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Overwinter population change of small mammals in southern Finland

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Patterns and variations in the overwinter population change of small mammals (shrews, voles, and mice) were studied on the basis of long-term data collected using snap trapping in autumn and spring 1981–2005 in southern Finland. In particular, attempts were made to reveal possible negative effects of mild winters on the wintering success of populations. The winter decline in density varied considerably both within and between species and groups. It was not significantly steeper in the coastal than in inland vole populations, but there were significant differences between the local populations of the southern coast. Small mammals seemed to overwinter more successfully in forests than in fields, and the negative effects of mild winters seemed to impact the populations of field habitats. The direct contribution of high ambient temperatures on the overwinter population change seemed to be largely restraining, but especially so in the depth of winter. There seemed to be indirect inverse effects involved. Population density exhibited only minor effects.

Introduction

Most animals live in a seasonal environment, where the number of individuals at the beginning of any one season is dependent on the survivors from the preceding season (e.g., Fretwell 1972, Boyce 1979). Winter is an obvious bottleneck for the long-term existence of populations, which in the harsh environmental conditions of high latitudes are confronted with especially hard challenges. Despite minor and occasional winter reproduction (Pucek *et al*. 1993, Norrdahl & Korpimäki 2002), small mammal populations, in general, only decline during the coldest period of the year. Density-dependent factors such as competition for food and predation, as well as density-independent climatic conditions govern winter mortality (e.g., Hansen *et al*. 1999, Merritt *et al*. 2001, Aars & Ims 2002, Lima *et al*. 2002, Stenseth *et al*. 2002, Hörnfeldt 2004). The winter decline generally accelerates with increasing winter length and severity (Hansson & Henttonen 1985, Dokuchaev 1989, Aars & Ims 2002), primarily due to food shortages (Stenseth *et al*. 2002, Huitu *et al*. 2003) or predation (Hanski *et al*. 2001, Korpimäki *et al*. 2002).

Prolonged unbroken periods of frost or snow are suggested to have a more negative impact on animals than several shorter periods interspersed with mild spells (e.g., Newton 1998), but the opposite is also well-known. The latter implies that, for wintering small mammals, severe winters with thick snow cover, providing shelter from cold and predation, could be more favourable than mild ones (Hansson & Henttonen 1985, Merritt 1985, Sonerud 1986, Sheftel 1989, Nybo & Sonerud 1990, Jędrzejewski & Jędrzejewska 1993, Pucek *et al.* 1993, Lindström & Hörnfeldt 1994, Merritt *et al.* 2001, Hörnfeldt 2004). In mild winters, the fluctuation of temperatures around the freezing point may be especially harmful by alternate freezing and thawing wetting the wintering microhabitats of small mammals ("frost seesaw effect", Solonen 2001, 2004; cf. also Merritt 1985). This effect is expected to be most intense in open low-lying habitats where the water from melted snow may cover large areas (Solonen 2004).

Seasonal variation in numbers belong to the basic characteristics of the long-term dynamics of populations. Many small mammal populations exhibit, in addition, more or less regular longer-term cyclic density fluctuations (e.g., Kalela 1962, Hansson & Henttonen 1985, Norrdahl 1995, Stenseth *et al.* 1996, Stenseth 1999, Sundell *et al.* 2004). In various localities in northern Europe, the previous regularity of vole cycles seemed to be decreasing (Lindström & Hörnfeldt 1994, Steen *et al.* 1996, Hansson 1999, Henttonen 2000, Solonen 2001, 2004, Laaksonen *et al.* 2002). In northern Sweden, an important feature of the persistent decline in density and amplitude for vole species is a clear decrease in wintering success (Hörnfeldt 2004, Hörnfeldt *et al.* 2005). Potential causal factors behind these kinds of changes include less favourable climatic conditions (Hörnfeldt 2004, Solonen 2004, Korslund & Steen 2006), increased predation (Lindström & Hörnfeldt 1994, Hörnfeldt *et al.* 2005), as well as a decrease in food quality (Agrell *et al.* 1995), environmental stress (Unangst & Wunder 2003), and diseases (Telfer *et al.* 2002, Niklasson *et al.* 2003).

In southern Finland, coastal and inland vole abundances seem to fluctuate in significant synchrony, but their general levels in good vole years are considerably higher inland than in coastal regions (Solonen 2004, Sundell *et al.* 2004). There is no significant correlation between regional autumn and spring vole abundances. The regional vole densities show no significant trends, but the coastal spring densities seemed to be declining. The highest peaks of the cycles appear to be levelling off as well (Solonen 2004, T. Solonen & P. Ahola unpubl. data).

