



Tawny owl prey remains indicate differences in the dynamics of coastal and inland vole populations in southern Finland

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Abstract Some studies suggest that mild winters decrease overwinter survival of small mammals or coincide with decreased cyclicality in vole numbers, whereas other studies suggest non-significant or positive relationships between mild winter conditions and vole population dynamics. We expect for the number of voles to be higher in the rich and low-lying habitats of the coastal areas than in the less fertile areas inland. We assume that this geographical difference in vole abundances is diminished by mild winters especially in low-lying habitats. We examine these relationships by generalized linear mixed models using prey remains of breeding tawny owls *Strix aluco* as a proxy for the abundance of voles. The higher number of small voles in the coastal area than in the inland area suggest that vole populations were denser in the coastal area. Vole populations of both areas were affected by winter weather conditions particularly in March, but these relationships differed between areas. The mild ends of winter with frequent fluctuations of the ambient temperature around the freezing point (“frost seesaw”) constrained significantly the coastal vole populations, while deep snow cover, in general after hard winters, was followed by significantly

lowered number of voles only in the inland populations. Our results suggest that coastal vole populations are more vulnerable to mild winters than inland ones. We also show that tawny owl prey remains can be used in a meaningful way to study vole population dynamics.

Keyword *Arvicola amphibius* · *Microtus agrestis* · Mild winters · *Myodes glareolus* · *Strix aluco* · Vole monitoring

Introduction

Recently, increasing irregularity has been reported in previously relatively regular vole cycles in Northern Europe (Lindström and Hörnfeldt 1994; Steen et al. 1996; Hansson 1999; Hörnfeldt 2004; Hörnfeldt et al. 2005; Bierman et al. 2006; Ims et al. 2008; Brommer et al. 2010). These observations, superficially related to local fluctuations in vole population size, may actually indicate a loss of essential ecosystem functions. Cornulier et al. (2013) conclude that the collapse of vole cycles is likely to be deleterious to vole predators and cause also other changes cascading down the food web.

Observations on the southern coast of Finland suggest that the formerly regular three-year vole cycles have been leveling off and the general abundance of voles has been declining (Solonen and Karhunen 2002). Solonen (2004) proposes the phenomenon to be due to mild and wet winters, causing a so-called “frost seesaw effect, i.e., a fluctuation of ambient temperatures around the freezing point”. The increasing frequency of such circumstances with alternating wet and cold periods is supposed to be especially disastrous to overwintering voles by wetting and freezing in turns their wintering cavities. In mild winters a lower proportion of voles seemed to survive from autumn to spring (Solonen 2006).

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According to a local snap-trapping time series in southern Finland, overwinter change in population size of small mammals varies considerably both within and between species and species groups (Solonen 2006). The change is not significantly steeper in the coastal than in inland vole populations, but there are significant differences between the local populations in the southern coastal area. Small mammals seemed to overwinter more successfully in forests than in fields, and the mild winters seemed to have negative effects especially on vole populations in field habitats. The direct contribution of high ambient temperatures to the overwinter population change seemed to be largely restraining, but especially so in midwinter. Also many other studies suggest that mild winters decrease overwinter survival or coincide with decreased cyclicality (Merritt et al. 2001; Aars and Ims 2002; Hörnfeldt 2004; Bierman et al. 2006; Boonstra and Krebs 2006; Korslund and Steen 2006; Hipkiss et al. 2008; Solonen and Ahola 2010; Magnusson et al. 2015). However, some studies suggest non-significant or positive relationships between mild winter conditions and vole population dynamics (Tkadlec et al. 2006; Hoset et al. 2009; Brommer et al. 2010; Korpela et al. 2013). This may be because mild winters may also periodically increase the depth of the snow layer, thus improving vole survival in the subnivean space. Thus, the depth of the snow cover does not depend straightforwardly on the winter temperature.

