Ornis Fennica 79:121–131. 2002

Effects of variable feeding conditions on the Tawny Owl *Strix aluco* near the northern limit of its range

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Received 15 May 2002, accepted 7 July 2002

Relationships between the wintering conditions, vole abundance, and food and breeding success of a population of Tawny Owls in Uusimaa, southern Finland, were studied during a 15-year period (1986–2000). There were no significant trends in the weather variables studied, though general experience suggested that winters were getting milder. The abundance of small microtine voles, the staple food for owls before the breeding season, fluctuated in three-year cycles, but the general level of vole abundance seems to have lowered after the 1980s. Correspondingly, during the first years of the study the proportion of small voles in the prey of owls was significantly higher than later. When voles were scarce, the proportion of alternative prey in the diet of owls was high. The number of nestings (denoting the breeding frequency of owls) could be predicted from the abundance of voles in spring. On average, the Tawny Owls of the district laid eggs and produced young slightly but not significantly more in "good" vole years than in "poor" ones. The difference was, however, significant in the breeding success of the local population studied. The number of young fledged correlated positively with the number of voles brought to the nest by parents. Significant relationships between the clutch size and fledgling production of owls and the vole abundance and weather variables studied emerged only when the data of the "poor" vole years were excluded. In such cases there was a significant negative relationship between the average clutch size and the "frost see-saw effect", the number of days in winter during which the temperature at least once fell from plus to minus °C. The latter variable was suggested to be negatively correlated with the abundance of voles. The relationship was similar also with the average fledgling production that was, however, largely determined by the clutch size.

1. Introduction

Near the northern border of its present range in southern Finland, the Tawny Owl *Strix aluco* is a relatively new resident inhabitant now well established for over a hundred years (von Haartman *et al.* 1963–1972, Mikkola 1983, Väisänen *et al.* 1998). In their northernmost range Tawny Owls are confronted not only with potential competition by their northern congener the Ural Owl *S.*

uralensis, and to a lesser extent probably also by the Great Grey Owl *S. nebulosa* (Korpimäki 1986), but particularly by their widely varying feeding conditions. Small rodents, the main food of owls especially before the breeding season (Linkola & Myllymäki 1969, Mikkola 1983, Jędrzejewski *et al.* 1994), have shown pronounced cyclic fluctuations in abundance (Kalela 1962, Hansson & Henttonen 1985, Hanski *et al.* 1991). In addition, hard winters, in particular in combination with food shortage, have been disastrous, and they have limited the distribution and abundance of the Tawny Owl (e.g., Saurola 1995). Therefore the development of the Finnish Tawny Owl population has been characterised by alternating increases and drawbacks.

Since the latest crash of Tawny Owls in Finland (in 1987), however, mild winters seem to have predominated, coinciding with a lower level of vole abundance, at least near the southern coast of Finland (Solonen *et al.* 1990, 1995). Intuitively, mild winters might be harmful for voles because ambient temperature fluctuates commonly around the freezing point, causing frequent alternate wet and cold periods that deteriorate their over-wintering conditions (Solonen 2001). Largely snowless winters also provide poor cover. Until recently, the general level of small microtine voles of the Finnish southern coast seemed to be in continued decline, and the earlier three-year cycles in their abundance seemed to be levelling off (Solonen 2001, 2002). This might have some effects on owls as well. In fact, the occurrence of the Long-eared Owl *Asio otus* and Tengmalm's Owl *Aegolius funereus*, nomadic vole specialists that are good indicators of vole abundance, has become more irregular than before (Solonen *et al.* 1995, Solonen 2001, 2002).

