtine rodents on the dynamics of least weasels *Mustela nivalis* – a hypothesis. – *Oikos* 50: 366–370.
- Henttonen, H. 2000. Long-term dynamics of the bank vole *Clethrionomys glareolus* at Pallasjärvi, northern Finnish taiga. – *Pol. J. Ecol.* 48: 87–96.
- Henttonen, H., Oksanen, T., Jortikka, A. et al. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? – *Oikos* 50: 353–365.
- Huitu, O., Norrdahl, K. and Korpimäki, E. 2003. Landscape effects on temporal and spatial properties of vole population fluctuations. – *Oecologia* 135: 209–220.
- Hurrell, J. W. 1995. Decadal trends in the north Atlantic oscillation: regional temperatures and precipitation. – *Science* 269: 676–679.
- Hurrell, J. W., Kushnir, Y. and Visbeck, M. 2001. The north Atlantic oscillation. – *Science* 291: 603–605.
- Hörnfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls and tularemia in northern Sweden. – *Oecologia* 32: 141–152.
- Hörnfeldt, B. 1986. Smådäggdjursinventering i PMK:s referensområden – rapport från verksamheten 1985. – *Naturvårdsverket, rapport 3256*. (In Swedish with English summary).
- Hörnfeldt, B. 1989. Smådäggdjursinventering i PMK:s referensområden – rapport från verksamheten 1988. – *Naturvårdsverket, rapport 3662*. (In Swedish with English summary).

- Hörnfeldt, B. 1991. Cycles of voles, predators, and alternative prey in boreal Sweden. – PhD thesis, Univ. of Umeå, Sweden.
- Hörnfeldt, B. 1994. Delayed density dependence as a determinant of vole cycles. – *Ecology* 75: 791–806.
- Hörnfeldt, B. 1995. Long-term decline in numbers of cyclic voles in northern Sweden. – WWF meeting on lemmings, Finse, Norway, pp. 21–24.
- Hörnfeldt, B. 1998. Miljöövervakningen visar på minskande sorkstammar! – *Fauna och Flora* 95: 137–144.
- Hörnfeldt, B. 2004. Miljöövervakning av smådäggdjur. http://www.eg.umu.se/personal/hornfeldt_birger/bh/sidor/index3.html
- Hörnfeldt, B., Löfgren, O. and Carlsson, B.-G. 1986. Cycles in voles and small game in relation to variations in plant production indices in northern Sweden. – *Oecologia* 68: 496–502.
- Hörnfeldt, B., Carlsson, B.-G., Löfgren, O. et al. 1990. Effects of cyclic food supply on breeding performance in Tengmalm's owl (*Aegolius funereus*). – *Can. J. Zool.* 68: 522–530.
- Kalela, O. 1957. Regulation of reproduction rate in sub-arctic populations of the vole *Clethrionomys rufocanus* (Sund.). – *Ann. Acad. Sci. Fenn.*, Ser. A, IV Biologica 34: 1–60.
- Klemola, T., Koivula, M., Korpimäki, E. et al. 2000. Experimental tests of predation and food hypotheses for population cycles of voles. – *Proc. R. Soc. Lond. B* 267: 351–356.
- Korpimäki, E. 1987. Clutch size, breeding success and brood size experiments in Tengmalm's owl *Aegolius funereus*: a test of hypotheses. – *Ornis. Scand.* 18: 277–284.
- Korpimäki, E. 1994. Rapid or delayed tracking of multi-annual vole cycles by avian predators? – *J. Anim. Ecol.* 63: 619–628.
- Korpimäki, E. and Hakkarainen, H. 1991. Fluctuating food supply affects the clutch size of Tengmalm's owl independent of laying date. – *Oecologia* 85: 543–552.
- Korpimäki, E. and Norrdahl, K. 1991. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. – *Ecology* 72: 814–826.
- Korpimäki, E. and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. – *Ecology* 79: 2448–2455.
- Korpimäki, E., Norrdahl, K., Klemola, T. et al. 2002. Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. – *Proc. R. Soc. Lond. B* 269: 991–997.