In this study, we examine how mild winters might explain the spatial differences and temporal changes in the abundance of voles, by using prey remains of breeding tawny owls *Strix aluco* Linnaeus 1758 as a proxy for the number of three species of voles in coastal and inland habitats in southern Finland. The species concerned included all the common arvicolines of the study areas in southern Finland, namely the large water vole *Arvicola amphibius* (Linnaeus 1758) as well as the small voles the field vole *Microtus agrestis* (Linnaeus 1761) and the bank vole *Myodes glareolus* (Schreber 1780). The water vole occurs in a range of habitats around rivers, streams and marshes in the lowlands (Batsaikhan et al. 2008). Steep riverbanks with lush grass and vegetation are preferred. In Fennoscandia the species lives a fossorial life during winter months, being so largely protected from climatic fluctuations. The field vole occurs in a wide range of habitats, including grasslands, woods, upland heaths, dunes, marshes, peat-bogs and river-banks, tending to prefer damp areas (Kryštufek et al. 2008). It occurs in a number of anthropogenic habitats, including meadows, field-margins and young forestry plantations. The bank vole inhabits all kinds of woodland, preferring densely-vegetated clearings, woodland edge, and river and stream banks in forests (Amori et al. 2008). It is also found in scrubs, parkland, and hedges.

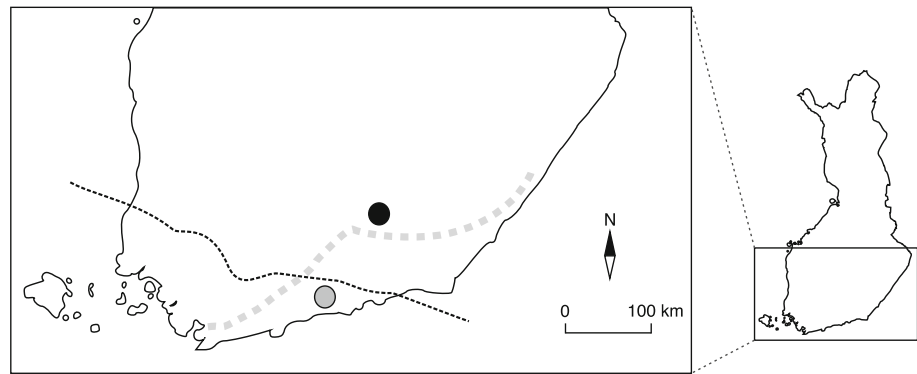
We expect that (1) due to the differences in the environmental conditions, the number of voles in tawny owl prey are higher in the rich and largely low-lying habitats of the coastal areas than in the less fertile areas in the interior of the country with a generally higher elevation (hypso-metric layer 0–50 and 50–200 m, respectively; Ahti et al. 1968; National Board of Survey 1979), suggesting that their populations are, in general, denser in the coastal than inland areas. (2) This geographical difference in vole abundances is diminished by mild winters, in particular during those periods when the ambient temperature fluctuates frequently around the freezing point, due to increased mortality especially in low-lying habitats. (3) The species inhabiting, in general, the most low-lying habitats as compared to surroundings (field voles rather than other species) should be affected most seriously. (4) A trend in the effect should coincide with a trend in the affecting weather factor. (5) Weather-induced deaths of voles probably take place during a relatively short period of time (weeks rather than months) and occur non-selectively over a wide range of individuals and populations in similar habitats as compared to other, more selective causes of death such as predation, diseases and aging.

Materials and methods

Study areas and field work

The field work was conducted in two local study areas ca. 70 km apart in different climatic zones (see Hämet-Ahti 1981) (Fig. 1). Our *coastal* study area of about 500 km² was situated in Uusimaa, near the southern coast of Finland (60°22'N, 25°15'E), in the hemiboreal climatic zone. Our *inland* study area of about 700 km² was located in and around the city of Lahti in Päijät-Häme, southern Finland (60°59'N, 25°39'E), in the boreal climatic zone. The hemiboreal zone, halfway between the temperate and boreal zones, is characterised by relatively cold winters and mild summers (Hämet-Ahti 1981). The boreal zone is characterised by long, usually very cold winters, and short, cool to mild summers. A distinct characteristic of the inland study area is also the prominent terminal moraine formation of Salpausselkä, the northern side of which differs from the southern lower-lying areas both geographically and climatically (Kersalo and Pirinen 2009). The areas consist of a mosaic of agricultural land (approximately 50 %), spruce-dominated forest (40 %) and water systems (10 %), mainly bays in the coastal area and lakes and streams in the inland area. The general densities of tawny owl territories were about 6–10 territories per 100 km² in the coastal area and 3–6 in the inland area. The habitats of owls were mainly rural but some of the

