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Are vole-eating owls affected by mild winters in southern Finland?

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Relationships between winter temperatures, vole abundance, and the occurrence and breeding of various vole-eating owls were studied on the basis of Finnish data collected in 1986–2000. The species included two resident generalists (Tawny Owl *Strix aluco* and Ural Owl *S. uralensis*) and two nomadic vole specialists (Long-eared Owl *Asio otus* and Tengmalm's Owl *Aegolius funereus*). Near the southern coast, spring vole abundance contributed significantly to the occurrence and breeding of owls, while in inland populations they seem already to be largely governed by the vole abundance of the preceding autumn. The mild winter temperatures contributed negatively to the abundance of vole specialists, whereas Tawny Owls of southern distribution seemed to be both positively and negatively affected. When only the good vole years were included in the analyses, the positive effect of high winter temperatures on the occurrence of resident species and their negative effect on the clutch size and breeding success of owls, in general, were emphasised. When the mildness of winters near the southern coast of Finland was characterised by the number of the days during which the ambient temperature at least once fell from plus to minus °C (the intensity of the "frost seesaw"), additional significant relationships between mild winters and the occurrence and breeding of owls emerged. The frost seesaw contributed negatively, in combination with the positive contribution of vole abundance, to the occurrence and breeding frequency of nomadic vole specialists, and explained alone a considerable proportion of the variation in the breeding effort of all the species. In mild winters a lesser proportion of voles seemed to survive from autumn to spring, providing an explanation for the negative effects of mild winters on owls.

1. Introduction

The close relationship between the fluctuating abundance of small microtine voles, and the occurrence and breeding success of vole-eaters is well known (e.g., Linkola & Myllymäki 1969, Mikkola 1983, Korpimäki 1985, Hanski *et al.* 1991, Brommer *et al.* 2002). Recently, increasing irregularity has been reported in previously relatively regular vole cycles in Northern Europe (Lindström & Hörnfeldt 1994, Steen *et al.* 1996, Hansson 1999, Henttonen 2000, Laaksonen *et al.* 2002). Observations on the southern coast of Finland suggest that the formerly regular three-year vole cycles were levelling off, and the general abundance of voles was declining (Solonen 2001, 2002, Solonen & Karhunen 2002). This was proposed to be due to mild and wet winters, causing a so-called "frost seesaw effect", i.e. fluctuation of winter temperatures around the freezing point. The increasing frequency of such circumstances with alternating wet and cold periods was supposed to be especially disastrous to over-wintering voles by alternatively wetting and freezing their wintering holes. Indirectly, the effect of mild winters was linked to observations on the occurrence and breeding of some vole-eating owls.

In this paper, the regional scale of the earlier reports is widened to cover the whole Finnish range of the species considered. I examine whether the recent fluctuations and trends in the occurrence and breeding of vole-eating owls in southern Finland vary in accordance with their known response to the abundance of voles, and whether some patterns observed might be due to mild winters and could be explained by the frost seesaw effect. The idea of the frost seesaw effect would be supported 1) by negative relationships between the mildness of winters and the vole abundance, as well as the occurrence and breeding of owls, 2) if the relationships are more pronounced in strict vole specialists than in generalists, and 3) if they are more pronounced near the milder southern coast than elsewhere in the Finnish range of the species. In particular, the occurrence of nomadic vole specialists and the breeding of resident vole-eaters should be negatively affected.

2. Material and methods

2.1. Study species and owl data

Four species of owls were suitable for study due to their ecological characteristics and the availability of data. They included two species of resident generalists and two species of nomadic vole specialists. The resident generalists were the Tawny Owl *Strix aluco* and Ural Owl *S. uralensis*, whose diets are largely composed of small voles (e.g., Mikkola 1983, Korpimäki & Sulkava 1987, Solonen & Karhunen 2002). The distribution of the Tawny Owl in Finland is clearly southern, while the occurrence of the Ural Owl is heavily concentrated in the inner parts of the country (e.g., Solonen 1994, Saurola 1995, Väisänen *et al.* 1998). The nomadic vole specialists were the Long-eared Owl *Asio otus* and Tengmalm's Owl *Aegolius funereus* that both are largely dependent on the availability of small voles (e.g., Korpimäki 1985, 1988). Accordingly, they occur in various parts of the country, following variations in the abundance of their staple food.