In resident generalists such as the Tawny Owl (e.g., Mikkola 1983), the response to a varying supply of over-wintering voles can be seen in the breeding frequency and clutch size, while the final breeding success is largely determined by the availability of food during the nestling period (Linkola & Myllymäki 1969, Lundberg 1981, Wendland 1984, Korpimäki & Sulkava 1987, Wallin 1988). In changing foraging conditions either the owls have to turn to some alternative prey, or their breeding success will drop (Andersson & Erlinge 1977, Keith *et al.* 1977). Tawny Owls are relatively flexible in their food habits (e.g., Wendland 1984) compared to some other species of owls, many of which are quite strict vole specialists (e.g., Mikkola 1983). Therefore it is probable that they will readily compensate the scarcity of voles by using some other kind of prey, and manage quite well breeding in variable food conditions.

In the present paper, we study the relationships between the wintering conditions, the abundance of voles, and the food and breeding success of Tawny Owls in Uusimaa, southern Finland, during a 15-year period. The main questions addressed are whether the winters are really getting milder and less snowy, and whether there are related changes in the vole abundance and in the food or breeding parameters of owls. As stated above, the weather variables characterising the mildness of winters were expected to be negatively related to the abundance of voles. The response of owls to the temporal variations and changes in the vole abundance was supposed to be dietary rather than reproductive. The variable food conditions were expected to affect the nesting frequency but to have relatively minor effects on the breeding success of Tawny Owls.

2. Material and methods

The field study was conducted in 1986–2000 in Uusimaa, near the southern coast of Finland (60°N, 25°E) (Fig. 1). The local main study area covered about 500 km^2 (Solonen 1993). During the study, there were annually more than 300 nest-boxes suitable for Tawny Owls available evenly throughout the study area. Including all habitats in the area, in general the densities of Tawny Owl territories were about 6–10 territories per 100 km^2, while some smaller local concentrations were as high as 42 per 100 km^2 (Solonen 1993). Thereby it seems that the availability of nesting holes did not restrict the size of the local Tawny Owl population studied. The habitats of owls were mainly rural but some of the territories may be characterised also as suburban. Owls preferred rich deciduous and mixed forests near fields, sparsely dispersed human habituation, and especially eutrophic water bodies.

A wide range of data on the winter weather (at

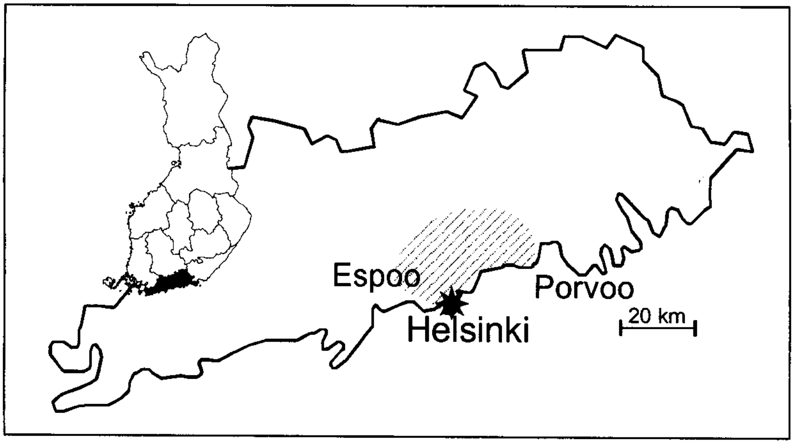

Fig. 1. The location of the study area in southern Finland. The shaded local main study area is situated in the middle of the southern coast of the province of Uusimaa; the larger scale study area is indicated by the borderline.

Helsinki-Vantaa Airport) were gathered from the reviews of the Finnish Meteorological Institute of 1985–2000. The weather variables considered in each winter (usually November, December, January, February, and March) included (1) the average winter ambient temperature (°C), (2) the length of the period when the temperature commonly fell or stayed below freezing point (d), (3) the number of frost days (temperature below 0 °C), (4) the number of days during which the temperature at least once rose and fell from plus to minus °C (later referred to as the "frost see-saw effect" (Solonen 2001)), (5) the number of days of snow cover (here also October and April included), and (6) the average depth of the snow cover in March (in the beginning of the breeding season of owls) (cm). When inter-correlated, only those variables of best fit were included in the final analyses.