In this study, I examine the overwinter change in small mammals on the basis of the results of snap trappings conducted from 1981 to 2005 in southern Finland. My goal is to clarify the role of some potential factors behind the recent changes in populations. I attempt to elucidate effects of weather, habitat, and population density on the wintering success of small mammals especially in the southernmost part of the country. Regional and local scales, as well as various groups of species (shrews, voles, mice) are considered. Following the frost seesaw hypothesis (Solonen 2001, 2004, Solonen & Karhunen 2002), I expect that irrespective of species the overwintering of small mammals is less successful (1) near the climatically mild southern coast of Finland than in colder inland regions, (2) in fields than in forests, and (3) in milder winters than in colder ones. The negative effects of mild winters should be evident especially in species and populations living in low-lying habitats. The magnitude of the overwinter population change should follow the preceding population density (Merritt *et al.* 2001, Stenseth *et al.* 2002, Hörnfeldt 2004).

Material and methods

Species and study areas

The groups of small mammals considered here consisted of shrews Soricidae (mainly common shrews *Sorex araneus*), small voles Microtinae of two genera (bank voles *Clethrionomys glareolus* and field voles *Microtus agrestis*), and mice Muridae (mainly yellow-necked mice *Apodemus flavicollis*). Due to small samples, mice were not, however, considered separately but included in other groups of small mammals. Near the southern coast of Finland, populations were monitored in three localities, Lohja (60°16´N, 24°12´E), Kirkkonummi (60°13´N, 24°24´E), and Sipoo (60°20´N, 25°12´E). The two former are situated 13 km apart and the two latter about 50 km from each other. In Lohja and Kirkkonummi the study period covered the years 1981–2005, and in Sipoo the years 1986–2000. Comparable data on inland voles, separated from the coastal areas by a distance of about 150 km and the geographical (Tikkanen 1994) and meteorological (Drebs *et al.*

2002) barrier of the ridges of Salpausselkä, collected during 1986–2000 (Heinola, 61°N, 26°E) were derived from published sources (Brommer *et al*. 2002, Sundell *et al*. 2004).

Trapping data

Trappings were conducted each autumn (late October–early November) and spring (early May) at several standard points along the catching lines. In Lohja and Kirkkonummi, the trapping areas included a spruce (*Picea abies)*-dominated wooded site and an abandoned field site. The characteristics of the field sites thus somewhat changed during the study period due to ecological succession but in Lohja the change concerning the trapping points itself was rather slow and minor. At each of these four sites, the trapping consisted of 16 points of three traps, the points situated about 25 m from each other, during two approximately 24-hr periods (totalling 384 trap nights). In Sipoo each trapping period was about 24 hrs, using 30 points of three traps, the points spaced evenly along a line of 1.5 km through a rich spruce forest area (totalling 90 trap nights). The results were expressed as individuals per 100 trap nights. For a regional vole index, I combined the results of the three separate coastal trapping localities. The inland trappings were conducted in June, i.e. some weeks later than the coastal ones so their catches might have increased due to the onset of reproduction. On the other hand, the increased predation in early summer probably had the opposite effect.

The catch indices describe the general level of populations in the surroundings, not only exactly in each local trapping site. Declines in catch indices in permanent sampling sites are not shown to be due to the repeated trappings there (Christensen & Hörnfeldt 2003). Removal trappings may, however, cause a temporary reduction in local densities.

I expressed the overwinter population change simply by the difference between the autumn and spring abundance indices. This measure, which is used to characterize the wintering success of small mammals as well (e.g., Pucek *et al*. 1993, Hörnfeldt 2004), in fact describes the combined effect of mortality, emigration, and immigration. For comparisons between different populations and habitats as well as to diminish the potential bias introduced by some local differences in trapping methods, the overwinter decline was expressed as a percentage. I also used spring trapping indices to characterize the result of the overwinter population change. Instead of deleting the zero values of the catch index, I arbitrarily replaced densities below the detection limit of trapping methods with a value of 0.001. This might produce some overestimates in the lower end of the variation but had no serious effects on the results.