The data on vole-eating owls were obtained from the annual reports of the Finnish programme monitoring common raptors and owls (Haapala & Saurola 1986, 1987, 1989, Haapala *et al.* 1990–1998, Taivalmäki *et al.* 1999, 2000, 2001), as well as from a local report on owls (Solonen 2002). The variables characterising the occurrence and breeding of owls in Uusimaa (about 10,000 km^2) near the southernmost coast (here referred to "coastal") and elsewhere within the Finnish range of the species (here referred to "inland") in 1986–2000 included 1) the number of territories recorded (the occurrence of the species), 2) the number of nests recorded (an estimate of the breeding frequency), 3) the average clutch size (the number of eggs laid per nest), and 4) the average fledgling production, or breeding success (the number of nearly fledged young per nesting attempt). These data have collected annually by competent persons using standard methods, so that annual samples seemed to be comparable enough for the purpose of the present study.

2.2. Vole abundance

Vole populations (*Clethrionomys* sp., *Microtus* sp.) were monitored in the coastal area by trapping in two localities, Sipoo (60°N, 25°E) (Solonen 2001, Solonen & Karhunen 2002) and Lohja–Kirkkonummi (60°N, 24°E) (Kimpari Bird Projects; Solonen 2002), situated about 50 km from each other. Small mammals were trapped each spring (early May) and autumn (late October–early November) at several standard points along the catching lines in 1986–2000. The results were expressed as individuals per 100 trap nights. In Sipoo each trapping period of about 24 hrs used 30 points of three traps each along a line of 1.5 km, for a total of 90 trap nights. In Lohja–Kirkkonummi there were two separate trapping areas 13 km apart (data combined). Both trapping areas included a wooded and a field site. The trapping consisted of 16 points of three traps at each site during two approximately 24-hr periods (total of 384 trap nights). For a regional vole index, the results of the separate trapping localities were averaged. Comparable inland data collected during 1986–2000 (Heinola, 61°N, 26°E) were derived from published sources (Brommer *et al.* 2002, Sundell *et al.* 2004). On the basis of vole abundance indices of the preceding autumn, the breeding seasons of owls were classified as belonging to either "good" or "poor" vole years, corresponding to good and poor vole years in the three-year vole cycles (Solonen & Karhunen 2002).

2.3. Weather conditions

The mean ambient temperature of winter, including months from December to February, from the coastal area at Helsinki-Vantaa airport (60°N, 25°E), and from the inland area at Jyväskylä, Central Finland (62°N, 25°E) were gathered from the 1985–2000 reviews of the Finnish Meteorological Institute. The number of days during which the ambient temperature at least once fell from plus to minus °C, i.e. the intensity of the frost seesaw, was considered as a possible explanation of the mechanism of the effect of mild winters on voles (Solonen 2001). This measure seems to characterise well the recent mildness of winters in southernmost Finland (Solonen & Karhunen 2002). More precisely, mildness here means the average vicinity of winter temperatures to freezing. In addition, the average depth of the snow cover in March at the beginning of the breeding season of owls was considered, because snow cover is known to be of significance for both voles and owls (e.g., Linkola & Myllymäki 1969, Hansson & Henttonen 1985, Jędrzejewski *et al.* 1994).

2.4. Statistical analyses

Fluctuations in various parameters were examined by Spearman rank correlation and trends by linear regression (Sokal & Rohlf 1981, Fowler & Cohen 1986). The dependent variables, characterising the occurrence and breeding of owls, were put with the independent variables into backward stepwise multiple regression analyses (Sokal & Rohlf 1981) to reveal the relative importance of voles and possible additional contributions of weather factors on owls (P-to-enter < 0.08, P-to-remove < 0.08). Similar analyses were performed also between the

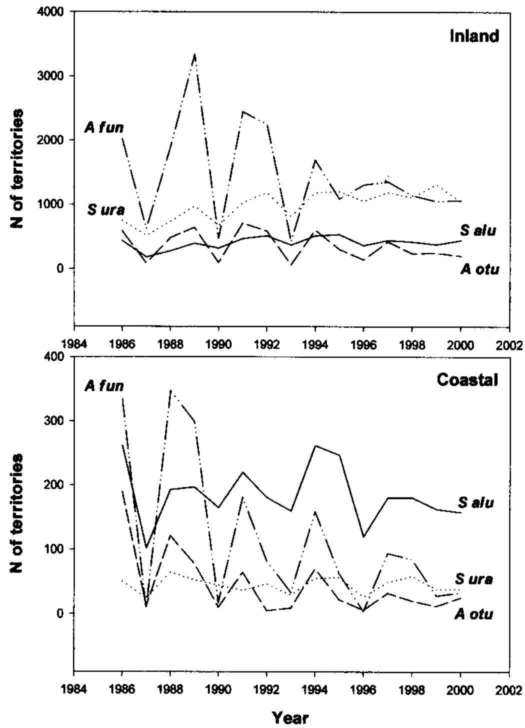

Fig. 1. Fluctuations in the numbers of owl territories recorded near the southern coast (Coastal) and elsewhere (Inland) in Finland in 1986–2000. Nomadic vole specialists: *A fun* = *Aegolius funereus*, *A otu* = *Asio otus*, and resident generalists: *S alu* = *Strix aluco*, *S ura* = *S. uralensis*.

vole abundance indices and winter weather factors to indicate possible mechanisms of the processes. The differences between the resident generalist and nomadic vole specialist owls, as well as those between the data from the coastal area and inland were examined. To eliminate the heavily confusing effect of the regularly cyclic vole crashes that were independent on winter temperatures, the analyses were also performed after excluding the data of poor vole years. In calculations, SigmaStat 2.03 statistical software was used.