Fig. 1 The location of the study areas. The coastal study area is marked as a grey circle and the inland study area as a black circle. The border of the hemiboreal climatic zone is indicated as a black dashed line. Terminal moraine formation of Salpausselkä is indicated as a thick light grey dashed line (the formation is at highest approximately 70 m and at widest 1.5 km)



territories may be characterised also as (sub)urban. Owls preferred rich deciduous and mixed forests near fields, sparsely dispersed human habitation, and especially eutrophic water bodies. The best tawny owl habitats often had a strong cultural impact, being situated around manor houses, which traditionally occupied the best habitats of the area.

In the coastal study area, vole abundance was studied from the prey of breeding tawny owls by analysing 51 nest bottom litter samples collected from 30 different locations (local territories) in 1986–1999 (Solonen and Karhunen 2002) (Fig. 2). In the inland study area, 78 nests from 34 local territories were analysed in 1995–2003 (Kekkonen et al. 2008) (Fig. 2). The total number of individual voles from the two study areas were 1164 and 1230, respectively. In the coastal area, the total number of water voles, field

voles and bank voles were 312, 661 and 191, and in the inland area 468, 620 and 142, respectively.

Food remains (bones) were separated from the litter by picking with tweezers. They were assorted and identified in appropriate categories. In each prey category, the number of individuals was counted on the basis of the most common individual bones found. The identification of mammals was based mainly on jawbones (mandibles) and limb bones, including hip-bones, femurs, tibiae, and humeri. Bones were classified as right or left side of the body and paired so that we did not overestimate the number of prey individuals. Species were determined by the unique morphological features of the bones. In species identification, we used both literature (Saurola 1995; Siivonen and Sulkava 2002) and reference collections.

The relationships between the annual mean number of small voles in nest samples and the vole catch indices of standard local snap trappings (Kekkonen et al. 2008; Solonen and Ahola 2010) were significantly positive ($r = 0.724$, $P = 0.003$; $r = 0.694$, $P = 0.019$) in coastal and inland field voles and ($r = 0.520$, $P = 0.034$; $r = 0.744$, $P = 0.011$) bank voles, respectively. In the coastal study area, the number of bank voles in prey remain samples correlated significantly positively with both the number of water voles ($r = 0.774$, $P = 0.002$) and field voles ($r = 0.719$, $P = 0.006$). In the inland area, the field vole numbers correlated positively with the number of water voles ($r = 0.924$, $P < 0.001$) and bank voles ($r = 0.775$, $P = 0.014$). In the total data, voles comprised 36.7 % of the total number of prey individuals in samples in the coastal study area and 38.9 % in the inland area.

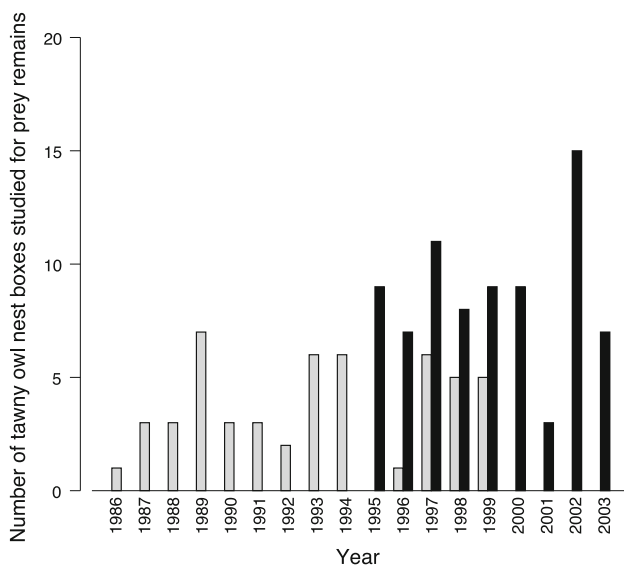


Fig. 2 Number of nest boxes which were studied for prey items in each year. Grey bars indicate boxes from the coastal study area and black bars indicate boxes from the inland study area. In some years data were available for only one of the study areas