Meteorological variables

Various aspects of winter weather were characterized by the average ambient temperatures and intensity of the frost seesaw. Temperatures were expressed as winter means or monthly averages, inclusive of months November to March, and were derived from the dense Finnish network of more than 500 meteorological data points (http://www.fmi.fi). Data for the coastal area came from Helsinki-Vantaa Airport (60°19´N, 25°58´E), and for the inland area from Jyväskylä, central Finland (62°14´N, 25°41´E), using the 1985–2000 reviews of the Finnish Meteorological Institute. In 1987–1998, the average winter means for the two regions were –4.1 (± 2.9 SD) and –7.7 (± 3.6 SD) °C, respectively. On the basis of the data from the southern coast, an attempt was made to explain the possible effects of winter temperatures by the intensity of the frost seesaw, characterized by the number of days during which the ambient temperature at least once fell from plus to minus °C (Solonen & Karhunen 2002). The weather variables showed no significant trends within the study period. However, in the long run, the 1990s were characterized by remarkably mild winters (Drebs *et al*. 2002).

Statistical methods

I examined the differences in the overwinter population change between the species, populations, and other groups considered with the Mann-Whitney rank sum test or with the Kruskal-

Wallis one-way analysis of variance on ranks (multiple comparisons with Dunn's method), the synchrony between fluctuations with the Spearman correlation, and trends using linear regression. The combined effects of potential density-dependent factors (such as competition and predation characterized by the autumn density) and density-independent factors (characterizing the temperature conditions of winters) on the spring abundance of small mammals were examined using the backward stepwise multiple regression analysis (Sokal & Rohlf 1981). To meet the assumptions of the method, the abundance indices were ln-transformed. In calculations, I used SigmaStat 3.1 and Wessa 1.1.16 (http://www.wessa.net) statistical softwares.

Results

The absolute and relative amplitudes of the overwinter population change of small mammals varied considerably both within and between the species and groups (Table 1). However, the winter decline was not significantly larger in the coastal as compared with that in the inland vole populations (Mann-Whitney test: $T_{12,15} \geq 141.0$, $P \geq 0.20$) and there were only a few significant differences between the local populations of the southern coast (Kruskal-Wallis one-way analysis of variance), the relative winter decline (%) being significantly lower in field voles than in bank voles (Dunn's test: $Q = 4.35$, $P < 0.05$) and shrews ($Q = 3.75$, $P < 0.05$). In small mammals,

Table 1. Autumn and spring densities (individuals per 100 trap nights), showing the overwinter population change, and the winter decline (%) of small mammals at various localities in southern Finland in 1981–2005 (*n* = the number of years included in the data).

Species group	Locality	Autumn mean ± SD	Spring mean ± SD	Decline (%) mean ± SD	*n*
Shrews	Lohja	4.0 ± 2.6	0.5 ± 0.7	83.6 ± 24.3	24
	Kirkkonummi	3.3 ± 1.9	0.8 ± 1.0	55.3 ± 58.9	24
	Sipoo	10.1 ± 4.7	2.5 ± 1.7	42.2 ± 130.6	14
Bank vole	Lohja	6.1 ± 5.3	1.1 ± 1.1	63.7 ± 45.6	24
	Kirkkonummi	5.8 ± 5.0	1.0 ± 1.1	65.4 ± 45.5	24
Field vole	Lohja	2.6 ± 3.4	0.5 ± 0.9	49.3 ± 60.6	24
	Kirkkonummi	2.2 ± 2.3	0.8 ± 0.9	32.0 ± 95.8	24
Voles	Lohja	8.7 ± 7.0	1.6 ± 1.4	47.3 ± 83.1	24
	Kirkkonummi	8.0 ± 6.5	1.8 ± 1.4	64.6 ± 34.7	24
	Sipoo	11.6 ± 7.4	1.0 ± 1.0	90.5 ± 9.9	14
	Coastal	9.9 ± 5.5	1.4 ± 1.1	81.3 ± 18.3	15
	Inland	21.3 ± 17.4	7.1 ± 9.5	44.3 ± 53.5	12
Small mammals	Lohja	13.6 ± 8.6	2.3 ± 1.9	70.9 ± 37.5	24
	Kirkkonummi	12.8 ± 7.0	2.7 ± 2.0	77.4 ± 14.2	24
	Sipoo	22.0 ± 9.9	3.7 ± 2.2	81.5 ± 10.3	14

Table 2. Overwinter population change (%) of various groups of small mammals in fields and forests near the southern coast of Finland in 1981–2005. The number of years (*n*), mean, SD and median values of change (%) as well as Mann-Whitney rank sum test statistic (*T*) and the significance of difference (*P*) between the median values of habitats are given.