3. Results

3.1. Fluctuations and trends

The fluctuations in the occurrence of both resident generalist and nomadic vole specialist owls in Finland in 1986–2000 showed broadly similar pat-

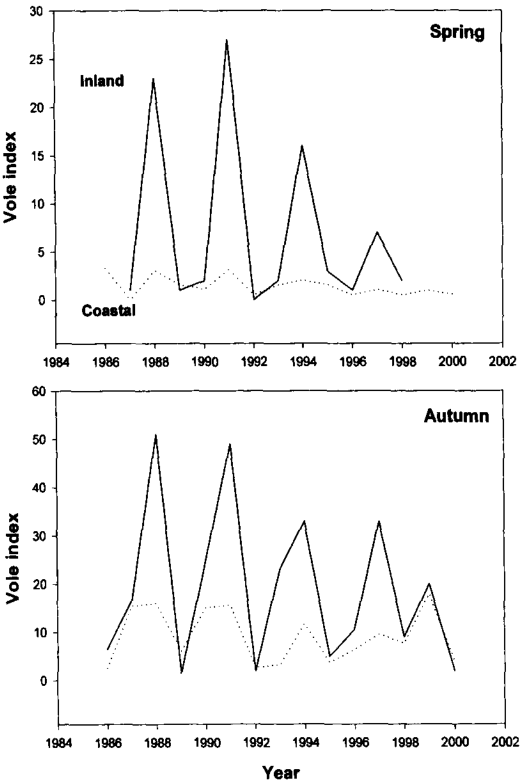

Fig. 2. Fluctuations in the spring and autumn vole abundance indices (individuals/ 100 trap nights) of the coastal area (Uusimaa) and those of an inland region (Heinola) in Finland in 1986–2000.

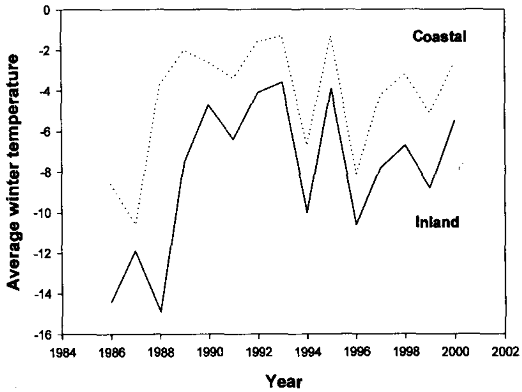

Fig. 3. Fluctuations in the mean mid-winter (December–February) temperature (°C) in the coastal area (Vantaa) and inland (Jyväskylä) in 1986–2000.

terns (Fig. 1). In the coastal region, the correlation was significant between each pair of the species considered ($r_S = 0.56–0.83$, $P < 0.05$, $n = 15$). The number of territories of the Tawny Owl and Ural Owl remained relatively stable (linear regression; $t_{13} = -0.61$, and $t_{13} = -0.22$, respectively, $P > 0.05$) while the occurrence of the vole specialists (Long-eared Owl and Tengmalm's Owl) significantly declined during the study period ($t_{13} = -2.51$, $P < 0.05$, and $t_{13} = -2.53$, $P < 0.05$, respectively). Elsewhere in Finland, the Tawny Owl numbers fluctuated in agreement with the coastal population of the species ($r_S = 0.59$, $P < 0.05$, $n = 15$) and remained at a relatively stable level ($t_{13} = 1.64$, $P = 0.13$, $n = 15$). The numbers of Ural Owl territories recorded showed no correlation with those of the other owl populations except Tawny Owls of the same region ($r_S = 0.66$, $P < 0.01$, $n = 15$), but they increased significantly ($t_{13} = 4.16$, $P < 0.01$). The numbers of Long-eared and Tengmalm's Owls fluctuated in considerable synchrony ($r_S = 0.91$, $P < 0.001$, $n = 15$), but showed no trends ($t_{13} = -1.20$, and $t_{13} = -1.26$, respectively, $P > 0.05$).