Statistical methods

To test the predictions, generalized linear mixed models were fitted to the data using the statistical package “lme4” in R (version 3.2.4; R Development Core Team 2013; Venables et al. 2014). The response variable consisted of the number of voles in the owl nest samples. The fixed

effects included a categorical explanatory variable “locality” (coastal, inland), as well as continuous variables “year” (trend) and various weather variables (Electronic Supplementary Material ESM S1). Weather variables included both large-scale and local indices, covering longer (winter) or shorter (monthly) periods of time. For characterising the winter weather conditions at large, we applied the winter index of the North Atlantic oscillation (NAO), averaging the monthly values of the index from December to March. NAO is the most prominent pattern of atmospheric variability over the northern hemisphere and it has a marked effect on European weather (Hurrell et al. 2001). The increasing positive values of the winter NAO indices [<http://www.cru.uea.ac.uk/cru/data/nao.htm> (accessed 23 March 2011)] indicate milder and wetter winter weathers in Europe. Effects of local weather conditions were examined using the local mean temperature of winter, including December, January, February and March, as well as the mean depth of the snow cover over winter (averaging the values in the middle of each of these months) (Finnish Meteorological Institute; Helsinki—Vantaa station for the coastal area and Lahti, Laune station for the inland area). In addition, we used the intensity of the frost seesaw, i.e., how often the subsequent daily minimum and maximum temperatures were on the different side of the freezing point during a defined period of time. To sharpen the analyses, in addition to the mean or total values of winter, we also used the respective monthly values of the weather variables. The tawny owl territory ID, indicating impacts of the local habitat (and individual birds), as well as the categorical variable “year”, indicating other annually varying unknown factors (not included when examining trends), characterised random effects on the intercepts of the vole numbers. Variables were centered to zero mean, describing average conditions.

Results

The total number of voles in the tawny owl prey samples were not significantly higher in the coastal area than in the inland area (Table 1). This was also the case with the water vole and field vole alone, while the bank vole numbers were significantly higher in the coastal area.

The effects of the explanatory weather variables studied somewhat varied between species and areas (Tables 2, 3, 4). Mild winters suggested high number of water voles and inland field voles but low number of bank voles. In most cases, various large-scale climatic factors (monthly NAO indices) explained well the number of different vole species. High December temperatures seemed to affect negatively particularly the coastal vole populations while the deep snow cover in March seemed to have a similar effect

Table 1 Local differences in the number of voles found in the tawny owl nest bottom samples ($n = 129$) in a coastal and in an inland area in southern Finland between 1986 and 2003 based on generalized linear mixed models with a random intercept for territory ID ($n = 64$; variance 0.333–0.464) and year ($n = 18$; variance 0.275–0.957) (see main text for details)

Fixed effects	Value	±SE	z	P
Water vole				
Coastal (intercept)	1.172	0.277	4.236	<0.001
Inland	−0.178	0.229	−0.777	0.437
Field vole				
Coastal (intercept)	1.882	0.264	7.143	<0.001
Inland	−0.223	0.226	−0.987	0.324
Bank vole				
Coastal (intercept)	0.865	0.205	4.209	<0.001
Inland	−0.634	0.254	−2.493	0.013
Voles total				
Coastal (intercept)	2.577	0.223	11.563	<0.001
Inland	−0.157	0.183	−0.858	0.391

on the inland populations. The frost seesaw effect, particularly in March, seemed to have a negative impact on the coastal field vole population.

There was a significant declining trend in the water vole numbers between 1986 and 2003 ($z = -5.755$, $P < 0.001$) due to highly significant trend in the inland area (1995–2003) ($z = -9.448$, $P < 0.001$) (Fig. 3). In the coastal area there was no trend (1986–1999) ($z = 0.353$, $P = 0.724$). In the field vole, the trend was negative throughout the study period (1986–2003) ($z = -5.903$, $P < 0.001$) as well as in the both study areas separately (coastal 1986–1999: $z = -4.140$, $P < 0.001$; inland 1995–2003: $z = -4.289$, $P < 0.001$) (Fig. 3). In the bank vole, there were no trends in the separate study areas ($z = -0.338$, $P = 0.735$ and $z = -0.739$, $P = 0.460$, in the coastal and inland areas, respectively). The spurious declining trend through the whole study period ($z = -2.270$, $P = 0.023$) is due to the higher vole numbers in the coastal area (Fig. 3). There was a significant positive trend in the intensity of the frost seesaw in March in the coastal study area ($t_{12} = 2.21$, $P = 0.024$). In other explanatory variables, there were no significant trends.