Group	Habitat	*n*	Mean ± SD	Median	*T*	*P*
Shrews and mice	Field	24	88.8 ± 16.9	93.9	705.0	0.016
	Forest	24	59.0 ± 43.9	69.0		
Voles	Field	24	36.7 ± 202.2	87.1	686.5	0.043
	Forest	24	48.1 ± 79.8	66.3		
Small mammals	Field	24	80.9 ± 33.3	88.4	708.0	0.014
	Forest	24	61.3 ± 47.1	72.6		

in general, it was, however, significantly larger in field habitats than in forests (Table 2).

The overwinter change of the local populations of bank voles of Lohja and Kirkkonummi fluctuated in considerable synchrony ($r_S = 0.54$, $P < 0.01$, $n = 24$) and in field voles ($r_S = 0.48$, $P < 0.05$, $n = 24$). There was also a synchrony in bank voles between Lohja and Sipoo ($r_S = 0.67$, $P < 0.01$, $n = 14$). In Kirkkonummi, the winter decline of bank voles increased significantly during the study period ($t_{1,22} = 2.41$, $P < 0.05$).

In general, small mammals seemed to benefit from mild winter months (Table 3). The effect of high temperatures in February on field voles was, however, negative. The intensity of the frost seesaw in February seemed to have significant negative effects on coastal voles at large. The autumn density reflected positively in spring densities of some vole populations but had a negative effect on shrews in Sipoo.

Discussion

Geographical and habitat variation

There seemed to be pronounced differences in the relative wintering success among the local small mammal populations. Similar differences have been reported at a large scale, for example in winter survival of shrews in western Siberia (Dokuchaev 1989, Sheftel 1989). Considerable regional and habitat differences in population dynamics of the bank vole over large geographical areas (Hansson *et al.* 2000, Hansson 2002) further reinforce the impression that highly vari-

Table 3. Effects of the preceding autumn population density (A) and local winter weather conditions, described alternatively and in various combinations by the winter (W) or monthly (D = Dec., J = Jan., F = Feb., M = Mar.) mean ambient temperature (*T*) or the intensity of the frost seesaw (S), on the spring abundance of some small mammal populations in southern Finland: a summary of the backward stepwise multiple regression analyses conducted. The best combination of the explaining variables included in the models, the direction (+/–) and contribution (partial r^2) of each variable to total variation explained (adjusted R^2) as well as *F* and *P* of the variance analyses are given. "E" means that all variables were eliminated from the model.

Population	Locality	Variables	r^2/R^2 (%)	*F*	*P*	df
Shrews	Lohja	SW +	39.0	9.3	0.010	1,12
	Kirkkonummi	E				
	Sipoo	A –	34.4		0.045	
		TW +	43.1		0.020	
		SM –	36.8		0.036	
		Total	44.2	4.4	0.031	3,10
Bank vole	Lohja	A +	45.7		0.011	
		TM +	39.4		0.022	
		Total	47.3	6.8	0.012	2,11
	Kirkkonummi	E				
Field vole	Lohja	TD +	76.7		< 0.001	
		TF –	43.6		0.014	
		Total	74.3	19.8	< 0.001	2,11
	Kirkkonummi	A +	33.6		0.038	
		TF –	33.5		0.038	
		Total	40.7	5.5	0.022	2,11
Voles	Sipoo	TW +	45.8		0.011	
		SF –	31.3		0.047	
		Total	36.0	4.7	0.034	2,11
	Coastal	TJ +	86.7		< 0.001	
		SF –	62.2		< 0.001	
		Total	84.6	39.5	< 0.001	2,12
	Inland	SD –	48.3		0.026	
		SM +	53.1		0.017	
		TW –	39.4		0.052	
		Total	50.8	4.8	0.034	3,8

able factors may be involved in the dynamics of local small mammal populations.

The present results do not clearly support the expectation that wintering voles managed worse near the Finnish southern coast than inland. This may be due to the differences in the trapping procedures and habitats as well as the small number of sampling localities. However, the relatively higher winter decline in the coastal *vs.* inland area and the reversed pattern in the variation between years would fit the hypothesis that the coastal populations are more governed by seasonal dynamics, while the inland populations are rather characterized by multiannual fluctuations.