Coastal and inland vole abundance indices fluctuated in significant synchrony (in spring, $r_S = 0.78$, $P < 0.01$, $n = 12$, and in autumn, $r_S = 0.66$, $P < 0.05$, $n = 13$), but their general levels in good vole years were considerably higher in the inland than in the coastal region (Fig. 2). There was no significant correlation between regional autumn and spring vole indices ($r_S = -0.08–0.22$, $P > 0.05$, $n = 12$ and 15). The regional vole indices showed no significant trends, but the coastal spring index decreased nearly significantly ($t_{13} = -1.98$, $P = 0.07$) during the study. The highest peaks of the cycles dropped pronouncedly as well. The regional mean winter temperatures fluctuated in significant synchrony ($r_S = 0.88$, $P < 0.001$, $n = 15$; Fig. 3), but they were considerably higher near the southern coast (averaging –4.3 ± 2.9 (SD) °C) than in central Finland (averaging –8.1 ± 3.7 (SD) °C).

3.2. Relationships between owls, voles and winter temperature

In the coastal area, spring vole abundance contributed significantly (positively), especially to the occurrence of Tawny Owls, the breeding effort of Ural Owls, and the occurrence and breeding frequency of the nomadic vole specialists (Table 1). In inland populations of owls, the occurrence and breeding seemed to be largely already governed by

Table 1. Backward stepwise multiple regression analyses of the contributions of vole abundance and winter temperature to the occurrence, breeding frequency, clutch size, and fledgling production of Tawny Owls (*Salu*), Ural Owls (*Sura*), Long-eared Owls (*Aotu*) and Tengmalm's Owls (*Afun*) in 1986–2000 in the coastal area (n = 15) and inland (n = 12).

Species	Dependent variable	Coastal Vs	R^2	F	P	Inland Vs	R^2	F	P
Salu	Occurrence	Sv	0.49	14.4	0.002	Ta	0.25	4.6	0.057
	Breeding freq.	Sv	0.33	7.9	0.015	Av	0.35	6.9	0.025
	Clutch size	Sv	0.30	7.0	0.020	Sv			0.013
						Av			0.017
						Ta			0.035
						Tot	0.73	10.9	0.003
	Fl. production	Sv	0.19	4.3	0.060	Sv	0.34	6.8	0.026
Sura	Occurrence	No				Av	0.22	4.1	0.071
	Breeding freq.	Av	0.29	6.4	0.027	Av	0.47	10.9	0.008
	Clutch size	Sv	0.54	17.4	0.001	Av	0.28	5.4	0.043
	Fl. production	Sv	0.55	17.8	<0.001	No			
Aotu	Occurrence	Sv			<0.001	Av			<0.001
		Te			0.006	Sv			<0.001
		Av			0.026	Tot	0.82	25.7	<0.001
		Tot	0.81	21.0	<0.001				
	Breeding freq.	Sv			0.002	Av			<0.001
		Ta			0.019	Sv			<0.001
		Av			0.043	Tot	0.82	25.6	<0.001
		Tot	0.71	12.1	<0.001				
	Clutch size	..				Ta			0.006
						Av			0.061
						Tot	0.52	7.2	0.014
	Fl. production	..				Ta	0.65	21.5	<0.001
Afun	Occurrence	Sv	0.61	22.6	<0.001	Av			0.002
						Sv			0.060
						Tot	0.66	11.7	0.003
	Breeding freq.	Sv	0.60	21.9	<0.001	Av	0.46	10.5	0.009
	Clutch size	Ta	0.39	8.5	0.014	Ta			0.001
						Av			0.008
						Tot	0.69	13.2	0.002
	Fl. production	No				Ta			<0.001
						Av			0.034
						Tot	0.71	14.5	0.002

The independent variables included were 1) the vole abundance index of preceding autumn (Av), 2) the spring vole abundance index (Sv), and 3) the mean ambient temperature in December–February (Ta). Explaining variables included in the models (Vs), adjusted R^2 as well as F and P of the variance analyses are given. "No" means that all variables were eliminated from the model.

the vole abundance of the preceding autumn. In the coastal area, the mean winter temperature contributed negatively to the occurrence and breeding frequency of Long-eared Owls and clutch size of Tengmalm's Owls. Clutch size and fledgling production of inland populations of both these species seemed to be similarly affected. In inland Tawny Owls, the occurrence seemed to be positively, while the clutch size was negatively affected by the mildness of winter.

When only the primarily good vole years were included in the analyses, the positive effect of high winter temperatures on the occurrence of resident species and their negative effect on the clutch size and breeding success of owls, in general, were emphasised (Table 2). When the mildness of winters in the coastal area was characterised by the intensity of the frost seesaw, additional significant relationships between mild winters and the occurrence and breeding of owls emerged (Table 3). The

Table 2. Backward stepwise multiple regression analyses of the contributions of vole abundance and winter temperature to the occurrence, breeding frequency, clutch size, and fledgling production of Tawny Owls (*Salu*), Ural Owls (*Sura*), Long-eared Owls (*Aotu*) and Tengmalm's Owls (*Afun*) in good vole years in 1986–2000 in the coastal area (n = 10) and inland (n = 8).

