

Research article

## Survival through bottlenecks of vole cycles: refuge or chance events?

KAI NORRDAHL\* and ERKKI KORPIMÄKI

Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland

(\*author for correspondence, tel.: +358-2-333 6008; fax: +358-2-333 6550; e-mail: kainor@utu.fi)

Received 24 May 2004; accepted 9 May 2005

Co-ordinating editor: J. Tuomi

**Abstract.** In small rodent populations with wide-amplitude fluctuations and low-density bottlenecks, the individuals that survive through the bottlenecks may gain major fitness advantages as they will be the founders of the following population expansion. Most hypotheses assume that there exists a physical or behavioural refuge from increased predation risk, and that the survivors are most likely individuals adapted to use such refuges. A recent hypothesis suggests that survival probability is habitat-dependent so that some otherwise sub-optimal habitats provide a spatial refuge from predation risk by the main predator(s). We used spatially replicated long-term (1981–2004) trapping and tracking data of voles (field vole *Microtus agrestis* and sibling vole *M. rossiaemeridionalis*) and their main predators (weasel *Mustela nivalis* and stoat *M. erminea*) to test predictions based on this hypothesis. We did not find support for the hypothesis. We did not find marked phase-dependent differences in the habitat-level distribution of *Microtus* voles. Habitat types with low *Microtus* vole abundance had, on average, comparable predator activity than the main *Microtus* vole habitats, indicating that there were no habitat-level refuges from predators. There appeared to be no permanent site-level refuges: the spatial distribution of voles varied from one bottleneck to another. This suggests that survival through bottlenecks is at least partly determined by chance events. We propose that in this kind of systems, where relatively short-lived prey are hunted by nomadic or widely ranging predators, short-term anti-predator responses may increase survival prospects as efficiently as more costly anti-predator adaptations, and there is no apparent need to maintain special adaptations to bottleneck situations that occur at infrequent intervals.

**Key words:** habitat selection, life history, *Microtus*, *Mustela*, population bottleneck, predation, refuge

### Introduction

In populations with wide-amplitude fluctuations and low-density bottlenecks, the individuals that survive through the bottlenecks may gain major fitness advantages as they will be the founders of the following population expansion. This general notion has evoked speculation and research on how well short-lived animals have been adapted for bottleneck-situations that occur at intervals longer than the life-span of an individual (Ylönen, 1994; Oksanen and

Lundberg, 1995; Kaitala *et al.*, 1997; Norrdahl and Korpimäki, 2000; Sundell and Norrdahl, 2002; Wolff, 2003). One of the most well-known model systems for this research has been the population cycles of northern rodents. The northern rodent cycles are large-scale phenomena characterized by multi-annual density oscillations, where differences between peak and lowest densities are typically 50–500-fold, bottleneck-densities are very low ( $< 1$  individual/ha), and the period of the cycle (interval between bottlenecks) varies between 3–5 years (Hansson and Henttonen, 1988; Korpimäki *et al.*, 2003, 2005b). The life-span of a vole is clearly shorter than the period of the cycles: only few voles live longer than one year and there are very few observations of voles surviving over two winters in the wild (Myllymäki, 1977a; Banks *et al.*, 2004).

Multi-annual cycles of small rodents have been studied intensively since they were described by Elton (1924). Despite  $> 75$  years of research, the cause of these population cycles is still a debated question. Most researchers agree that trophic interactions drive multi-annual high-amplitude cycles of northern rodent populations, although the relative importance of rodent-predator and plant-rodent interactions may vary between species and geographic areas (Jedrzejewski and Jedrzejewska, 1996; Korpimäki and Krebs, 1996; Oksanen and Oksanen, 2000; Turchin *et al.*, 2000; Ergon *et al.*, 2001; Hanski *et al.*, 2001; Turchin and Batzli, 2001; Klemola *et al.*, 2002b; Korpimäki *et al.*, 2002, 2005b). Even if there is no full consensus of the role of predation in the mechanism driving the cycles, radio telemetry studies have revealed that predation is the main mortality factor in the northern small rodent populations with multi-annual cycles (Norrdahl and Korpimäki, 1995, 1998; Steen, 1995; Banks *et al.*, 2000; Gilg, 2002). Therefore predation has been evoked as a key factor in the models focusing on adaptive vs. non-adaptive behaviour in fluctuating vole populations (Ylönen, 1994; Oksanen and Lundberg, 1995; Kaitala *et al.*, 1997; Ruxton and Lima, 1997).

Several hypotheses make predictions of which voles survive through the population bottlenecks, and what would be adaptive behaviour for a vole confronting a bottleneck-situation. The ‘null’ hypothesis would be that the survivors are a random sample of the population. As survival is a hit of luck determined by chance events, an adaptive response would be not to adapt to bottleneck-situations at all, or possibly a ‘terminal investment’ (*sensu* Clutton-Brock, 1984) if the survival prospects are very low. All other hypotheses assume that survival through the bottleneck is not a random process, and that there exists some kind of a refuge where the survival probability is higher than outside the refuge. The hypothesis of Ylönen *et al.* (2003) assumes that survival probability is habitat-dependent so that some otherwise sub-optimal habitats provide a spatial refuge from the predation risk by the main predator(s). Other hypotheses assume that the refuge is not habitat-dependent, but may be available in most habitats. The local refuge may be a physical place, a small

hole or other safe micro-scale site, as in the hypothesis of Sundell and Norrdahl (2002), but it may as well be a behavioural one (Ylönen, 1994; Banks *et al.*, 2000). By using a refuge, the animal should increase its probability to survive through the bottleneck, and hence the use of a refuge would be adaptive behaviour in most cases (e.g. Ylönen, 1994; Oksanen and Lundberg, 1995).

Despite a long history of intensive research, the validity of these hypotheses remains an open question. One reason for this lack of knowledge is the low density of animals in the bottleneck situations, which makes both observational and experimental field work difficult. When densities are  $\ll 1$  individual/ha, collection of observational data from inconspicuous small mammals becomes very laborious, and few research projects have enough resources for such studies. Experimental introduction of new individuals, or transfer of caught individuals to experimental sites, may change intra- or inter-specific interactions in a way that makes the results misleading. Therefore, it is not clear, whether the previous results obtained from small-scale field or laboratory experiments are reliable, or just experimental or laboratory artefacts (Mappes *et al.*, 1998; Norrdahl and Korpimäki, 2000; Wolff, 2003).

Assuming that the results obtained from small-scale experiments are valid, previous results suggest that behavioural responses to an experimentally elevated predation risk are common but short-term, and hence should not play a major role (Norrdahl and Korpimäki, 2000). When transferred to predator-free fences, voles originating from low density populations reproduce at a similar rate than voles originating from increasing populations, which also suggest that possible behavioural or physiological adaptations are short-term (Klemola *et al.*, 2002a). Selective predation on one sex or size class may occasionally have population level consequences (Klemola *et al.*, 1997; Norrdahl and Korpimäki, 1998), but generally indirect effects of vole-eating predators on the population structure or population growth in main prey appear to be small compared to the lethal effects on prey survival (Norrdahl *et al.*, 2004). As these results do not give clear support for the hypotheses suggesting that the quality or behaviour of voles would be essentially different in the low phase compared to other phases of the population cycles, the existence of physical (spatial) refuges becomes an even more interesting suggestion.