Due to their geographical location, the forest-dominated inland landscapes of the present study may exhibit more continental (dryer and harder) winters than the coastal, more agricultural ones. Commonly occurring higher abundance peaks of small mammals and their numerical declines are more pronounced in continental than in coastal regions (e.g., Hörnfeldt 2004, Solonen 2004, cf. Henttonen *et al.* 1989). In a continental climate, the cyclic fluctuations of small mammals may also be more regular (e.g., Sheftel 1989), while their winter mortality may be higher than in more maritime regions (e.g., Dokuchaev 1989). The typical average winter declines of 77% (± 23% SD) in bank voles and 86% (± 17% SD) in yellow-necked mice in deciduous forests of lowland, temperate Europe (Pucek *et al.* 1993) seem to be relatively similar to those found in southernmost Finland. However, differences between ecologically different species and populations are probably common.

Effects of temperature

Mild winters seemed to have both positive and negative effects on the overwinter population change of small mammals (cf. Merritt *et al.* 2001). Seemingly contradicting results may be explained by the fact that high temperatures indicate the absolute mildness of winters, while the intensity of the frost seesaw indicates temperatures around the freezing point. Thus, the mildness *per se* seemed to be favourable but temperatures fluctuating around the freezing point were unfavourable.

Mild weather conditions seemed to have negative effects on small mammals especially in the depth of winter. As expected, this mostly concerned populations in field habitats. This might be due to the frost seesaw effect being more intense in open low-lying habitats than in wooded mounds where the water from melted snow does not cover such large areas as commonly occurs in flat open terrain. This kind of heterogeneity of habitats also offers refuges for some proportion of small mammals (cf. also Merritt 1985, Ylönen *et al.* 1991, Wijnhoven *et al.* 2005, Korslund & Steen 2006). Therefore, since shrews and bank voles prefer forests, they are probably less vulnerable to the frost seesaw effect than field voles, which mainly occupy open habitats.

The effects of mild winters obviously extend over large rather than only local areas. At present they are probably more pronounced in the mild and wet climate of the low-lying southern coast than elsewhere in Finland (Solonen 2004). In southern Finland, winter temperatures decrease and snow cover increase north-eastwards while precipitation is highest in the southern coastal areas (Drebs *et al.* 2002). Because these factors, known to influence wintering small mammals (e.g., Marchand 1982, Merritt 1985, Pucek *et al.* 1993, Merritt *et al.* 2001, Korslund & Steen 2006), are more or less entangled together and with other factors, including predation (Sonerud 1986, Nybo & Sonerud 1990, Jędrzejewski & Jędrzejewska 1993, Pucek *et al.* 1993, Lindström & Hörnfeldt 1994, Merritt *et al.* 2001), such general indices as mean temperature and frost seesaw index used in this study hardly describe the complicated effects of high and fluctuating winter temperatures comprehensively. In heterogeneous habitats, local measurements of various environmental factors are needed to detect these effects in more detail.

Density-dependent factors

The variations in wintering success are often explained by the population density of the preceding autumn, suggesting the importance of density-dependent factors (Pucek *et al.* 1993, Merritt *et al.* 2001, Stenseth *et al.* 2002, Hörnfeldt 2004). In the present study, however, the effect of population density on the overwinter decline and the consequent spring density of small mammals seemed to be minor and rather positive than negative. This may be due to the low densities of populations and the small size of samples. The effect of population density may be overshadowed by various other ecological factors such as weather conditions and predation, which is commonly suggested to be a most important agent in the winter mortality of small mammals (Erlinge *et al*. 1983, Henttonen *et al*. 1987, Jędrzejewski & Jędrzejewska 1993, Pucek *et al*. 1993, Hansen *et al*. 1999, Hanski *et al*. 2001, Merritt *et al*. 2001).

Conclusions

The widely synchronous fluctuations of the overwinter population decline in various small mammal populations suggest a dominant role of some large-scale extrinsic factor such as winter weather. This interpretation is reinforced by the relationships between the variables characterizing temperature conditions of winters and the spring abundance of various small mammal populations. The effects of mild winter temperatures seem to be detrimental or favourable, being complicated by the negative influences of the frost seesaw.