Species	Dependent variable	Coastal Vs	R^2	F	P	Inland Vs	R^2	F	P
Salu	Occurrence	Sv	0.32	5.2	0.052	Ta	0.56	10.0	0.019
	Breeding freq.	No				Ta	0.46	7.0	0.038
	Clutch size	No				Ta	0.72	18.9	0.005
	Fl. production	No				Ta	0.62	12.3	0.013
Sura	Occurrence	No				Ta	0.50	8.0	0.030
	Breeding freq.	No				No			
	Clutch size	Sv	0.48	9.2	0.016	No			
	Fl. production	Sv	0.43	7.7	0.024	No			
Aotu	Occurrence	Ta			0.016	No			
		Sv			0.051				
		Av			0.073				
		Tot	0.84	16.4	0.003				
	Breeding freq.	Ta			0.003	No			
		Av			0.030				
		Tot	0.69	11.0	0.007				
	Clutch size	..				No			
	Fl. production	..				Ta	0.60	11.3	0.015
Afun	Occurrence	Sv	0.56	12.3	0.008	No			
	Breeding freq.	Sv	0.56	12.3	0.008	No			
	Clutch size	Sv	0.37	6.2	0.038	Av			0.004
						Sv			0.004
						Ta			0.007
						Tot	0.93	33.1	0.003
	Fl. production	No				Ta			0.003
						Av			0.057
						Tot	0.79	14.5	0.008

The independent variables included were 1) the vole abundance index of preceding autumn (Av), 2) the spring vole abundance index (Sv), and 3) the mean ambient temperature in December–February (Ta). Explaining variables included in the models (Vs), adjusted R^2 as well as F and P of the variance analyses are given. "No" means that all variables were eliminated from the model.

frost seesaw contributed negatively, in combination with the positive contribution of the vole abundance, to the occurrence and breeding frequency of nomadic vole specialists, and explained alone a considerable proportion of the variation in the breeding effort of all the species. In good vole years, the relative role of the frost seesaw effect in these relationships was emphasised.

In good vole years of the coastal area, the mildness of winter contributed negatively also to the proportion between the spring and autumn vole abundance (temperature: $R^2 = 0.37$, $F_{1,8} = 6.3$, $P < 0.05$; frost seesaw: $R^2 = 0.27$, $F_{1,8} = 4.4$, $P > 0.05$). The snow cover in March explained a considerable proportion of the variation in the spring vole abundance (positive contribution; $R^2 = 0.48$, $F_{1,8} = 9.4$, $P < 0.05$).

4. Discussion

4.1. Relationships between the vole abundance and owls

The occurrence and breeding of vole-eating owls were, as expected, largely determined by the abundance of voles. Especially the occurrence and breeding frequency of vole specialists near the southern coast of Finland seemed to be affected. In the coastal area, much of the variation in these parameters was explained mainly by the spring vole index, whereas elsewhere it was the vole abundance of the preceding autumn. These observations suggest that over-wintering voles manage better inland than in the coastal region. The levelling of the vole cycles and the declining trends in

Table 3. Backward stepwise multiple regression analyses of the contributions of vole abundance and the mildness of winter to the occurrence, breeding frequency, clutch size, and fledgling production of Tawny Owls (*Salu*), Ural Owls (*Sura*), Long-eared Owls (*Aotu*) and Tengmalm's Owls (*Afun*) in the coastal area in 1986–2000 in all years (n = 15) and when only the good vole years of each 3-year cycle were included (n = 10).

Species	Dependent variable	All years Vars	R^2	F	P	Good vole years Vars	R^2	F	P
Salu	Occurrence	No				Sv	0.32	5.2	0.052
	Breeding freq.	No				No			
	Clutch size	No				Fr	0.44	8.0	0.022
	Fl. production	No				Fr	0.41	7.2	0.028
Sura	Occurrence	No				No			
	Breeding freq.	No				No			
	Clutch size	No				Fr	0.67	19.6	0.002
	Fl. production	No				Sv	0.43	7.7	0.024
Aotu	Occurrence	Sv			<0.001	Fr			<0.001
		Fr			0.001	Av			0.008
		Av			0.008	Sv			0.022
		Tot	0.86	28.7	<0.001	Tot	0.94	48.7	<0.001
	Breeding freq.	Sv			0.004	Fr			<0.001
		Fr			0.005	Av			0.009
		Av			0.017	Tot	0.83	23.1	<0.001
		Tot	0.76	16.1	<0.001				
Afun	Occurrence	Sv			0.003	Fr			0.007
		Av			0.019	Av			0.053
		Fr			0.071	Tot	0.59	7.5	0.018
		Tot	0.73	13.8	<0.001				
	Breeding freq.	Sv			0.003	Fr			0.007
		Av			0.016	Av			0.032
		Fr			0.029	Tot	0.62	8.3	0.014
		Tot	0.75	14.9	<0.001				
	Clutch size	Fr	0.62	20.6	<0.001	Fr	0.67	19.3	0.002
	Fl. production	Fr	0.43	10.1	0.009	Fr	0.51	10.3	0.013