In this paper, we focus on habitat-related differences in the distribution of voles throughout density cycles by using spatially replicated long-term trapping and tracking data. Our main purpose is to find out whether the data would support the hypothesis suggesting that habitat-level refuges play a crucial role in the survival of voles through the population bottlenecks (Ylönen *et al.*, 2003). The core idea in this hypothesis is that different habitats are optimal for reproduction and survival: sub-populations living in habitats with a high recruitment rate should have a high local extinction risk during population declines, whereas otherwise sub-optimal habitats may have characteristics that

ensure high survival rates through population lows. Using the least weasel (*Mustela nivalis nivalis*) and the field vole (*Microtus agrestis*) living in northern Europe as a model system, Ylönen *et al.* (2003) suggested that field voles reach high population densities in meadows and fields but survive through population lows mainly in sub-optimal wet habitats (bogs and other wet habitats along ditches, creeks and slow flowing rivers). They suggested that least weasels cannot hunt efficiently in the wet habitats because of habitat structure (wet, soft bottom with grassy hummocks) and the presence of large and aggressive water voles (*Arvicola terrestris*).

The optimality of different habitats for small rodents is a multifaceted question. One definition based on the concept of sink-source dynamics is that a high quality habitat is a source habitat, where long-term average reproductive output is high (van Horne, 1983; Pulliam, 1988). However, inter-specific interactions with competitors or predators can have a strong impact on population increase rates, and therefore the measurements of reproductive output or densities may reflect variation in competition or predation pressures rather than in resources given by the habitat. In this kind of a situation, the classification of habitats may be drastically different depending on whether the index of habitat quality (reproductive output, or density) is measured without competitors or predators, or with them. Especially if the consequences of inter-specific interactions are not included in the term 'habitat quality', the quality of a habitat cannot be inferred solely by measuring densities or even reproductive outputs (e.g. van Horne, 1983). However, for the purpose of testing the hypothesis of Ylönen *et al.* (2003), we chose for our comparisons those habitat types that were mentioned in the paper, and accepted as a starting point the claim that meadows and fields are optimal habitats for field voles whereas wet habitats, which are core habitats for water voles, are sub-optimal habitats for field voles. The ground floor of the third chosen habitat type, forests, is dominated by mosses and shrubs, whereas grasses and herbs are less common. As grasses and herbs form the bulk of the diet of *Microtus* spp. voles (e.g. Hansson, 1971; Stenseth *et al.*, 1977; Batzli, 1985; Faber and Ma, 1986), forests have low food resources for these species, and can therefore be classified as a sub-optimal habitat compared to habitats covered by a rich grass and herb vegetation.

From this starting point, we predicted that (1) there should be phase-related differences in the distribution of *Microtus* voles between different habitats. Assuming that the scenario described in the paper by Ylönen *et al.* (2003) is valid, we also predicted that (2) wet habitats, which are core habitats for water voles, should have proportionally more *Microtus* voles in the low phase of the vole cycle than in the other phases of the population cycle, and that (3) these habitats should inhabit less small mustelid predators than the more optimal *Microtus* vole habitats, meadows and fields with grassy vegetation. A rejection

of prediction 1 would indicate that possible refuges operate at a scale smaller than habitat patches. A rejection of predictions 2–3 would mean that the scenario presented in the paper by Ylönen *et al.* (2003) is unlikely, although it would not necessarily mean that there are no habitat-level differences in survival probabilities. In addition, we assessed differences in the quality of main habitats for *Microtus* voles. As a crude bioassay of habitat quality, we compared body condition indices and litter sizes of field voles between the habitats.

## Methods

### *Study area and vole data*

The study area was situated in western Finland, in the municipalities of Kauhava and Lapua (63° N, 22° E). In these municipalities, pine- or spruce-dominated boreal forests cover ca. 65% and agricultural fields ca. 26% of the total area (Huitu *et al.*, 2003; map of the study area in Figure 1 of Hakkarainen *et al.*, 2003), and the rest of the area consists mainly of inhabited areas and watercourses (rivers and small lakes). Trapping sites in Kauhava were situated within an area of 5 × 2 km, whereas the trapping sites in Lapua were within an area of 7 × 3 km. The distance between these two areas was ca. 15 km. As previous studies have shown that the population dynamics of voles within the two trapping areas are tightly synchronized (Korpimäki and Wiehn, 1998; Huitu *et al.*, 2003; Korpimäki *et al.*, 2005a), we pooled the data from these two areas for our analyses.

The proportion of agricultural fields was higher in the vicinity of the trapping sites of Lapua (> 70%) than in the vicinity of the trapping sites of Kauhava (< 40%), but the main habitat types trapped were the same in both areas: forests, agricultural fields, and linear wet habitats along minor watercourses (large ditches – rivulets). The latter habitats (hereafter, water vole habitats) are suitable habitat for water voles. During the study period (1981–2004), we had three regular trapping sites in forests (one in a pine-dominated forest, two in spruce-dominated forests) and 5–6 trapping sites in agricultural fields (two in uncultivated fields, 3–4 in small ditches within cultivated fields). The number of comparable trappings in water vole habitats was 2–3 (two mainly along largest drainage ditches or rivulets, 0–1 along medium-sized drainage ditches).

Each trapping site was trapped in late spring (May) and autumn (September–early October). Within each forest or agricultural field site, we placed 50–100 mouse snap traps (commercial Finnish metal traps) in a grid with ca. 10 m intervals between the traps. The number of rows in a grid as well as the length of rows varied between sites, but the grid area was between 0.5–1.0 ha. One trapping period lasted four nights, and the traps were checked daily.

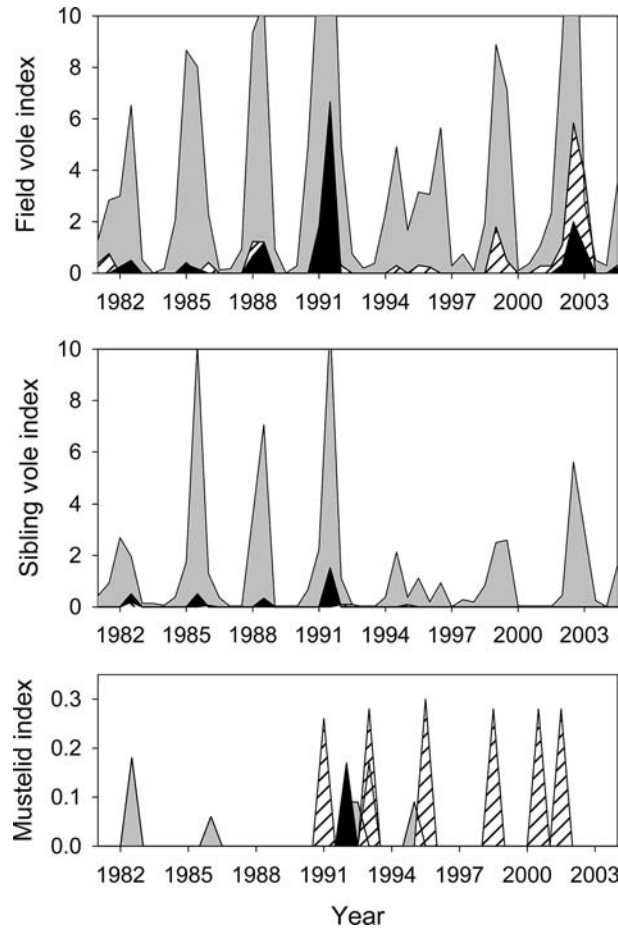


Figure 1. The mean trap indices (individuals per 100 trap nights) of field voles, sibling voles and small mustelids (pooled number of least weasels and stoats) in regular spring and autumn snap trappings in Kauhava and Lapua, western Finland, during 1981–2004. Grey area refers to mean trap indices in agricultural fields, black to mean indices within forests, and slashed to water vole habitats. Peak values have been truncated at index value 10 to emphasise patterns at population lows.