Discussion

Coastal tawny owl nests had more vole remains than inland nests. Prey remains accumulate in the nest box during the nestling period, which lasts about 1 month. In our study areas, tawny owls laid their eggs, in general, in late March–early April (Kekkonen et al. 2008; Solonen 2014). Thus

Table 2 Relationships between the number of individuals in tawny owl prey samples and various winter weather factors in coastal and inland populations of the water vole *Arvicola amphibius* in southern Finland revealed by generalized linear mixed models

Variable	Estimate	±SE	z	P
Coastal				
Feb NAO	0.299	0.080	3.7	0.000
Dec temp	-0.263	0.080	-3.3	0.001
Jan NAO	-0.177	0.111	-1.6	ns
Mar snow	-0.021	0.014	-1.5	ns
Feb frost	0.056	0.040	1.4	ns
Feb temp	0.076	0.060	1.3	ns
Mar NAO	0.176	0.141	1.2	ns
Mar frost	-0.072	0.069	-1.1	ns
Dec NAO	-0.104	0.107	-1.0	ns
Dec snow	0.022	0.031	0.7	ns
Winter NAO	0.110	0.215	0.5	ns
Dec frost	-0.031	0.062	-0.5	ns
Winter snow	-0.019	0.038	-0.5	ns
Jan frost	-0.016	0.045	-0.3	ns
Jan temp	-0.020	0.057	-0.3	ns
Feb snow	0.006	0.024	0.2	ns
Mar temp	0.019	0.113	0.2	ns
Winter temp	-0.014	0.101	-0.1	ns
Winter frost	0.001	0.020	0.0	ns
Jan snow	-0.001	0.024	-0.0	ns
Inland				
Mar snow	-0.043	0.022	-2.0	ns
Feb NAO	0.397	0.225	1.8	ns
Mar NAO	0.444	0.285	1.6	ns
Feb snow	0.058	0.040	1.4	ns
Mar temp	0.312	0.219	1.4	ns
Feb temp	0.164	0.116	1.4	ns
Feb frost	0.132	0.121	1.1	ns
Mar frost	0.094	0.091	1.0	ns
Dec NAO	-0.158	0.161	-1.0	ns
Winter frost	0.033	0.047	0.7	ns
Jan frost	-0.069	0.132	-0.5	ns
Jan snow	0.019	0.038	0.5	ns
Dec temp	-0.044	0.106	-0.4	ns
Winter temp	0.084	0.218	0.4	ns
Winter NAO	0.115	0.330	0.3	ns
Jan NAO	-0.068	0.237	-0.3	ns
Winter snow	-0.006	0.051	-0.1	ns
Jan temp	-0.012	0.166	-0.1	ns
Dec snow	0.004	0.055	0.1	ns
Dec frost	-0.007	0.112	-0.1	ns

The significance level using Bonferroni correction is 0.05/20 = 0.0025

ns not significant

Table 3 Relationships between the number of individuals in tawny owl prey samples and various winter weather factors in coastal and inland populations of the field vole *Microtus agrestis* in southern Finland revealed by generalized linear mixed models