The independent variables included were 1) the vole abundance index of preceding autumn (Av), 2) the spring vole abundance index (Sv), and 3) intensity of the frost see-saw (Fr). Explaining variables included in the models (Vs), adjusted R^2 as well as F and P of the variance analyses are given. "No" means that all variables were eliminated from the model.

vole specialists near the southern coast reinforce this impression.

Specialist mammalian predators are suggested to be a driving force of the cyclic fluctuations of small rodents (Henttonen *et al.* 1987, Korpimäki *et al.* 2002), while avian predators (including nomadic vole specialists) should stabilise their numbers (Andersson & Erlinge 1977, Korpimäki 1985, Korpimäki & Norrdahl 1989, 1991, Hanski *et al.* 1991). If this were the case, a decline of mammalian specialists (mustelids) might explain the levelling of the vole cycles. The increase of avian vole-eaters might also explain the decline in the level of vole populations. On the basis of the present data, as well as the nation-wide data on other avian vole-eaters (Taivalmäki *et al.* 2001), the trends in the abundance of avian vole-eaters, if they exist, are, however, rather declining than increasing.

4.2. Mild winters and the occurrence and breeding of vole-eaters

Mild winter temperatures contributed negatively to the breeding effort of owls. They seemed to have a negative effect also on the occurrence and breeding frequency of Long-eared Owls in the coastal area, but a positive effect on those of the inland population of Tawny Owls. This suggests that the mildness of winters had deteriorated regional attractiveness for owls near the southern coast and improved their over-wintering conditions elsewhere.

Relationships between the intensity of the frost seesaw and the variables characterising the occurrence and breeding of owls were negative, following the logic of adverse effects of mild winters due to the frost seesaw effect on voles (Solonen 2001). Significant relationships emerged most pronouncedly in good vole years, when also the role of the autumn vole abundance was emphasised. This suggests that in poor vole years voles were generally too scarce even without the effect of the frost seesaw to be effectively preyed upon by predators.

In vole specialists the clutch size and breeding success seemed to be heavily affected by mild winters. This conforms to the assumption that they are more susceptible to the variations in vole abundance than generalists whose diets include much alternative prey, especially in poor vole years (e.g., Mikkola 1983). Of the generalists examined, the Tawny Owl seemed to be both more sensitive and more vulnerable to the negative effects of mild winters than the Ural Owl of more inland distribution.

4.3. Effects of mild winters on voles

In the coastal area, a lesser proportion of voles seemed to survive from autumn to spring in mild winters than at other times. Though the relationship between the intensity of the frost seesaw and abundance of voles seemed to be weak, it might provide an explanation to the negative effects of mild winters on owls (see below). In addition, in mild winters the snow cover is thinner affecting voles negatively (cf. Hansson & Henttonen 1985, Lindström & Hörnfeldt 1994).

The effects of mild winters obviously extend over large rather than only local areas. At present, however, they probably are more pronounced near the milder climate of the southern coast than elsewhere in Finland. Vole populations are known to fluctuate on large scales (e.g., Hansson & Henttonen 1985, Sundell *et al.* 2004). There are, in addition, some smaller-scale temporal and spatial variations in the rhythm of the abundance fluctuations of voles that may confuse the recorded outcome of the effect of mild winters. This might be due to the frost seesaw effect being more intense in open lowland habitats than in wooded highlands where the water from melted snow does not cover such large areas as commonly occurs in flat open terrain. Correspondingly, similar smaller scale heterogeneity of habitats also offers refuges for some proportion of vole populations. Therefore, since Bank Voles *Clethrionomys glareolus* prefer forests, they are probably less vulnerable to the frost seesaw effect than Field Voles *Microtus agrestis*, which mainly occupy open habitats. In accordance with the above, the long-term trapping data suggest that the earlier fluctuation synchrony between Bank Voles and Field Voles near the southern coast of Finland was disappearing, and that especially the levels of Field Voles were declining (Kimpari Bird Projects, unpubl.).