Mixed-flour (wheat + rye) bread was used as bait. Within linear water vole habitats, we used larger traps (commercial Finnish metal traps for rats) and we had to put the traps in a row instead of a grid. During years 1981–1989, these traps were put in one long line per site (two sites). From 1990 onwards, we divided the traps to 3–5 separate places (ditches or rivulets) per site (three sites). The total length of trap line in each of these water vole habitat sites varied between 300–500 m. Each trapping period in a water vole habitat lasted three nights (four nights during 1981–1989), and we used dried apple and mixed-flour bread as bait. Both bait types are suitable for *Microtus* voles

(Myllymäki *et al.*, 1971; Korpimäki and Norrdahl, 1991; Koivunen *et al.*, 1996). The total number of trap nights was 58796 in agricultural fields, 28500 in forests, and 14249 in water vole habitats.

Four species of voles have been trapped in the study area: field vole (mean body mass of trapped voles 27.9 g,  $n=1513$ ), sibling vole (*Microtus rossia-meridionalis*; 24.5 g,  $n=1268$ ), bank vole (*Clethrionomys glareolus*; 17.7 g,  $n=2603$ ), and water vole (141.3 g,  $n=202$ ) (Norrdahl and Korpimäki, 2002). The other vole species have a long local history (Jaarola *et al.*, 1999), but sibling voles are most likely recent immigrants: the species probably arrived to the study area in hay transportations from Karelian Isthmus during the 1940's (Sulkava and Sulkava, 1967). The two *Microtus* species are ecologically fairly similar species, although sibling voles appear to be more colonial and therefore also more vulnerable to patch-searching predators (Norrdahl and Korpimäki, 1993; Norrdahl *et al.*, 2004).

Previous studies have shown that the population dynamics of *Microtus* voles and bank voles are characterized by synchronous multi-annual oscillations, where the dominant period (interval between successive bottlenecks) is 3 years (Klemola *et al.*, 2002b; Korpimäki *et al.*, 2005a). Regular multi-annual population oscillations in bank voles appear to be a mere reflection of the density cycles in *Microtus* species: densities of common predators track the population cycles of *Microtus* voles, and these predators may switch to hunt in habitats occupied by bank voles when the densities of *Microtus* voles decline (Hanski and Henttonen, 1996; Oksanen *et al.*, 2000). Densities of water voles oscillate widely, but there appears to be no significant synchrony with the population fluctuations of smaller voles (Korpimäki *et al.*, 2005a). Yet, during the deepest population declines of smaller voles, also the densities of water voles have declined to low numbers.

For this study, we calculated the mean trap indices (individuals/100 trap nights) of the two *Microtus* voles for each habitat type and season during 1981–2004. In addition, we made a trapping site-level analysis of the presence/absence of the *Microtus* species for the 12 trapping sites used in this study.

The years were classified as increase, peak, or decline years according to the density change of *Microtus* voles from spring to the next spring (in accordance with Krebs and Myers, 1974): in increase years, densities of voles increased whereas, in decline years, densities clearly declined. In peak years, vole populations increased until a density peak in late summer or early autumn and thereafter densities started to decline so that the mean density of voles from spring to the next spring was higher than during either increase or decline years. During 1994–1996 the cyclic pattern was unclear and therefore these years were not classified. In the 3-year cycles studied, population bottlenecks are short but deep. In our classification, decline years reflect the

situation just prior to bottlenecks, whereas increase years reflect the situation from the deepest bottleneck to the start of a new population expansion (i.e. survivors).

Field and sibling voles trapped with snap traps during years 1984–1992 and 1997–1999 were weighed (to the nearest 0.5 g, in the latter period to the nearest 0.1 g), sexed, and their reproductive status was checked using the length (first period) or the mass (latter period) of testes, or width and condition of uterus together with signs of wear in nipples as a criterion for classification (four categories: immature, mature, pregnant, lactating). The number of embryos or, if the animal was not visibly pregnant but had recently given birth, the number of fresh scars in uterus were used as an index of litter size. The body length of the animals (from snout to vent) was measured to the nearest 1 mm. Also the size of embryos (length, from older embryos also weight to the nearest 0.1 g) was measured. As an index of body condition we used the residuals of non-linear regression (polynomial function) between log-transformed body mass and body length (Norrdahl and Korpimäki, 2002). The residuals were calculated separately for both genders and species, and the weight of embryos was subtracted from the weight of the mother before calculations. Voles from water vole habitats were trapped with larger traps than voles from other habitats, and larger traps are less sensitive than smaller traps. According to our experience, also the larger rat traps should capture effectively voles weighing > 20 g, and therefore we included only voles weighing > 20 g to our analyses of body condition and litter size.

#### *Predator data*

Several species of predators hunt voles in the study area. Radio tracking revealed that predation was the main mortality factor (>95% of deaths) in adult *Microtus* voles (Norrdahl and Korpimäki, 1995, 1998). Two species of small mustelid predators, the least weasel (*Mustela nivalis nivalis*) and the stoat (*M. erminea*), were alone responsible for ca. 75% of deaths in radio-tracked voles. The least weasel (mean body mass in northern Finland: males 48 g,  $n=48$ ; females 35 g,  $n=40$ ) can be considered to be a specialist predator of *Microtus* voles, whereas the larger stoat (males 205 g,  $n=74$ ; females 105 g,  $n=26$ ) is a semi-generalist hunting all species of small rodents as well as small birds (Rinta-Jaskari, 1990; Korpimäki *et al.*, 1991).

To get a crude estimate of the relative hunting pressure by small mustelids in the three habitat types, we analysed snow tracking data collected during years 1989–1992 and 1997–2000 in the same municipalities as the vole data. Snow track lines were skied each spring (late February–March) and autumn (November–December) to get an index of carnivore activity. Snow tracks were counted soon after a snowfall, so that tracks made by animals only during the



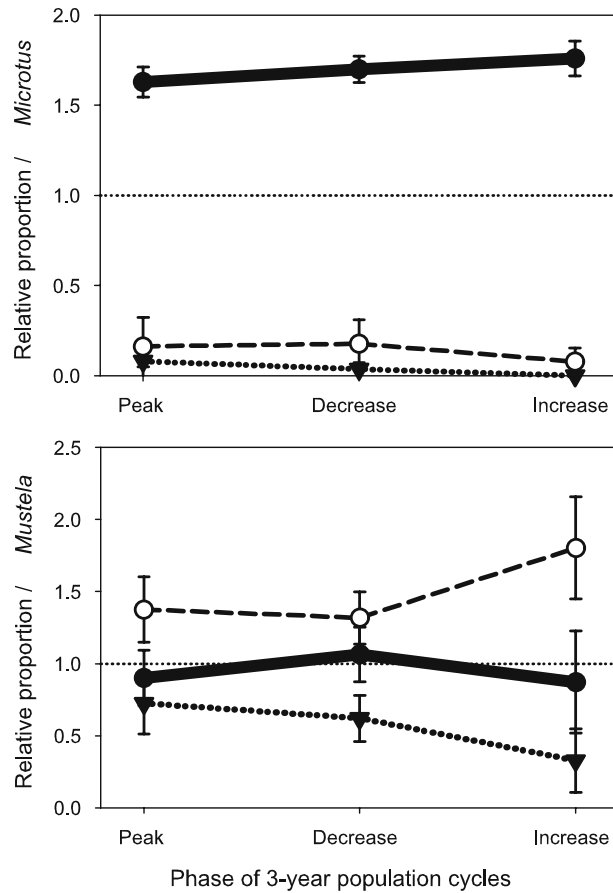


Figure 2. The relative proportion ( $\pm$ S.E.) of *Microtus* spp. voles (upper panel) and *Mustela* spp. carnivores (lower panel) observed in different habitats in the different phases of 3-year vole cycles in Kauhava and Lapua, western Finland. The relative proportion was calculated as the number of individuals observed divided by the number of individuals expected under even distribution. For *Microtus* spp., we used bi-annual snap trapping data collected during years 1981–1993 and 1997–2004. For *Mustela* spp., we used bi-annual snow tracking data collected during years 1989–1993 and 1997–2000. Thick line refers to agricultural fields, dashed line with circles to water vole habitats, and dotted line to forests.

previous one or two nights were visible. Identification of species was based on track dimensions (Korpimäki *et al.*, 1991).