Steep winter population declines suggest that fields may provide suboptimal habitats for overwintering small mammals. This may be the case only locally and only under certain conditions. In autumn, fields provide plenty of food, such as grass, seeds, and invertebrates, that attract various small mammals from surrounding habitats. In unfavourable weather conditions of mild winters, low-lying fields may become ecological traps, decreasing the densities of small mammals by increasing mortality. Spatial dynamics of animals provide an additional explanation for local variations in overwinter population change.

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References

Aars, J. & Ims, R. A. 2002: Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. — *Ecology* 83: 3449–3456.

Agrell, J., Erlinge, S., Nelson, J., Nilsson, C. & Persson, I. 1995: Delayed density-dependence in a small-rodent population. — *Proc. R. Soc. Lond. B* 262: 65–70.

Boyce, M. S. 1979: Seasonality and patterns of natural selection for life histories. — *Am. Nat.* 114: 569–583.

Brommer, J. E., Pietiäinen, H. & Kolunen, H. 2002: Reproduction and survival in a variable environment: Ural owls and the three-year vole cycle. — *Auk* 119: 544–550.

Christensen, P. & Hörnfeldt, B. 2003: Long-term decline of vole populations in northern Sweden: a test of the destructive sampling hypothesis. — *J. Mammal.* 84: 1292–1299.

Dokuchaev, N. E. 1989: Population ecology of *Sorex* shrews in North-East Siberia. — *Ann. Zool. Fennici* 26: 371–379.

Drebs, A., Nordlund, A., Karlsson, P., Helminen, J. & Rissanen, P. 2002: *Climatological statistics of Finland 1971–2000*. — Finnish Meteorological Institute, Helsinki.

Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I. N., Nilsson, T., von Schantz, T. & Sylvén, M. 1983: Predation as a regulating factor on small rodent populations in southern Sweden. — *Oikos* 40: 36–52.

Fretwell, S. D. 1972: *Populations in a seasonal environment*. — Princeton Univ. Press, Princeton.

Hansen, T. F., Stenseth, N. C. & Henttonen, H. 1999: Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. — *Am. Nat.* 154: 129–139.

Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. 2001: Small-rodent dynamics and predation. — *Ecology* 82: 1505–1520.

Hansson, L. 1999: Intraspecific variation in dynamics: small rodents between food and predation in changing landscapes. — *Oikos* 85: 159–169.

Hansson, L. 2002: Dynamics and trophic interactions of small rodents: landscape and regional effects on spatial variation? — *Oecologia* 130: 259–266.

Hansson, L. & Henttonen, H. 1985: Gradients in density variations of small rodents: the importance of latitude and snow cover. — *Oecologia* 67: 394–402.

Hansson, L., Jędrzejewska, B. & Jędrzejewski, W. 2000: Regional differences in dynamics of Bank Vole populations in Europe. — *Polish J. Ecol.* 48 (Suppl.): 163–177.

Henttonen, H. 2000: Long-term dynamics of the bank vole *Clethrionomys glareolus* at Pallasjärvi, northern Finnish taiga. — *Polish J. Ecol.* 48 (Suppl.): 87–96.

Henttonen, H., Oksanen, T., Jortikka, H. & Haukisalmi, V. 1987: How much do weasels shape microtine cycles in northern Fennoscandian taiga? — *Oikos* 50: 353–365.

Henttonen, H., Haukisalmi, V., Kaikusalo, A., Korpimäki, E., Norrdahl, K. & Skarén, U. A. P. 1989: Long-term population dynamics of the common shrew *Sorex araneus* in Finland. — *Ann. Zool. Fennici* 26: 349–355.

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

Hörnfeldt, B., Hipkiss, T. & Eklund, U. 2005: Fading out of vole and predator cycles? — *Proc. R. Soc. Lond. B* 272: 2045–2049.

Huitu, O., Koivula, M., Korpimäki, E., Klemola, T. & Norrdahl, K. 2003: Winter food supply limits growth of northern vole populations in the absence of predation. — *Ecology* 84: 2108–2118.

Jędrzejewski, W. & Jędrzejewska, B. 1993: Predation on rodents in Białowieża Primeval Forest, Poland. — *Ecography* 16: 47–64.

Kalela, O. 1962: On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. — *Ann. Acad. Sci. Fenn. Ser. A IV Biol*. 66: 1–38.

Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N. C. 2002: Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. — *Proc. R. Soc. Lond. B* 269: 991–997.

Korslund, L. & Steen, H. 2006: Small rodent winter survival: snow conditions limit access to food resources. — *J. Anim. Ecol.* 75: 156–166.

Laaksonen, T., Korpimäki, E. & 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.