- Korpimäki, E., Klemola, T., Norrdahl, K. et al. 2003a. Vole cycles and predation. – *Trends Ecol. Evol.* 18: 494–495.
- Korpimäki, E., Norrdahl, K., Huitu, O. et al. 2003b. Predator-induced synchrony in population oscillations of coexisting small mammal species. – In: Huitu, O., Temporal and spatial synchrony in small mammal population fluctuations, PhD thesis. Univ. of Turku, Finland.
- Krebs, C. J. and Myers, J. H. 1974. Population cycles in small mammals. – *Adv. Ecol. Res.* 8: 267–399.
- Laaksonen, T., Korpimäki, E. and Hakkarainen, H. 2002. Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. – *J. Anim. Ecol.* 71: 23–31.
- Lambin, X. and Graham, I. M. 2003. Testing the specialist predator hypothesis for vole cycles. – *Trends Ecol. Evol.* 18: 493.
- Lindén, H. 1988. Latitudinal gradients in predator–prey interactions, cyclicity and synchronism in voles and small game populations in Finland. – *Oikos* 52: 341–349.
- Lindström, E. 1989. Food limitation and social regulation in a red fox population. – *Holarct. Ecol.* 12: 70–79.
- Lindström, E. R. and Hörnfeldt, B. 1994. Vole cycles, snow depth and fox predation. – *Oikos* 70: 156–160.
- Lindström, E., Angelstam, P., Widén, P. et al. 1987. Do predators synchronize vole and grouse fluctuations?—An experiment. – *Oikos* 48: 21–124.
- Lindström, E. R., Andrén, H., Angelstam, P. et al. 1994. Disease reveals the predator: sarcoptic mange, red fox predation and prey populations. – *Ecology* 75: 1042–1049.
- Lindström, E., Brainerd, S. M., Helldin, J. O. et al. 1995. Pine marten – red fox interactions: a case of intraguild predation? – *Ann. Zool. Fenn.* 32: 123–130.
- Lindström, J., Ranta, E. and Lindén, H. 1996. Large-scale synchrony in the dynamics of capercaillie, black grouse and hazel grouse populations in Finland. – *Oikos* 76: 221–227.
- Löfgren, O. 1995. Niche expansion and increased maturation rate of *C. glareolus* in the absence of competitors. – *J. Mammal.* 76: 1100–1112.
- Lövblad, G., Kindbom, K., Grennfelt, P. et al. 1995. Deposition of acidifying substances in Sweden. – *Ecol. Bull.* 44: 17–34.
- Marström, V., Keith, L. B., Engren, E. et al. 1989. Demographic responses of arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). – *Can. J. Zool.* 67: 658–668.
- Marström, V., Kenward, R. E. and Engren, E. 1988. The impact of predation on boreal tetraonids during vole cycles: an experimental study. – *J. Anim. Ecol.* 57: 859–872.
- Marschner, H. 1995. Mineral nutrition of higher plants, 2nd edn. – Academic Press.
- Mulder, J. L. 1990. The stoat *Mustela erminea* in the Dutch dune region, its local extinction and possible cause: the arrival of the fox *Vulpes vulpes*. – *Lutra* 33: 1–21.
- Niklasson, B., Kinnunen, L., Hörnfeldt, B. et al. 1999. A new picornavirus isolated from bank voles (*Clethrionomys glareolus*). – *Virology* 255: 86–93.
- Niklasson, B., Heller, K. E., Schoenecker, B. et al. 2003a. Development of type 1 diabetes in wild bank voles associated with islet autoantibodies and the novel Ljungan virus. – *Int. J. Exp. Diabetes Res.* 4: 35–44.
- Niklasson, B., Hörnfeldt, B., Nyholm, E. et al. 2003b. Type 1 diabetes in Swedish bank voles (*Clethrionomys glareolus*): signs of disease in both colonized and wild cyclic populations at peak density. – *Ann. N. Y. Acad. Sci.* 1005: 170–175.