The data was originally collected for larger-scale monitoring and experimental purposes (Korpimäki *et al.*, 2002 and unpublished data), and we had to reanalyse the original field data to get habitat-specific predator indices. We used data collected around 20 agricultural field areas (each 2.5–5 km<sup>2</sup>). At each site, six lines (length 0.5–2.2 km) per season were skied, and the lines as well as all observed predator tracks were drawn on a map. Based on the maps, we divided the original track lines to parts along habitat boundaries. For each

main habitat type (agricultural fields, water vole habitats, and forest edges) including at least 0.3 km of continuous track line, we calculated predator activity indices (individuals per 300 m of track line) from the central 300 m of the longest continuous part of the track line. Small rodent tracks were counted but not mapped, and therefore we had to use the same mean rodent index value (small rodent tracks per 300 m of track line) for all parts of a track line. A crude estimate of predator-prey ratios was calculated by dividing the habitat-specific mustelid predator index (*Mustela* spp. individuals per 300 m of track line) with the rodent index. After counting habitat-specific index values for each track line, we calculated habitat-specific mean values for each area, and used these mean values in our analyses.

As we only had tracking data from snowy periods, we also calculated the mean catch index of small mustelids (individuals/100 trap nights) in each habitat type. The small mustelids trapped were incidental by-catch of the regular vole trappings. As the number of small mustelids captured during the study period was low (15 individuals), we also calculated the same catch indices of small mustelids from a larger trapping data collected by the members of the Ornithological Society of Suomensekä during 1973–2003. This larger data has been collected from western Finland using approximately same methods as those used in our study (for details, see Huitu *et al.*, 2003). The total number of trap nights in the data collected by the ornithological society was 117862 in agricultural fields, 83083 in forests, and 17679 in water vole habitats.

## Results

### *Voles*

During the study period (years 1981–2004), both field voles and sibling voles were captured in all three main habitats: agricultural fields, forests, and along watercourses (water vole habitats) (Figure 1). Mean abundances of *Microtus* voles in agricultural fields (including uncultivated grasslands) were clearly higher than expected under even distribution, whereas the opposite was true for the other habitats (Figure 2). Mean density indices in agricultural fields were 8–12 times (field vole) or 24–36 times (sibling vole) higher than in forests or water vole habitats (Table 1), although it should be kept in mind that the trap indices from water vole habitats were not fully comparable to the indices from other habitats because of larger traps and different layout of trap stations. Density indices of *Microtus* voles in forests and water vole habitats were positively related to densities in agricultural fields (Table 1). We did not observe significant phase-related differences in the habitat-level distribution of *Microtus* voles (Figure 2). However, during the lowest population bottlenecks,

*Table 1.* The mean trap indices (individuals per 100 trap nights) of field voles, sibling voles and small mustelids (pooled number of least weasels and stoats) in regular spring and autumn snap trappings at Kauhava and Lapua, western Finland, during 1981–2004. Trapping sites were situated in agricultural fields, forests, or linear water vole habitats along ditches and rivulets. *r* refers to Pearson correlation coefficient between the mean trap indices from forest or water vole habitat vs. the mean trap index of the same species in agricultural fields

Species	Habitat	Mean	S.E.	<i>N</i>	<i>r</i>	<i>p</i>
Field vole	Agricultural fields	3.60	0.63	49	–	–
	Forests	0.31	0.15	49	0.70	<0.0001
	Water vole habitats	0.46	0.15	48	0.68	<0.0001
Sibling vole	Agricultural fields	1.39	0.34	49	–	–
	Forests	0.06	0.03	49	0.76	<0.0001
	Water vole habitats	0.04	0.02	48	0.37	0.01
Mustelids*	Agricultural fields	0.011	0.005	49	–	–
	Forests	0.007	0.005	49	–	–
	Water vole habitats	0.035	0.013	48	–	–

\* Correlation coefficients were not calculated for mustelids because of low numbers of trapped individuals.

field voles and sibling voles were captured only from agricultural fields (Figure 1). Also long-term presence/absence data from 12 trapping sites indicates that the two vole species were widely distributed at highest population peaks, but occurred only in agricultural fields at population lows (Table 2). Within the agricultural trapping sites, the distribution pattern varied from population low to another: the proportion of trapping periods with no individuals of the species was clearly higher at the level of individual trapping sites (field vole: range 0.23–0.41; sibling vole: 0.48–0.71) than in the pooled data (field vole: 0.04; sibling vole: 0.27) (Table 2).

The mean body condition indices of field voles were more dependent on season than on habitat type (Table 3). However, the seasonal pattern differed between habitats: within and around agricultural fields the seasonal peak in mean body condition was in autumn, whereas in the other habitats the seasonal peak was in summer (Table 3; Figure 3). The litter size of field voles appeared to be better explained by season and body condition index than by habitat (Table 3), although the power of this test was hampered by the low sample sizes outside agricultural fields ( $n = 19$  litters for forests,  $n = 5$  for water vole habitats, and  $n = 54–177$  for other habitats: small ditches within cultivated fields, grasslands, and small ditches between cultivated fields and grasslands).

### *Predators*

Although trapping indices of field voles and sibling voles were much higher in agricultural fields than in the other habitats, the distribution of the main predators, small mustelids, did not follow the same pattern. Both mean snow



A more detailed analysis of habitat-specific differences in predator indices revealed that both mustelid predator index and predator-to-prey ratio index were generally higher in water vole habitats than in agricultural fields: in 15 out of 16 cases mean mustelid index was higher in water vole habitats than in agricultural fields, and in 12 out of 16 cases also the predator-to-prey ratio was higher in water vole habitats than in agricultural fields (Figure 5). These differences were mainly due to stoats: habitat type did not explain a significant proportion of variation in the activity indices of least weasels, but explained much of the variation in the case of stoats (Table 4). However, the interaction term habitat by season was significant for least weasels (Table 4): in spring, the mean activity index for least weasels was higher in forests than in agricultural fields or water vole habitats, whereas the opposite was true in autumn (Figure 4). Despite seasonal differences in habitat-level distribution of least weasel activity, we did not observe significant phase-related differences in the habitat-level distribution of small mustelids (Figure 2). For other carnivore species, either habitat or habitat by season interaction did not explain a significant proportion of variation in the activity indices. Yet, the few American mink and otters we observed were always in water vole habitats.

## Discussion

### *Sub-optimal habitats offer no refuge for *Microtus voles**

According to our long-term trapping and tracking data, *Microtus* vole abundances were continuously higher in agricultural fields and grasslands than in

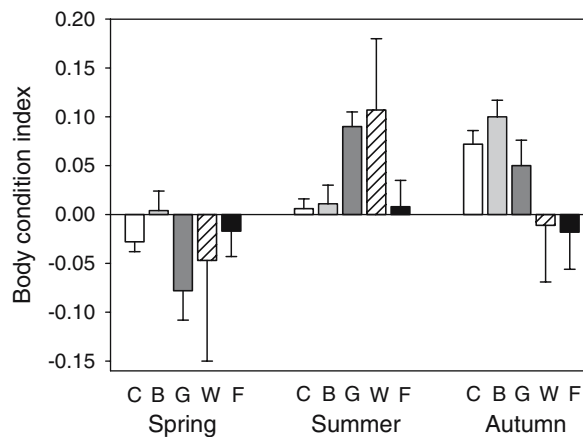


Figure 3. The seasonal mean ( $\pm$  S.E.) body condition index of field voles in different habitats in Kauhava and Lapua, western Finland, during years 1984–1992 and 1997–1999. Spring refers to March–April, summer to May–August, and autumn to September–November. The habitats denoted with letters are: C=cultivated fields (mainly spring-sown crops), B=ditches between cultivated fields and grasslands, G=grasslands (including both perennial hay fields and uncultivated grasslands), W = wet but grassy water vole habitats, and F=forests.