Mild winters do not necessarily affect the primary factors causing cyclicity in vole populations, unless it is by affecting the numbers of mammalian predators (cf. Hanski *et al.* 1991, Korpimäki *et al.* 2002, Sundell *et al.* 2004). Their direct numerical effect on voles is logically stronger when there are plenty of voles than when voles are scarce. Mild winters may only cut off the highest peaks of vole abundance, making the cyclicity less pronounced. Their effect on voles was thus similarly stabilising in the manner of the nomadic vole specialists (Korpimäki 1985, Korpimäki & Norrdahl 1989).

4.4. Conclusions and prospects

The significant relationships emerging in this study fit rather well the predictions tested from the frost seesaw hypothesis. However, the statistical relationships revealed naturally provide only support for the ideas presented rather than hard evidence. Especially the most probable link between the frost seesaw effect and owls, i.e. the abundance of voles, needs further examination.

As expected, the present results suggest that the negative effects of the unfavourable weather on the wintering conditions of voles were of large scale. Therefore the populations of vole-eaters probably reflect indirectly the regional fluctuations in vole abundance more precisely than the vole trapping samples of relatively restricted spatial cover.

Direct relationships between vole abundance and owls are reflected in the diet of owls. Therefore, long-term studies on the diets of owls provide a tool to examine also the large-scale effects of climatic factors on voles and vole-eating birds of prey.

Such studies are of current interest, because climate change appears to be shifting the zone of high winter temperatures adverse for voles and their predators little by little further northwards. At present this zone covers southernmost Finland, where the low coastal districts seem to be especially vulnerable in terms of the wintering conditions for small mammals.

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Vaikuttavatko Etelä-Suomen leudot talvet myyriä syöviin petolintuihin?

Talvien leutouden, myyrien runsauden ja myyriä syövien petolintujen esiintymisen ja pesinnän välisiä suhteita tutkittiin Suomessa vuosina 1986–2000 kerätyn aineiston valossa. Tarkasteltaviin myyränsyöjiin kuului kaksi paikkauskollista yleispetoa (lehtopöllö ja viirupöllö) sekä kaksi vaeltelevaa myyräspesialistia (sarvipöllö ja helmipöllö).

Pöllöjen esiintyminen ja pesintä riippuivat selvästi keväisestä myyrärunsaudesta, mutta sisämaassa kevään pöllötilanne voitiin arvioida jo edellisen syksyn myyräkannan perusteella. Tästä voidaan päätellä myyrien säilyvän talven yli paremmin sisämaassa kuin rannikolla. Leudot talvet vaikuttivat negatiivisesti etenkin myyriin erikoistuneisiin pöllölajeihin, mutta eteläinen lehtopöllö näytti sekä hyötyvän että kärsivän. Hyvinä myyrävuosina talven leutouden myönteiset vaikutukset paikkalintupöllöjen esiintymiseen ja kielteiset vaikutukset pöllöjen pesintään yleensä korostuivat.

Kun talven leutoutta kuvattiin niiden päivien lukumäärällä, jolloin ilman lämpötila (°C) ainakin kerran laski nollan alapuolelle ("pakkassahan" voimakkuus), paljastui uusia riippuvuussuhteita talven leutouden ja pöllöjen välillä. Pakkassaha vaikutti myyrärunsauden vastaisesti myyräspesialistien esiintymiseen ja pesintään, ja selitti yksin huomattavan osan kaikkien tutkittujen pöllölajien pesintäpanoksen vaihtelusta. Leutoina talvina pienempi osuus myyristä näytti selviytyvän syksystä kevääseen, mikä selittäisi leutojen talvien haitallisen vaikutuksen pöllöihin.

References

Andersson, M. & Erlinge, M. 1977: Influence of predation on rodent populations. — Oikos 29: 591–597.

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.

Fowler, J. & Cohen, L. 1986: Statistics for Ornithologists. — BTO Guide 22.

Haapala, J., Korhonen, J. & Saurola, P. 1990: Breeding of raptors and owls in Finland in 1989. — Lintumies 25: 2–10. (In Finnish with English summary)

Haapala, J., Korhonen, J. & Saurola, P. 1991: Breeding and population trends of common raptors and owls in Finland in 1990. — Lintumies 26: 2–13. (In Finnish with English summary)

Haapala, J., Korhonen, J. & Saurola, P. 1994: Breeding and population trends of common raptors and owls in Finland in 1993. — Linnut 29 (2): 20–24. (In Finnish with English summary)

Haapala, J., Korhonen, J. & Saurola, P. 1995: Breeding and population trends of common raptors and owls in Finland in 1994. — Linnut 30 (2): 20–25. (In Finnish with English summary)

Haapala, J., Korhonen, J. & Saurola, P. 1996: Breeding and population trends of common raptors and owls in Finland in 1995. — Hippiäinen 26 (2): 4–11. (In Finnish with English summary)