The vole populations of the study area were monitored by small-scale trapping from spring 1986 to spring 2000. In a central locality (Sipoo, Hindsby), small mammals were trapped each spring and autumn at 30 standard points along a line of about 1.5 km with three snap traps at each point (total of 90 traps) throughout a 24-hour period. The catch results were expressed as individuals per 100 trap nights. On the basis of the vole index of the preceding autumn (in 1986 that of the same spring), the study years of the breeding seasons of the owl species concerned were classified as "good" (indices ranging from 5.6–23.3; n = 10) or "poor" (2.2–12.2; n = 5), corresponding to good and poor vole years in the three-year vole cycles. From the point of view of Tawny Owls, the habitat distribution of the trapping line might have been concentrated in forests, but old fields were also included. However, the proportions of forest and open habitat seemed roughly to correspond to those of the district at large.

The prey of the Tawny Owl during the breeding season was studied by analysing 51 nest bottom litter samples collected from 30 different locations (local territories) (Karhunen 2001). To exclude the effect of different habitats as far as possible, most urban sites were excluded, since there the diet of owls may be largely composed of birds (Gilbert 1989, Zalewski 1994; T. Solonen, own obs.). The samples represented both good (33) and poor (18) vole years. To study possible long-term dietary shifts of owls in relation to vole abundance, the nest samples of two periods (1986–1992 and 1993–1999) were compared. For the former and the latter period, respectively, 16 and 17 samples of good vole years and six and 12 samples of poor vole years were examined. An attempt was made to make the spatial distribution of samples of different periods as similar as possible.

Food remains (bones, feathers *etc.*) 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 bones of limbs, including hip-bones, femurs, tibiae, and humeri. Birds were classified into four approximate size categories (large/mean

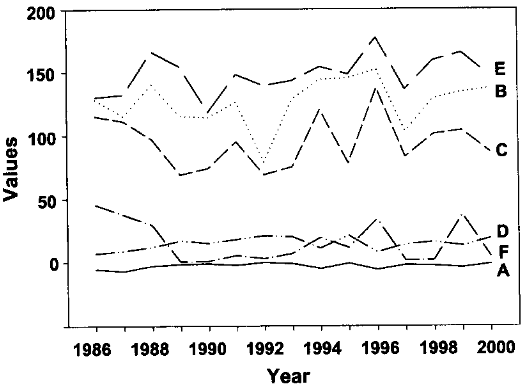

Fig. 2. Variations of the weather variables studied from winter 1985/1986 to winter 1999/2000 at Helsinki-Vantaa Airport, southern Finland (from data of the Finnish Meteorological Institute). Years denotes the spring (breeding season of owls) after the winter considered. Values: A = average winter temperature (°C); B = length of the frost period (d); C = number of frost days; D = intensity of the "frost see-saw effect" (d); E = number of days with snow cover; F = depth of the snow cover in March (cm).

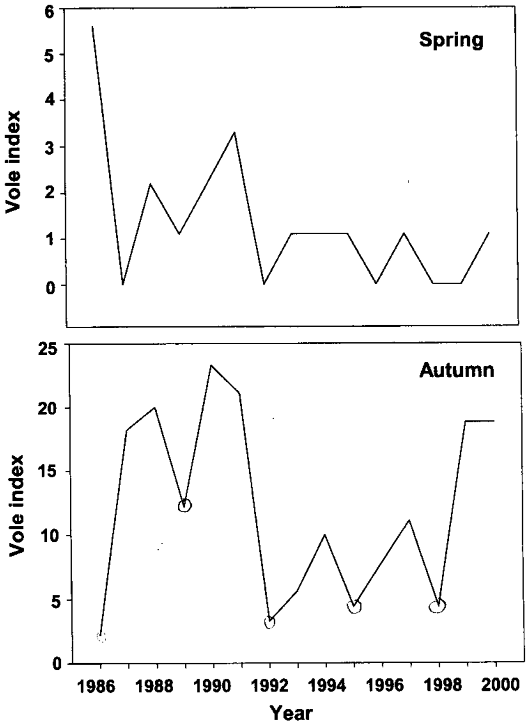

Fig. 3. Fluctuations in the abundance of small microtine voles in the study area in 1986–2000 on the basis of spring and autumn catches by snap-traps. The vole index denotes individuals per 100 trap nights. Data from autumn 2000 are missing.