Table 3. Analysis of variance tables for the effect of habitat, season, their interaction, and sex or body condition index (residual of sex-specific non-linear regression between body mass and body length) on (a) the body condition index, or (b) the litter size of field voles. For a detailed description of habitats and seasons, see Figure 3. df refers to degrees of freedom, f–F-statistics, and *p* to the probability of F-statistics

	df	Sum of squares	Mean square	f	<i>p</i>
<i>a. Body condition index</i>					
Habitat	4	0.13	0.03	1.28	0.28
Season	2	0.19	0.09	3.56	0.03
Habitat × Season	8	0.69	0.09	3.30	0.001
Sex	1	0.01	0.01	0.48	0.49
Error	1098	28.63	0.03		
<i>b. Litter size</i>					
Habitat	4	10.27	2.57	1.40	0.23
Season	2	13.56	6.78	3.71	0.03
Habitat × Season	7	15.52	2.22	1.21	0.30
Body condition index	1	9.70	9.70	5.31	0.02
Error	298	544.66	1.83		

supposedly sub-optimal habitats, forests and wet habitats inhabited by water voles (water vole habitats). We did not observe marked phase-related differences in the habitat-level distribution of the two voles, although during deepest population lows, *Microtus* voles were trapped only from the supposed prime habitats (agricultural fields with grassy vegetation). Our results did not support our first prediction (there should be phase-related differences in the distribution of *Microtus* voles between different habitats), and even less our second prediction (water vole habitats should have proportionally more *Microtus* voles in the low phase of the vole cycle than in other phases of the population cycle).

In contrast to main prey densities, mean predator activity indices were almost as high in forests as in agricultural fields, and even higher in water vole habitats. Also mean predator-to-prey ratio indices appeared to be higher in water vole habitats than in agricultural fields. We did not observe marked phase-related differences in the habitat-level distribution of carnivore activity. Thus, our results did not either support our third prediction (wet water vole habitats should sustain less small mustelid predators than the more optimal *Microtus* vole habitats, meadows and fields with grassy vegetation).

Although our results are based on crude indices of prey and predator abundances, the picture given by different indices was clear and consistent. Therefore we can with relative confidence refute the suggestion that wet water vole habitats (or forests) would provide a habitat-level refuge from the action of predators at population bottlenecks of *Microtus* voles (Ylönen *et al.*, 2003).

There are two main reasons why the hypothesis of Ylönen *et al.* (2003) did not work in our study system. First, the model presented in the paper (a general model for a specialist predator and a prey species with risky and safe habitats)

included an assumption that predators can hunt their prey to extinction in optimal habitats, whereas in the sub-optimal habitats prey are vulnerable only when density exceeds a critical threshold (in the model,  $M^*$ ) (Ylönen *et al.*, 2003). This assumption obviously does not hold in our study system: predators can and apparently do eradicate *Microtus* voles from patches of sub-optimal habitats. Second, the general model included only one specialist predator and one prey species. This simplification may lead to misleading results in multi-species assemblages, where the distribution and habitat-level survival probability or offspring production of the focal species may depend on the distribution of competitors or other prey/predator species. At least in northern Europe, the most productive habitat patches as well as the wet but grassy habitat patches are often occupied by superior competitors (water vole or root vole *Microtus oeconomus* in the case of field vole, larger mustelids in the case of weasels; e.g. Myllymäki, 1977b; Henttonen *et al.*, 1977; Henttonen and Hansson, 1984; Erlinge and Sandell, 1988; Aunapuu and Oksanen, 2003). Interference competition with larger species, or predation by larger predators, may have a strong impact on habitat selection, reproductive output, or survival prospects.

For a field vole, a move from grassy meadows and fields to wet water vole (or root vole) habitats may be a shift from the side of Scylla to the side of Charybdis: a least weasel may kill most voles in a patch it encounters, but a stoat may be an even worse option. When vole densities decline, least weasels

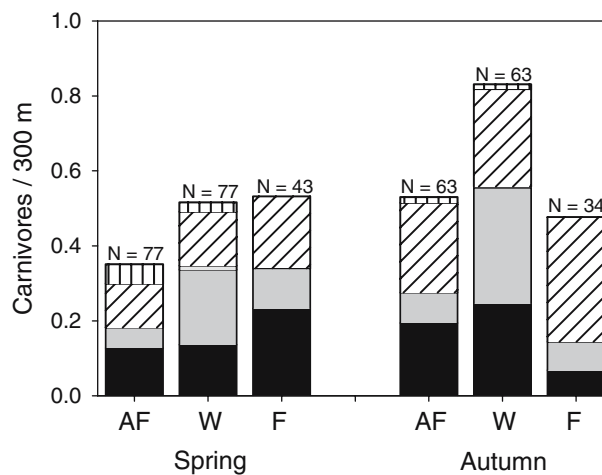


Figure 4. The seasonal mean snow track indices (individuals/300 m of snow track line) of carnivores in different main habitats in Kauhava and Lapua, western Finland, during 1989–1993 and 1997–2000. Spring refers to February–March, autumn to November–December (in few cases early January). Habitats denoted with letters are: AF = agricultural fields, W = water vole habitats along watercourses, and F = forests and forest edges. Black parts refer to least weasels, grey to stoats, pale grey to minks and otters, slashed to red fox, and vertical lining to cats. Sample size ( $N$ ) equals the number of agricultural areas (each 2.5–5 km<sup>2</sup>) with the habitat type studied times the number of years with tracking within the habitat type in the area.

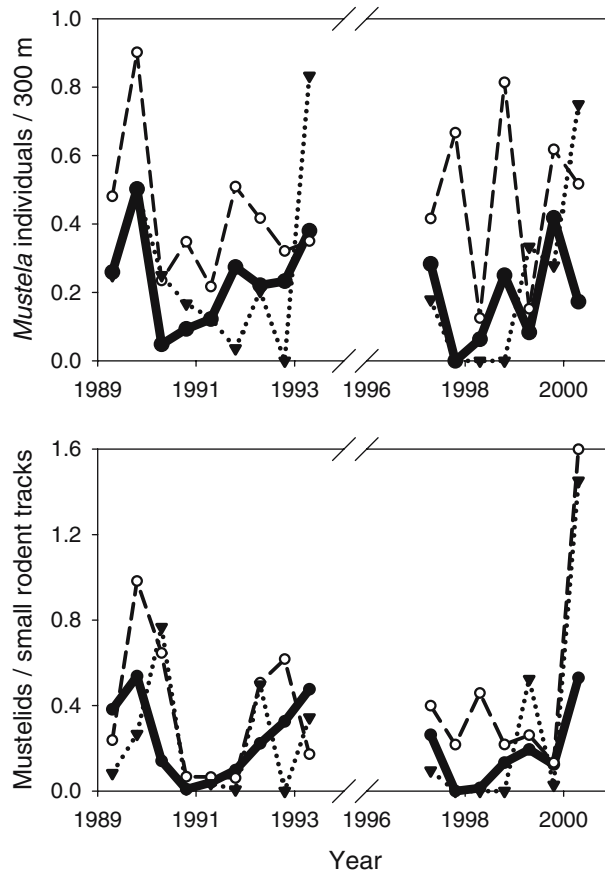


Figure 5. The mean snow track indices of small mustelids (individuals/300 m of snow track line; upper panel) and the mean predator-to-prey ratio indices (track index of mustelids divided by the number of rodent tracks/300 m of snow track line; lower panel) in different main habitats in Kauhava and Lapua, western Finland, during 1989–1993 and 1997–2000. Thick line with dots refers to agricultural fields, slashed line with circles to water vole habitats, and dotted line with triangles to forests and forest edges.