Variable	Estimate	±SE	z	P
Coastal				
Dec temp	-0.348	0.087	-4.0	0.000
Mar frost	-0.202	0.061	-3.3	0.000
Winter frost	-0.053	0.020	-2.7	ns
Jan frost	-0.119	0.044	-2.7	ns
Winter temp	-0.258	0.099	-2.6	ns
Dec frost	-0.143	0.068	-2.1	ns
Jan temp	-0.125	0.059	-2.1	ns
Feb snow	0.051	0.024	2.1	ns
Jan NAO	-0.259	0.125	-2.1	ns
Mar temp	-0.232	0.123	-1.9	ns
Winter snow	0.069	0.038	1.8	ns
Mar snow	0.028	0.017	1.7	ns
Feb temp	-0.065	0.074	-0.9	ns
Feb NAO	-0.112	0.127	-0.9	ns
Winter NAO	-0.219	0.255	-0.9	ns
Dec snow	0.032	0.039	0.8	ns
Mar NAO	0.136	0.183	0.7	ns
Dec NAO	0.037	0.137	0.3	ns
Jan snow	-0.007	0.028	-0.3	ns
Feb frost	-0.006	0.052	-0.1	ns
Inland				
Mar snow	-0.035	0.008	-4.3	0.000
Feb NAO	0.323	0.089	3.6	0.000
Mar NAO	0.407	0.116	3.5	0.000
Feb temp	0.153	0.049	3.2	0.002
Feb frost	0.129	0.056	2.3	ns
Winter snow	-0.043	0.023	-1.9	ns
Mar temp	0.193	0.112	1.7	ns
Winter temp	0.182	0.103	1.8	ns
Winter NAO	0.226	0.167	1.4	ns
Dec snow	-0.036	0.026	-1.4	ns
Winter frost	0.029	0.024	1.2	ns
Jan frost	0.070	0.066	1.1	ns
Jan snow	-0.015	0.020	-0.8	ns
Jan temp	0.055	0.087	0.6	ns
Dec NAO	-0.052	0.092	-0.6	ns
Jan NAO	0.062	0.129	0.5	ns
Feb snow	0.008	0.024	0.3	ns
Mar frost	0.011	0.049	0.2	ns
Dec frost	-0.004	0.060	-0.1	ns
Dec temp	-0.004	0.056	-0.1	ns

The significance level using Bonferroni correction is 0.05/20 = 0.0025

ns not significant

Table 4 Relationships between the number of individuals in tawny owl prey samples and various winter weather factors in coastal and inland populations of the bank vole *Myodes glareolus* in southern Finland revealed by generalized linear mixed models

Variable	Estimate	±SE	z	P
Coastal				
Dec temp	-0.192	0.070	-2.7	ns
Mar frost	-0.100	0.051	-2.0	ns
Jan NAO	-0.135	0.090	-1.5	ns
Feb frost	0.039	0.032	1.2	ns
Feb NAO	0.102	0.085	1.2	ns
Dec snow	0.023	0.023	1.0	ns
Feb snow	0.015	0.019	0.8	ns
Winter snow	0.017	0.030	0.6	ns
Dec NAO	-0.042	0.084	-0.5	ns
Jan frost	-0.016	0.038	-0.2	ns
Winter temp	-0.031	0.086	-0.4	ns
Dec frost	-0.018	0.051	-0.4	ns
Winter NAO	-0.055	0.181	-0.3	ns
Feb temp	0.014	0.051	0.3	ns
Mar NAO	0.035	0.124	0.2	ns
Winter frost	-0.004	0.016	-0.2	ns
Jan snow	-0.002	0.019	-0.1	ns
Mar temp	0.010	0.093	0.1	ns
Jan temp	-0.003	0.049	0.2	ns
Mar snow	-0.000	0.012	-0.0	ns
Inland				
Dec NAO	-0.219	0.045	-4.9	0.000
Mar snow	-0.027	0.009	-3.1	0.002
Mar frost	-0.088	0.034	-2.6	ns
Dec frost	-0.103	0.047	-2.2	ns
Winter frost	-0.046	0.021	-2.2	ns
Jan NAO	-0.168	0.100	-1.7	ns
Mar NAO	0.187	0.142	1.3	ns
Winter NAO	-0.183	0.155	-1.2	ns
Feb NAO	0.122	0.113	1.1	ns
Feb snow	0.019	0.020	1.0	ns
Winter temp	-0.080	0.109	-0.7	ns
Jan snow	0.012	0.018	0.7	ns
Dec snow	-0.015	0.026	-0.6	ns
Winter snow	-0.013	0.024	-0.5	ns
Feb frost	-0.030	0.063	-0.5	ns
Jan temp	-0.026	0.080	-0.3	ns
Mar temp	-0.020	0.114	-0.2	ns
Feb temp	-0.010	0.063	-0.2	ns
Jan frost	0.009	0.064	0.1	ns
Dec temp	-0.003	0.051	-0.1	ns