weight about 350 g, thrush-sized/90 g, medium/23 g, and small/11 g) based on limb-bones (femurs, tibio-tarsi, tarso-metatarsi, humeri, ulnae, metacarpals) as well as sternums, beaks, and feathers. Amphibians (mainly frogs *Rana* spp.) were counted on the basis of iliums, femurs, tibiae, or humeri. Some invertebrates were detected due to the presence of remains of their chitin cuticle. In species identification, we used both literature (Siivonen & Sulkava 1994, Saurola 1995) and reference collections. In estimating the importance of each prey category, individual weights derived from literature (von Haartman *et al.* 1963–1972, Korpimäki & Sulkava 1987, Siivonen & Sulkava 1994) were used.

The local data on the breeding of Tawny Owls were derived from the population of the main study area. The larger scale data (Solonen *et al.* 1990, 1995, Solonen 2002) included observations of the whole population of the district (Fig. 1). The variables studied included (1) the number of nestings recorded (as an estimate of the breeding frequency of the owls), (2) the average clutch size (the number of eggs laid per nest), and (3) the average fledgling production or breeding success (the number of nearly fledged young per nesting attempt).

Statistical methods followed mainly the general standards (Sokal & Rohlf 1981, Fowler & Cohen 1986). Spearman rank correlation was used in examining trends. Due to the small sample size or non-parametric nature of variables also relationships between variables were studied, mostly using a Spearman rank correlation. The significance of difference between proportions was studied with a G-test (adjusted using Williams' correction). Weather factors' effects on vole abundance, as well as their suspected consequent effects on the breeding of Tawny Owls, were studied by backward stepwise multiple regression analyses (P-to-enter < 0.10, P-to-remove < 0.10). When needed, the data were normalised by log-transformation. In calculations, SigmaStat statistical software was used.

3. Results

3.1. Winter weather and vole abundance

During the study period (from the winter 1985/1986 to 1999/2000), there were no obvious temporal trends in the weather variables studied (r_S varied from –0.16 to 0.38, $P > 0.05$, $n = 15$) (Fig. 2). However, the intensity of the frost see-saw effect increased ($r_S = 0.93$, $P < 0.001$, $n = 15$) while the average depth of the snow cover in March decreased ($r_S = -0.66$, $P < 0.01$, $n = 15$) significantly with the increasing average winter temperature.

The abundance of small microtine voles (Bank Voles *Clethrionomys glareolus*, and *Microtus* spp., mainly or possibly entirely Field Voles *M. agrestis*; the occurrence of the Sibling Vole *M. rossiaemeridionalis* was not ascertained) fluctuated in three-year cycles — poor vole years were followed by two years of higher vole densities (Fig. 3). On the basis of the vole abundance in the preceding autumn, poor vole years for breeding owls were 1987, 1990, 1993, 1996, and 1999. Not surprisingly, the vole densities in autumn were much higher than those in spring. On the basis of spring catches, the abundance of small voles declined nearly significantly during the study period ($r_S = -0.48$, $P = 0.07$, $n = 15$). In autumn, the amount of catches varied considerably and there was no clear trend ($r_S = -0.17$, $P > 0.05$, $n = 14$). However, during the latter half of the study period, the general level of the vole abundance seemed to be largely lower than in earlier autumns (Fig. 3).