change from residents to nomads, travelling even several kilometres per day in their search of prey patches (Oksanen *et al.*, 1992; Oksanen and Henttonen, 1996). When a least weasel encounters a patch of voles, it probably stops to hunt. However, the weasel may not be able to extirpate all voles living in the patch because of two constraints. First, a weasel is far from a perfect predator: a high percent of attacks are unsuccessful (Jedrzejewski *et al.*, 1992). Second, the energetic needs of a least weasel are so high, that even 16-h intervals between meals may be fatal (Brown and Lasiewski, 1972; Gillingham, 1984). When distances between prey patches are long, a weasel should leave a patch after a few hours of unsuccessful hunting, or it will have a high risk to starve before it will find another prey patch and manage to catch a prey from that



Table 4. Analysis of variance tables for the effect of habitat, season, and their interaction on the mean snow track index of (a) least weasels, or (b) stoats. For a detailed description of habitats and seasons, see Figure 4

	df	Sum of squares	Mean square	f	p
<i>a. Least weasel</i>					
Habitat	2	0.10	0.05	0.77	0.46
Season	1	0.00	0.00	0.03	0.87
Habitat × Season	2	0.97	0.48	7.59	0.0006
Error	344	21.95	0.06		
<i>b. Stoat</i>					
Habitat	2	2.63	1.32	24.42	<0.0001
Season	1	0.10	0.10	1.82	0.18
Habitat × Season	2	0.26	0.13	2.41	0.09
Error	344	18.54	0.05		

patch. This should make the stops by weasels in prey patches short (as also suggested by Koivisto and Pusenius, 2003). The temporary nature of weasel residence may be illustrated by the results obtained between 1992 and 1994 in our study area: we radio-collared a total of 11 least weasels, and only three of them stayed in the vicinity (< 1 km) of the trapping site for more than 2 weeks; the rest disappeared or were killed by avian predators within a few days (mean  $\pm$  S.E. =  $3.9 \pm 0.6$  tracking days,  $N=8$ ; K. Norrdahl and E. Korpimäki, unpublished data). In contrast, the larger stoat survives longer periods without food, and is able to utilize many other prey types (other small rodents and small birds; Korpimäki *et al.*, 1991; Aunapuu and Oksanen, 2003). Therefore, a stoat living in a water vole (or root vole) patch is more likely to kill all field voles from the habitat patch than a least weasel.

#### *Short-term vs. long-term differences in habitat quality*

We observed significant habitat-level differences in the body condition of field voles and in the distribution of their main predators, weasels and stoats. However, the relative order of habitat quality appeared to change from spring to autumn, except in the case of stoats which were continuously more abundant in water vole habitats than in the other habitats. The apparently stereotypic habitat selection behaviour in stoats in comparison to the more flexible habitat use in least weasels is in accordance with previous observations made in northern Norway (Aunapuu and Oksanen, 2003).

The observed timing of seasonal peak in the body condition of field voles may be explained by the seasonal pattern of food availability. The main plants cultivated in the study area are spring-sown cereals. Sowing is done in May, grain crop is harvested in August–October, and most agricultural fields are ploughed in September–November. Therefore the quantity of food (total plant

biomass as well as the quantity of seeds) in cereal fields increases throughout summer towards a seasonal peak in early autumn. In grasslands and non-cultivated habitats, such as water vole habitats, the seasonal peak of grass and herb growth is in May–June. Later the quality of many food plants appears to decline (e.g. Batzli, 1985; Huhtanen and Jaakkola, 1994; Lesage *et al.*, 2000; Gustavsson and Martinsson, 2004). Thus, the timing of the seasonal peak in the quantity of high-quality food is different in agricultural fields and other habitats. The observed timing of seasonal peaks in the body condition of field voles appears to reflect this difference well.

In autumn, least weasel activity indices were, on average, lower in forests than in the other habitats, whereas the opposite was true in spring. A possible explanation for this observation is that, as the densities of main prey (*Microtus* voles) declined from autumn to spring, weasels partly switched from habitats occupied by main prey to habitats with more alternative prey (bank voles and small birds). Whatever the actual cause behind the observation was, the common lesson given by the field vole and weasel data is that short-term data can give a misleading picture of long-term patterns. In our study system, marked seasonal habitat-level differences appeared to negate each others in longer time scales. In other ecosystems the pattern may be the same, or it may be the opposite: differences that are of minor importance in seasonal time scale may accumulate so that they play an important role in evolutionary time scales. Whatever the situation, speculations on what happens in longer (evolutionary) time scales may lead to completely wrong tracks if they are based on observations collected during a very restricted time period.

#### *Adaptive anti-predator strategy for a field vole-type prey*

We did not observe significant phase-dependent differences in the habitat-level distribution of *Microtus* voles. If any habitat type was more important for long-term survival than others, our results suggest that it was grassy agricultural fields, which are supposed to be optimal habitat for these species. During the lowest population bottlenecks, field voles and sibling voles were captured only from agricultural fields. However, within this main habitat type, there appeared to be no permanent refuges: the distribution of voles between the trapping sites varied from one bottleneck to another. This suggests that survival through bottlenecks is at least partly determined by chance events. This conclusion has implications for the optimality of different anti-predator strategies.

Many previous predator-prey models including predator-induced anti-predator adaptations have assumed that the most effective anti-predator adaptations are very costly, such as extremely low mobility or a relatively long delay in reproduction (Oksanen and Lundberg, 1995; Kaitala *et al.*, 1997; Mappes and Ylönen, 1997). An alternative view is that high temporal variation

in predation risk should favour rapid switches between anti-predator and feeding behaviours (the predation risk allocation hypothesis; Lima and Bednekoff, 1999). At least two observations indicate that the optimal anti-predator strategy for a field-vole type prey should be closer to the latter alternative. First, the temporary nature of predator residence in systems with patch-searching predators suggests that short-term anti-predator responses to the presence of predators may be enough to bring a prey individual through the most risky periods. Short-term anti-predator responses should also give the advantage that the prey can utilize periods between predator visits better than if the anti-predator responses would be longer-term, and the individual may also switch rapidly from one predator avoidance strategy to another strategy (e.g. terminal investment, or dispersal) if local predation risk stays at high levels for prolonged periods. Second, in radio telemetry studies performed within our study areas, lowest predation risk was not associated with lowest mobility but with intermediate mobility (Banks *et al.*, 2000). If intermediate mobility is an effective behavioural strategy for predator avoidance, a prey individual may maximize its survival prospects without paying a high price in terms of food gain or encounters with the opposite sex. A small or moderate reduction in current reproductive investment may be compensated with increased survival prospects, especially when the probability that current offspring would survive and reproduce successfully is low.

An important point to note in the probable effectiveness of short-term/low-cost anti-predator strategies is that this kind of behavioural strategies should work well in most phases of population growth. The frequency of predator visits is probably much higher when vole populations are declining than when they are increasing, but for a short-lived vole individual the current risk to be depredated (i.e. presence of a predator) is probably the most important cue to use in behavioural decisions (Ylönen, 1994; Lima and Bednekoff, 1999; Koivisto and Pusenius, 2003). If the same behavioural strategy works well in population bottlenecks than in the other phases of population dynamics, there is no need to maintain special adaptations for infrequent bottleneck situations. This would be especially true if the survival probability through periodic population bottlenecks is largely determined by chance events, as our results suggest.