- Norrdahl, K. and Korpimäki, E. 1995. Mortality factors in a cyclic vole population. – *Proc. R. Soc. Lond. B* 261: 49–53.
- Nybo, J. O. and Sonerud, G. A. 1990. Seasonal changes in diet of hawk owls *Surnia ulula*: importance of snow cover. – *Ornis Fenn.* 67: 45–51.
- Odsjö, T. 1993. The Swedish Environmental Specimen Bank with reference to the National Contaminant Monitoring Programme in Sweden. – *Sci. Tot. Environ.* 139/140: 147–156.
- Odsjö, T., Bignert, A., Olsson, M. et al. 1997. The Swedish Environmental Specimen Bank – application in trend monitoring of mercury and some organohalogenated compounds. – *Chemosphere* 34: 2059–2066.
- Oksanen, T., Oksanen, L., Schneider, M. et al. 2001. Regulation, cycles and stability in northern carnivore-herbivore systems: back to first principles. – *Oikos* 94: 101–117.
- Oli, M. K. 2003a. Population cycles of small rodents are caused by specialist predators: or are they? – *Trends Ecol. Evol.* 18: 105–107.
- Oli, M. K. 2003b. Response to Korpimäki et al.: vole cycles and predation. – *Trends Ecol. Evol.* 18: 495–496.
- Ögren, E. 1996. Premature dehardening in *Vaccinium myrtillus* during a mild winter: a cause for winter dieback? – *Funct. Ecol.* 10: 724–732.
- Östlund, L., Zackrisson, O. and Axelsson, A.-L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. – *Can. J. For. Res.* 27: 1198–1206.
- Saitoh, T. and Nakatsu, A. 1997. The impact of forestry on the small rodent community of Hokkaido, Japan. – *Mammal Study* 22: 27–38.
- Schoenecker, B., Heller, K. E. and Freimanis, T. 2000. Development of stereotypes and polydipsia in wild caught bank

- voles (*Clethrionomys glareolus*) and their laboratory-bred offspring: is polydipsia a symptom of diabetes mellitus? – *Appl. Anim. Behav. Sci.* 68: 349–357.
- Siivonen, L. 1948. Structure of short-cyclic fluctuations in numbers of mammals and birds in the northern parts of the northern hemisphere. – *Papers Game Res.* 1: 1–166.
- Siivonen, L. 1968. Nordeuropas däggdjur. – P. A. Norstedt & Söners förlag, Stockholm.
- Small, R. J., Marcström, V. and Willebrand, T. 1993. Synchronous and non-synchronous population fluctuations of some predators and their prey in central Sweden. – *Ecography* 16: 360–364.
- Sonerud, G. A. 1986. Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. – *Holarct. Ecol.* 9: 33–47.
- Steen, J. B., Steen, H., Stenseth, N. C. et al. 1988. Microtine density and weather as predictors of chick production in willow ptarmigan, *Lagopus l. lagopus*. – *Oikos* 51: 367–373.
- Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. – *Oikos* 87: 427–461.
- Stenseth, N. C., Mysterud, A., Ottersen, G. et al. 2002. Ecological effects of climate fluctuations. – *Science* 297: 1292–1296.
- Strann, K.-B., Yoccoz, N. G. and Ims, R. A. 2002. Is the heart of Fennoscandian rodent cycle still beating? A 14-year study of small mammals and Tengmalm's owls in northern Norway. – *Ecography* 25: 81–87.
- Strengbom, J., Nordin, A., Näsholm, T. et al. 2002. Parasitic fungus mediates change in nitrogen-exposed boreal forest vegetation. – *J. Ecol.* 90: 61–67.
- Strengbom, J., Walheim, M., Näsholm, T. et al. 2003. Regional differences in the occurrence of understorey species reflect nitrogen deposition in Swedish forests. – *Ambio* 32: 91–97.
- Yoccoz, N. G., Stenseth, N. C., Henttonen, H. et al. 2001. Effects of food addition on the seasonal density-dependent structure of bank vole *Clethrionomys glareolus* populations. – *J. Anim. Ecol.* 70: 713–720.