There was a nearly significant positive relationship between the vole index of the autumn and that of the next spring ($r_S = 0.47$, $P = 0.08$, $n = 14$). There were no clear relationships between the spring vole abundance index and the single winter weather variables studied either in the total data ($r_S = -0.33$ to 0.35, $P > 0.05$, $n = 14$) or when the poor vole years were excluded ($r_S = -0.37$ to 0.49, $P > 0.05$, $n = 9$). The spring vole abundance could, however, be predicted from a linear combination of the autumn vole density, the length of the frost period, and the number of snow cover days (backward stepwise multiple regression analysis; $F_{3,10} = 4.04$, $P < 0.05$, $R^2 = 0.55$).

3.2. Composition and changes of diet in good and poor vole years

A total of 3194 prey individuals were identified in 51 nests (Table 1). Mammals clearly predominated (59.4%), followed in abundance by amphibians (17.5%) and birds (17.0%). The most abundant prey species group was the *Microtus* voles (20.7%). By biomass, the importance of mammals (64.3%) and birds (23.5%) was emphasised. The most important single prey species was the Water Vole *Arvicola terrestris* (33.0%).

In good vole years (33 nests, 2157 prey items), the most abundant prey category was small voles (30.9%) (Table 2). The proportion of *Microtus* voles was 23.9%. Considerable proportions of prey individuals were in amphibians (16.6%) and birds (16.0%). By biomass, Water Voles dominated (38.0%) and were followed by birds (21.4%) and small voles (13.9%).

In poor vole years (18 nests, 1 037 prey items), the most abundant prey categories were amphib-

Table 1. Diet composition of Tawny Owls on the basis of nest bottom samples (n = 51) collected in 1986–1999 from 30 local territories in southern Finland.

Prey species or category	Number	%	Biomass %
Hedgehogs	1	0.0	0.3
Shrews	284	8.9	1.2
Moles	12	0.4	0.5
Bats	8	0.3	0.0
Squirrels	4	0.1	0.7
Bank Voles	191	6.0	2.6
Water Voles	312	9.8	33.0
Field Voles	661	20.7	9.9
Mice	326	10.2	2.9
Rats	82	2.6	12.6
Weasels	7	0.2	0.2
Unidentified mammals	8	0.3	0.3
Large-sized birds	30	0.9	6.3
Thrush-sized birds	265	8.3	14.3
Medium-sized birds	186	5.8	2.6
Small birds	61	1.9	0.4
Amphibians	560	17.5	12.1
Beetles	191	6.0	0.1
Crayfish	5	0.2	0.1
Total	3194	100	100

ians (19.5%) and birds (19.0%) (Table 2). The proportion of small voles was only 17.8%. By biomass, the most important prey category was birds (28.4%). The Water Vole was, however, again the most important single prey species (21.2%). Important alternative prey also included rats *Rattus norvegicus* (16.7%) and amphibians (14.8%). The proportion of small voles was only 9.2%.

Table 2. Diet composition of Tawny Owls in "good" (n = 9) and "poor" (n = 5) vole years of 1986–1999 in southern Finland. The significance of the difference between proportions was tested by a G-test (adjusted using Williams' correction) (ns = not significant).

Prey category	Good years		Poor years		G	P
	n	%	n	%		
Small voles	667	30.9	185	17.8	53.8	< 0.001
Water Voles	253	11.7	59	5.7	36.4	< 0.001
Birds	345	16.0	197	19.0	4.7	< 0.050
Amphibians	358	16.6	202	19.5	4.2	< 0.050
Rats	50	2.3	32	3.1	2.3	ns
Mice	196	9.1	130	12.5	11.0	< 0.001
Shrews	142	6.6	142	13.7	55.7	< 0.001
Others	146	6.8	90	8.7	4.8	< 0.050
Total	2157	100	1037	100		
Number of nests	33		18			

Table 3. Changes in the diet composition of Tawny Owls between 1986–1992 and 1993–1999 in "good" and "poor" vole years in southern Finland. The significance of differences between the periods was tested with a G-test (adjusted using Williams' correction) (ns = not significant).