## Conclusions

We did not find support for our predictions that there should be marked phase-related differences in the habitat-level distribution of *Microtus* voles, or that otherwise sub-optimal habitats would provide a spatial refuge from the predation risk by the main predator(s). The distribution of voles between the trapping sites varied from one bottleneck to another. These results suggest that

survival through bottlenecks is at least partly determined by chance events, rather than habitat- or site-level refuges. To conclude, our results are in disagreement with the suggestion that field voles survive through population bottlenecks in otherwise sub-optimal habitats, especially in wet habitats occupied by water voles (Ylönen *et al.*, 2003).

Our study system included relatively short-lived prey hunted by nomadic or widely ranging predators. Based on our present and previous results, we propose that in this kind of systems selection should favour short-term/low-cost anti-predator behaviours rather than adaptations leading to longer-term reduction in foraging or reproductive activities, in accordance with the predation risk allocation hypothesis (Lima and Bednekoff, 1999). A short-term reduction in foraging activity or reproductive effort may be enough to bring the prey individual through the most risky period. This strategy should work well in most phases of population growth. As short-term/low-cost anti-predator behaviours may increase survival prospects as efficiently as more costly anti-predator adaptations, and the same behavioural adaptations may work as well in bottleneck situations as in most other phases of population growth, there is no apparent need to maintain special adaptations to bottleneck situations that occur at infrequent intervals.

Although our results indicated that the hypothesis by Ylönen *et al.* (2003) is not valid in a system with voles and small mustelid predators, this does not mean that the general model presented in the paper should be totally rejected. We propose that the general model presented by Ylönen *et al.* (2003) should only be considered in a limited set of ecosystems, where the main predators are relatively large-sized or avian, and cannot therefore enter all habitats where prey can live. A model ecosystem might include a mixture of open vegetation and thicket, prey which can utilize both vegetation types and predators which cannot hunt effectively in thicket. If thicket provides less food resources for prey than open habitats, the system might fulfil the critical assumptions of the model by Ylönen *et al.* (2003).

Our results also serve as an example warning of the potential hazards of extrapolating conclusions based on short-term data to evolutionary time scales. In our study system, significant seasonal differences in relative habitat quality appeared to negate each others in longer time scales. This suggests that the significant habitat-level differences we observed in short-term data played a minor if any role in evolutionary meaningful time scales.

### **Acknowledgements**

We thank Mikko Hast, Ossi Hemminki, Timo Hyrsky, Mikko Hänninen, Tero Klemola, Jouni Klinga, Minna Koivula, Jesse Laaksonen, Olli Norrdahl and Jari Valkama for help in the field work, and Otso Huitu, Tero Klemola and

two anonymous reviewers for comments on the ms. The study was financially supported by the Academy of Finland (grant nos. 36207, 71079 and 50777 to KN, and grant nos. 8202013, 880696 and 8206140 to EK).

## References

- Aunapuu, M. and Oksanen, T. (2003) Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. *Evol. Ecol.* **17**, 371–392.
- Banks, P., Norrdahl, K. and Korpimäki, E. (2000) Nonlinearity in the predation risk of prey mobility. *Proc. R. Soc. Lond. B* **267**, 1621–1625.
- Banks, P.B., Norrdahl, K., Nordström, M. and Korpimäki, E. (2004) Dynamic impacts of feral mink predation on vole metapopulations in the outer archipelago of the Baltic Sea. *Oikos* **105**, 79–88.
- Batzli, G.O. (1985) Nutrition. In R.H. Tamarin (ed.) *Biology of New World Microtus* Special Publication No. 8, American Society of Mammalogists, pp. 779–811.
- Brown, J.H. and Lasiewski, R.C. (1972) Metabolism of weasels: the cost of being long and thin. *Ecology* **53**, 939–943.
- Clutton-Brock, T.H. (1984) Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* **123**, 212–229.
- Elton, C. (1924) Periodic fluctuations in the numbers of animals: their causes and effects. *Br. J. Exp. Biol.* **2**, 119–163.
- Ergon, T., Lambin, X. and Stenseth, N.C. (2001) Life-history traits of voles in a fluctuating population respond to the immediate environment. *Nature* **411**, 1043–1045.
- Erlinge, S. and Sandell, M. (1988) Coexistence of stoat, *Mustela erminea*, and weasel, *Mustela nivalis*: social dominance, scent communication and reciprocal distribution. *Oikos* **53**, 242–246.
- Faber, J. and Ma, W.C. (1986) Observations on seasonal dynamics in diet composition of the field vole, *Microtus agrestis*, with some methodological remarks. *Acta Theriol.* **31**, 479–490.
- Gilg, O. (2002) The summer decline of the collared lemming (*Dicrostonyx groenlandicus*) in high arctic Greenland. *Oikos* **99**, 499–510.
- Gillingham, B.J. (1984) Meal size and feeding rate in the least weasel (*Mustela nivalis*). *J. Mammal.* **65**, 517–519.
- Gustavsson, A.-M. and Martinsson, K. (2004) Seasonal variation in biochemical composition of cell walls, digestibility, morphology, growth and phenology in timothy. *Euro. J. Agronomy* **20**, 293–312.
- Hakkarainen, H., Mykrä, S., Kurki, S., Korpimäki, E., Nikula, A. and Koivunen, V. (2003) Habitat composition as a determinant of reproductive success of Tengmalm's owls under fluctuating food conditions. *Oikos* **100**, 162–171.
- 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., Henttonen, H., Korpimäki, E., Oksanen, L. and Turchin, P. (2001) Small-rodent dynamics and predation. *Ecology* **82**, 1505–1520.
- Hansson, L. (1971) Habitat, food and population dynamics of the field vole *Microtus agrestis* (L.) in south Sweden. *Viltrevy* **8**, 268–378.
- Hansson, L. and Henttonen, H. (1988) Rodent dynamics as community processes. *Trends Ecol. Evol.* **3**, 195–200.
- Henttonen, H. and Hansson, L. (1984) Interspecific relations between small rodents in European boreal and subarctic environments. *Acta Zool. Fennica* **172**, 61–65.
- Henttonen, H., Kaikusalo, A., Tast, J. and Viitala, J. (1977) Interspecific competition between small rodents in subarctic and boreal ecosystems. *Oikos* **29**, 581–590.
- Huhtanen, P.P. and Jaakkola, S. (1994) Influence of grass maturity and diet on ruminal dry matter and neutral detergent fibre digestion kinetics. *Arch. Tierernähr.* **47**, 153–167.