Lima, M., Merritt, J. F. & Bozinovic, F. 2002: Numerical fluctuations in the northern short-tailed shrew: evidence of non-linear feedback signatures on population dynamics and demography. — *J. Anim. Ecol.* 71: 159–172.

Lindström, E. & Hörnfeldt, B. 1994: Vole cycles, snow depth and fox predation. — *Oikos* 70: 156–160.

Marchand, P. J. 1982: An index for evaluating the temperature stability of a subnivean environment. — *J. Wildl. Manage*. 46: 518–520.

Merritt, J. F. 1985: Influence of snowcover on survival of *Clethrionomys gapperi* inhabiting the Appalachian and Rocky Mountains of North America. — *Acta Zool. Fennica* 173: 73–74.

Merritt, J. F., Lima, M. & Bozinovic, F. 2001: Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. — *Oikos* 94: 505–514.

Newton, I. 1998: *Population limitation in birds*. — Academic Press, San Diego.

Niklasson, B., Hörnfeldt, B., Nyholm, E., Niedrig, M., Donoso-Mantke, O., Gelderblom, H. R. & Lernmark, Å. 2003: 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. 1995: Population cycles in northern small mammals. — *Biol. Rev*. 70: 621–637.

Norrdahl, K. & Korpimäki, E. 2002: Changes in population structure and reproduction during a 3-year population cycle of voles. — *Oikos* 96: 331–345.

Nybo, J. O. & Sonerud, G. A. 1990: Seasonal changes in diet of hawk owls *Surnia ulula*: importance of snow cover. — *Ornis Fennica* 67: 45–51.

Pucek, Z., Jędrzejewski, W., Jędrzejewska, B. & Pucek, M. 1993: Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. — *Acta Theriol*. 38: 199–232.

Sheftel, B. I. 1989: Long-term and seasonal dynamics of shrews in Central Siberia. — *Ann. Zool. Fennici* 26: 357–369.

Sokal, R. R. & Rohlf, F. J. 1981: *Biometry*. — Freeman, New York.

Solonen, T. 2001: Has owl prey availability deteriorated due to mild winters in southern Finland? — *Linnut* 36(2): 6–9. [In Finnish with English summary].

Solonen, T. 2004: Are vole-eating owls affected by mild winters in southern Finland? — *Ornis Fennica* 81: 65–74.

Solonen, T. & Karhunen, J. 2002: Effects of variable food conditions on the tawny owl *Strix aluco* near the northern limit of its range. — *Ornis Fennica* 79: 121–131.

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, H., Ims, R. A. & Sonerud, G. A. 1996: Spatial and temporal patterns of small-rodent population dynamics at a regional scale. — *Ecology* 77: 2365–2372.

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., Bjørnstad, O. N. & Saitoh, T. 1996: A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. — *Proc. R. Soc. Lond. B* 263: 1117–1126.

Stenseth, N. C., Viljugrein, H., Jędrzejewski, W., Mysterud, A. & Pucek, Z. 2002: Population dynamics of *Clethrionomys glareolus* and *Apodemus flavicollis*: seasonal components of density dependence and density independence. — *Acta Theriol*. 47, Suppl. 1: 39–67.

Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. 2004: Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. — *J. Anim. Ecol*. 73: 167–178.

Telfer, S., Bennett, M., Bown, K., Cavanagh, R., Crespin, L., Hazel, S., Jones, T. & Begon, M. 2002: The effects of cowpox virus on survival in natural rodent populations: increases and decreases. — *J. Anim. Ecol*. 71: 558–568.

Tikkanen, M. 1994: The landforms of Finland. — *Terra* 106(3): 181–192. [In Finnish with English abstract].

Unangst, E. T. & Wunder, B. A. 2003: Body-composition dynamics in meadow voles (*Microtus pennsylvanicus*) of southeastern Colorado. — *Am. Midl. Nat*. 149: 211–218.

Wijnhoven, S., van der Velde, G., Leuven, R. S. E. W. & Smits, A. J. M. 2005: Flooding ecology of voles, mice and shrews: the importance of geomorphological and vegetational heterogeneity in river floodplains. — *Acta Theriol*. 50: 453–472.

Ylönen, H., Altner, H.-J. & Stubbe, M. 1991: Seasonal dynamics of small mammals in an isolated woodlot and its agricultural surroundings. — *Ann. Zool. Fennici* 28: 7–14.