The significance level using Bonferroni correction is $0.05/20 = 0.0025$

ns not significant

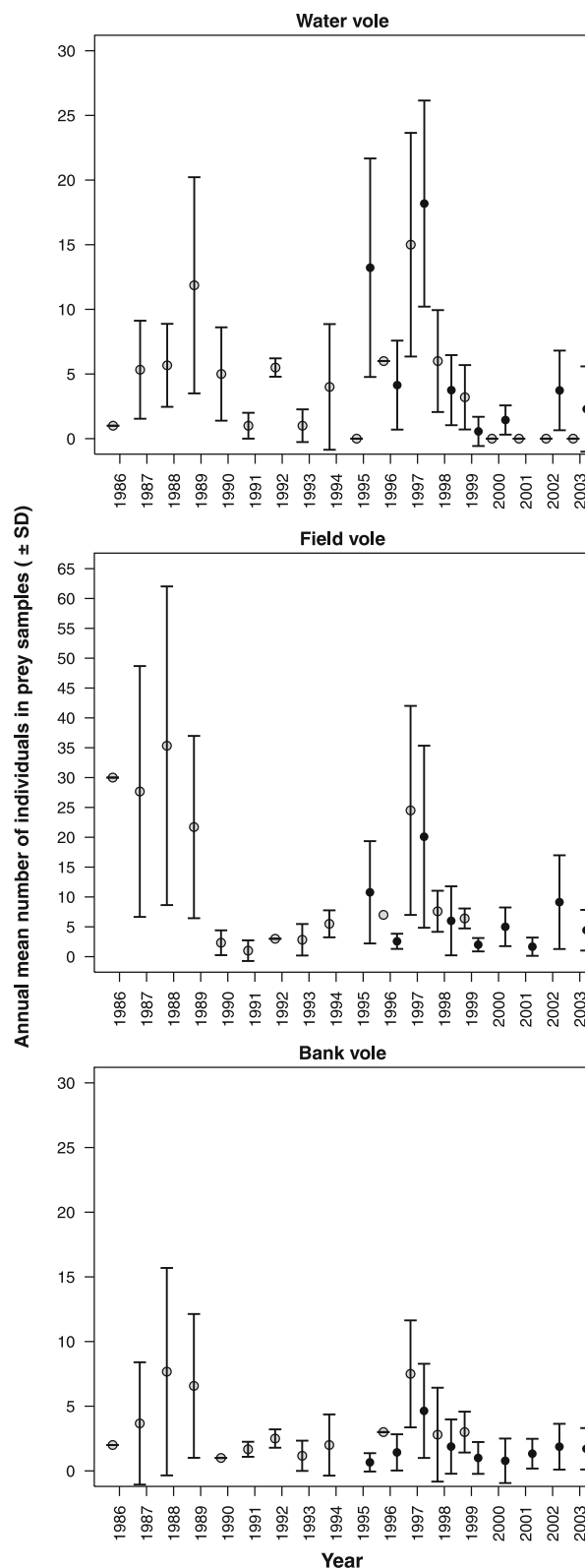


Fig. 3 Mean number and standard deviations of the three vole species found in the nest boxes during the study period. Grey circles present coastal study area and black circles inland study area in each year. In some years data were available for only one of the study areas. The vertical axis scales are different among the panels

there were nestlings in the nest in late April–early June, at a time when the snow has already melted in both areas. Thus the hunting success can be expected to be similar in both areas. The higher number of small voles (in particular bank voles) in the tawny owl prey samples in the coastal area suggest that vole populations were denser in the coastal than in the inland area.

In accordance with the expectations, high December temperatures and frequent occurrence of the frost seesaw in March were followed by lower number of small voles (in particular field voles) in the coastal area. However, mild Decembers (high NAO), in general, seemed to have a similar effect on inland bank voles. Mild ends of winter (high NAO in February and March) seemed to be favourable to inland field voles and (especially coastal) water voles. The depth of the snow cover in March showed a significant effect only on the inland populations of voles. Deep snow cover in March was followed by low number of all the vole species. The average snow cover in March amounted to 17.4 cm in the coastal area and to 31.2 cm in the inland area.