- Huitu, O., Norrdahl, K. and Korpimäki, E. (2003) Landscape effects on temporal and spatial properties of small rodent population fluctuations. *Oecologia* **135**, 209–220.
- Jaarola, M., Tegelström, H. and Fredga, K. (1999) Colonization history in Fennoscandian rodents. *Biol. J. Linn. Soc.* **68**, 113–127.
- Jedrzejewski, W. and Jedrzejewska, B. (1996) Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. *Acta Theriol.* **41**, 1–34.
- Jedrzejewski, W., Jedrzejewska, B. and McNeish, E. (1992) Hunting success of the weasel *Mustela nivalis* and escape tactics of forest rodents in Bialowieza National Park. *Acta Theriol.* **37**, 319–328.
- Kaitala, V., Mappes, T. and Ylönen, H. (1997) Delayed female reproduction in equilibrium and chaotic populations. *Evol. Ecol.* **11**, 105–126.
- Klemola, T., Koivula, M., Korpimäki, E. and Norrdahl, K. (1997) Small mustelid predation slows population growth of *Microtus* voles: a predator reduction experiment. *J. Anim. Ecol.* **66**, 607–614.
- Klemola, T., Korpimäki, E. and Koivula, M. (2002a) Rate of population change in voles from different phases of the population cycle. *Oikos* **96**, 291–298.
- Klemola, T., Tanhuanpää, M., Korpimäki, E. and Ruohomäki, K. (2002b) Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos* **99**, 83–94.
- Koivisto, E. and Pusenius, J. (2003) Effects of temporal variation in the risk of predation by least weasel (*Mustela nivalis*) on feeding behaviour of field vole (*Microtus agrestis*). *Evol. Ecol.* **17**, 477–489.
- Koivunen, V., Korpimäki, E., Hakkarainen, H. and Norrdahl, K. (1996) Prey choice of Tengmalm's owls (*Aegolius funereus funereus*): preference for substandard individuals? *Can. J. Zool.* **74**, 816–823.
- Korpimäki, E. and Krebs, C.J. (1996) Predation and population cycles of small mammals. *BioScience* **46**, 753–763.
- 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 Wiehn, J. (1998) Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos* **83**, 259–272.
- Korpimäki, E., Norrdahl, K. and Rinta-Jaskari, T. (1991) Responses of stoats and least weasels to fluctuating voles abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia* **88**, 552–561.
- Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. and Stenseth, N.C. (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., Oksanen, L., Oksanen, T., Banks, P.B., Batzli, G.O. and Henttonen, H. (2003) Vole cycles and predation. *Trends Ecol. Evol.* **18**, 494–495.
- Korpimäki, E., Norrdahl, K., Huitu, O. and Klemola, T. (2005a) Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proc. R. Soc. Lond.* **B272**, 193–202.
- Korpimäki, E., Oksanen, L., Oksanen, T., Klemola, T., Norrdahl, K. and Banks, P.B. (2005b) Vole cycles and predation in temperate and boreal zones of Europe. *J. Anim. Ecol.* (in press).
- Krebs, C.J. and Myers, J.H. (1974) Population cycles in small mammals. *Adv. Ecol. Res.* **8**, 267–399.
- Lesage, L., Crete, M., Huot, J. and Quillet, J.P. (2000) Quality of plant species utilized by northern white-tailed deer in summer along a climatic gradient. *Ecoscience* **7**, 439–451.
- Lima, S.L. and Bednekoff, P.A. (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* **153**, 649–659.
- Mappes, T. and Ylönen, H. (1997) Reproductive effort of female bank voles in a risky environment. *Evol. Ecol.* **11**, 591–598.
- Mappes, T., Koskela, E. and Ylönen, H. (1998) Breeding suppression in voles under predation risk of small mustelids: laboratory or methodological artifact? *Oikos* **82**, 365–369.
- Myllymäki, A. (1977a) Demographic mechanism in the fluctuating populations of the field vole *Microtus agrestis*. *Oikos* **29**, 468–493.

- Myllymäki, A. (1977b) Interactions between the field vole *Microtus agrestis* and its microtine competitors in Central-Scandinavian populations. *Oikos* **29**, 570–580.
- Myllymäki, A., Paasikallio, A. and Häkkinen, U. (1971) Analysis of a 'standard trapping' of *Microtus agrestis* (L.) with triple isotope marking outside the quadrat. *Ann. Zool. Fenn.* **8**, 22–34.
- Norrdahl, K. and Korpimäki, E. (1993) Predation and interspecific competition in two *Microtus* voles. *Oikos* **66**, 149–158.
- Norrdahl, K. and Korpimäki, E. (1995) Mortality factors in a cyclic vole population. *Proc. R. Soc. Lond. B* **261**, 49–53.
- Norrdahl, K. and Korpimäki, E. (1998) Does mobility or sex of voles affect risk of predation by mammalian predators?. *Ecology* **79**, 226–232.
- Norrdahl, K. and Korpimäki, E. (2000) The impact of predation risk from small mustelids on prey populations. *Mammal Rev.* **30**, 147–156.
- Norrdahl, K. and Korpimäki, E. (2002) Changes in individual quality during a 3-year population cycle of voles. *Oecologia* **130**, 239–249.
- Norrdahl, K., Heinilä, H., Klemola, T. and Korpimäki, E. (2004) Predator-induced changes in population structure and individual quality of *Microtus* voles: a large-scale field experiment. *Oikos* **105**, 312–324.
- Oksanen, L. and Lundberg, P. (1995) Optimization of reproductive effort and foraging time in mammals: the influence of resource level and predation risk. *Evol. Ecol.* **9**, 45–56.
- Oksanen, L. and Oksanen, T. (2000) The logic and realism of the hypothesis of exploitation ecosystems. *Am. Nat.* **155**, 703–723.
- Oksanen, T. and Henttonen, H. (1996) Dynamics of voles and small mustelids in the taiga landscape of northern Fennoscandia in relation to habitat quality. *Ecography* **19**, 432–443.
- Oksanen, T., Oksanen, L. and Norberg, M. (1992) Habitat use of small mustelids in north Fennoscandian tundra: a test of the hypothesis of patchy exploitation ecosystems. *Ecography* **15**, 237–244.
- Oksanen, T., Oksanen, L., Jedrzejewski, W., Jedrzejewska, B., Korpimäki, E. and Norrdahl, K. (2000) Predation and the dynamics of the bank vole *Clethrionomys glareolus*. *Pol. J. Ecol.* **48**(Suppl.), 197–217.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *Am. Nat.* **132**, 652–661.
- Rinta-Jaskari, T. (1990) *Kärpän (Mustela erminea) ja lumikon (Mustela nivalis) talvirivinto eteläpohjalaisella peltolakeudella: vuosittainen, lajisäisäinen ja lajienvälinen vaihtelu*. MSc thesis Dept. of Zoology, Univ. of Oulu, Finland.
- Ruxton, G.D. and Lima, S.L. (1997) Predator-induced breeding suppression and its consequences for predator-prey population dynamics. *Proc. R. Soc. Lond. B* **264**, 409–415.
- Steen, H. (1995) Untangling the causes of disappearance from a local population of root voles, *Microtus oeconomus*: a test of the regional synchrony hypothesis. *Oikos* **73**, 65–72.
- Stenseth, N.C., Hansson, L. and Myllymäki, A. (1977) Food selection of the field vole *Microtus agrestis*. *Oikos* **29**, 511–524.
- Sulkava, S. and Sulkava, P. (1967) On the small-mammal fauna of Southern Ostrobothnia. *Aquilo Ser. Zool.* **5**, 18–29.
- Sundell, J. and Norrdahl, K. (2002) Body size-dependent refuges in voles: an alternative explanation of the Chitty effect. *Ann. Zool. Fenn.* **39**, 325–333.
- Turchin, P. and Batzli, G.O. (2001) Availability of food and the population dynamics of arvicoline rodents. *Ecology* **82**, 1521–1534.
- Turchin, P., Oksanen, L., Ekerholm, P., Oksanen, T. and Henttonen, H. (2000) Are lemmings prey or predators? *Nature* **405**, 562–565.
- van Horne, B. (1983) Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* **47**, 893–901.
- Wolff, J.O. (2003) Laboratory studies with rodents: facts or artifacts? *BioScience* **53**, 421–427.
- Ylönen, H. (1994) Vole cycles and antipredatory behaviour. *Trends Ecol. Evol.* **9**, 426–430.
- Ylönen, H., Pech, R. and Davis, S. (2003) Heterogeneous landscapes and the role of refuge on the population dynamics of a specialist predator and its prey. *Evol. Ecol.* **17**, 349–369.