Haapala, J., Korhonen, J. & Saurola, P. 1997: Breeding and population trends of common raptors and owls in Finland in 1996. — Linnut-vuosikirja 1996: 41–53. (In Finnish with English summary)

Haapala, J., Korhonen, J. & Saurola, P. 1998: Breeding and population trends of common raptors and owls in Finland in 1997. — Linnut-vuosikirja 1997: 39–54. (In Finnish with English summary)

Haapala, J., Lehtonen, J. T., Korhonen, J. & Saurola, P. 1993: Breeding and population trends of common raptors and owls in Finland in 1992. — Linnut 28 (1): 18–27. (In Finnish with English summary)

Haapala, J., Lehtonen, J. & Saurola, P. 1992: Breeding and population trends of common raptors and owls in Finland in 1991. — Lintumies 27: 2–13. (In Finnish with English summary)

Haapala, J. & Saurola, P. 1986: Breeding of raptors and owls in Finland in 1986. — Lintumies 21: 258–267. (In Finnish with English summary)

Haapala, J. & Saurola, P. 1987: Breeding of raptors and owls in Finland in 1987. — Lintumies 22: 245–251. (In Finnish with English summary)

Haapala, J. & Saurola, P. 1989: Breeding and population trends of common raptors and owls in Finland in 1988. — Lintumies 24: 27–36. (In Finnish with English summary)

Hanski, I., Hansson, L. & Henttonen, H. 1991: Specialist predators, generalist predators, and the microtine rodent cycle. — J. Anim. Ecol. 60: 353–367.

Hansson, L. 1999: Intraspesific variation in dynamics: small rodents between food and predation in changing landscapes. — Oikos 86: 159–169.

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

Henttonen, H. 2000: Long-term dynamics of the bank vole Clethrionomys glareolus at Pallasjärvi, northern Finnish taiga. — In: Bujalska, G. & Hansson, L. (eds.), Bank vole biology: recent advances in the population biology of a model species. — 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.

Jędrzejewski, W., Jędrzejewska, B., Zub, K., Ruprecht, A. L. & Bystrowski, C. 1994: Resource use by Tawny Owls Strix aluco in relation to rodent fluctuations in Bialowieza National Park, Poland. — J. Avian Biol. 25: 308–318.

Korpimäki, E. 1985: Rapid tracking of microtine populations by their avian predators: possible evidence for stabilizing predation. — Oikos 45: 281–284.

Korpimäki, E. 1988: Diet of breeding Tengmalm's Owls Aegolius funereus: long-term changes and year-to-year variation under cyclic food conditions. — Ornis Fenn. 65: 21–30.

Korpimäki, E. & Norrdahl, K. 1989: Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. — Oikos 54: 154–164.

Korpimäki, E. & 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., 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.

Korpimäki, E. & Sulkava, S. 1987: Diet and breeding performance of Ural Owls Strix uralensis under fluctuating food conditions. — Ornis Fenn. 64: 57–66.

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.

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

Linkola, P. & Myllymäki, A. 1969: Der Einfluss der Kleinsäugerfluktuationen auf das Brüten einiger kleinsäugerfressender Vögel im südlichen Häme, Mittelfinnland 1952–1966. — Ornis Fenn. 46: 45–78.

Mikkola, H. 1983: Owls of Europe. — Poyser, Calton. 397 pp.

Saurola, P. (ed.) 1995: Owls of Finland. — Kirjayhtymä, Helsinki. 272 pp. (In Finnish with English summary)

Sokal, R. R. & Rohlf, F. J. 1981: Biometry. — Freeman, New York. 859 pp.

Solonen, T. 1994: Factors affecting the structure of Finnish birds of prey communities. — Ornis Fenn. 71: 156–169.

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. 2002: Monitoring of breeding owls in western Uusimaa, southern Finland, until 2000. — Tringa 29: 34–41. (In Finnish with English summary)

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

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.

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.

Taivalmäki, J.-P., Haapala, J. & Saurola, P. 1999: Breeding and population trends of common raptors and owls in Finland in 1998. — Linnut-vuosikirja 1998: 38–53. (In Finnish with English summary)

Taivalmäki, J.-P., Haapala, J. & Saurola, P. 2000: Breeding and population trends of common raptors and owls in Finland in 1999. — Linnut-vuosikirja 1999: 25–39. (In Finnish with English summary)

Taivalmäki, J.-P., Haapala, J. & Saurola, P. 2001: Breeding and population trends of common raptors and owls in Finland in 2000. — Linnut-vuosikirja 2000: 44–54. (In Finnish with English summary)

Väisänen, R. A., Koskimies, P. & Lammi, E. 1998: Distribution, numbers and population changes of Finnish breeding birds. — Otava, Helsinki. 567 pp. (In Finnish with English summary)