Following the expectations, the effect of the frost seesaw was most pronounced on the field voles that occupy, in general, more low-lying habitats than the other species. However, the frequent occurrence of the frost seesaw in March, in particular, may have an impact on the bank voles as well. It is well-known that besides forests, bank voles inhabit various more open lowland habitats (Amori et al. 2008). The significant positive trend in the intensity of the frost seesaw in March in the coastal study area coincided with the pronounced negative trend in the field vole population. As expected, the most pronounced effects seemed to be due to short-term factors, and they occurred over a wide range of populations.

Impacts of winter weather conditions on the population dynamics of voles

The geographical difference in vole abundance between the study areas diminished in mild winters, particularly during those periods when the ambient temperature fluctuated frequently around the freezing point. This was probably due to increased mortality particularly in the field vole populations of the coastal area (cf. Solonen 2006). The opposite trends in the intensity of the frost seesaw in March and in the number of coastal field voles reinforce this impression. Our results also suggest that the deaths of voles mainly took place during relatively short periods of time (within months) and non-selectively over various species and populations.

Our results suggest that coastal vole populations are more vulnerable to mild winters than inland ones. This is in accordance with some earlier findings (Solonen and

Karhunen 2002; Solonen 2004, 2006). However, there are studies (Tkadlec et al. 2006; Hoset et al. 2009; Brommer et al. 2010; Korpela et al. 2013; Gouveia et al. 2015) which have shown a positive or a non-significant relationship between a mild winter and vole population size in the following spring. The present results suggest that the discrepancy between the results of some studies may be due to the differences in the thickness of the snow cover between areas or years considered, as well as between the periods of winter time examined. When the snow cover is thick, the effect of mildness on the survival of voles diminishes or disappears. If the period of time during winter when the effect is examined is too long, the relationships between the explanatory and response variables may be diluted to insignificant.

Decline and long-term depression of mean densities of the grey-sided vole *Myodes rufocanus* (Sundevall 1846) and the field vole have occurred in managed forest landscapes of Sweden since the 1970s (Magnusson et al. 2015). When winter survival of voles was poor during a number of years when winters were mild suggests that there was a common driver related to the climate which affected vole survival. However, for the grey-sided vole, it is probable that climate is not the dominating driver due to different timing of the decline. Instead, habitat loss was concluded as being a potential cause of the decline of grey-sided vole densities. Even though the Swedish landscape has changed favourably for the needs of the field vole, field vole densities have been low. This suggests, that there is another factor than landscape structure which affects field vole densities. Recently, field vole populations in Sweden have recovered. At the same time there were favourable snow conditions for field vole survival. This suggests that the climate is a decisive factor affecting field vole dynamics. The depth of the snow cover during winter may be correlated directly with vole demography, having both direct and delayed effects (Boonstra and Krebs 2006). The overwinter survival may be a function of overwinter food availability that depends on the snow conditions of the previous winter.

Indirect measurements of vole abundance

We used the owl hunting success upon voles as a proxy for vole abundance in the field. These kinds of indirect measurements of vole abundance have their pros and cons. The prey remains method covers much larger areas, longer periods and a wider spectrum of individuals and species than is, in general, the case with direct methods such as local snap trappings (e.g., Balàuskienė 2005; Solonen et al. 2015). Though the analysis of food remains of vole-eating birds of prey may be spatially more comprehensive than other indirect methods or direct trapping as a tool for

monitoring of small mammals, the collecting of samples as well as picking and identifying prey remains is still quite laborious. There may be difficulties in the interpretation of the results of the prey remain analyses as well. For instance, snow cover may reflect the fact that after snowy winters, tawny owls breed late (Solonen et al., personal observations). In the nest bottoms of late broods there tend to be less voles and more birds, probably because especially young thrushes are easy prey. Thus there may be a degree of difficulty in separating the effects of snow on the voles and on the owls.

In conclusion, our results show that with some caution tawny owl prey remains can be used in a meaningful manner to study vole population dynamics. This is a most rewarding finding, because the study of owl prey remains is a classical topic in ornithology. We are sure there is a wealth of data of various species, which could be used in totally new contexts.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest. All applicable institutional and/or national guidelines for the care and use of animals were followed.

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