Prey category	1986–1992		1993–1999		G	P
	n	%	n	%		
Good vole years	5		4			
Small voles	378	34.6	289	27.1	14.1	< 0.001
Water Voles	109	10.0	144	13.5	10.8	< 0.010
Birds	161	14.7	184	17.3	3.8	ns
Amphibians	164	15.0	194	18.2	5.8	< 0.050
Rats	26	2.4	24	2.3	0.1	ns
Mice	93	8.5	103	9.7	1.5	ns
Shrews	71	6.5	71	6.7	0.0	ns
Others	90	8.2	56	5.3	12.3	< 0.001
Total	1092	100	1065	100		
Number of nests	16		17			
Poor vole years	2		3			
Small voles	104	30.7	81	11.6	88.3	< 0.001
Water Voles	31	9.1	28	4.0	23.8	< 0.001
Birds	63	18.6	134	19.2	0.1	ns
Amphibians	53	15.6	149	21.3	11.1	< 0.001
Rats	10	2.9	22	3.2	0.1	ns
Mice	31	9.1	99	14.2	15.0	< 0.001
Shrews	17	5.0	125	17.9	127.5	< 0.001
Others	30	8.8	60	8.6	0.0	ns
Total	339	100	698	100		
Number of nests	6		12			

In good vole years, the prey of Tawny Owls included small voles and Water Voles significantly more than in poor vole years (Table 2). In poor vole years owls brought other kinds prey significantly more to the nest, including birds, amphibians, mice and shrews. During the first half of the study period the proportion of small voles in the prey of Tawny Owls was significantly higher than later, both in good and poor vole years (Table 3). Out of the alternative prey, the proportion of amphibians correspondingly increased. The proportion of Water Voles increased only in good vole years, while the proportions of mice and shrews increased only in poor years.

There was a significant positive relationship between the numbers of *Microtus* and *Clethrionomys* voles in the diet samples of Tawny Owls ($r = 0.73$, $P < 0.001$, $df = 49$). The number of small voles was significantly related both to the number of Water Voles ($r = 0.58$, $P < 0.001$, $df = 49$) and to the number of rats and mice ($r = 0.29$, $P = 0.04$, $df = 49$).

3.3. Contributions of weather factors and vole abundance on the nesting of owls

The number of nestings of Tawny owls in the district (the breeding frequency) (averaging 100.5 ± 30.7 SD, n = 15) could be roughly predicted from the spring vole abundance measured. It was the only significant independent variable out of the ones indicating vole abundance and wintering conditions put in a backward stepwise multiple regression analysis to explain the breeding frequency of owls ($F_{1,13} = 7.04$, $P < 0.05$, $R^2 = 0.35$).

On average, in good vole years (n = 9) Tawny Owls of the district did not lay eggs (3.90 ± 0.55 SD vs. 3.36 ± 0.39 SD) and produce young (2.83 ± 0.50 SD vs. 2.40 ± 0.35 SD) per breeding attempt significantly more than in poor vole years (n = 5) (unpaired two-tailed t-test; $t_{12} = 1.93$, $P > 0.05$, and $t_{12} = 1.72$, $P > 0.05$; respectively). In the diet sample nests studied, the difference in the breeding success between the good and poor vole years (3.5 vs. 2.7) was, however, significant ($T = 305$, $P < 0.001$, $n_1 = 33$, $n_2 = 18$) (Mann-Whitney rank sum test).

The vole catch index of the preceding autumn has no significant relationship between either the average clutch size ($r_S = 0.30$, $P > 0.05$, $n = 14$) or the average number of young fledged per breeding attempt ($r_S = 0.15$, $P > 0.05$, $n = 14$) in the Tawny Owl population of the district. No significant correlation was found between the spring vole catch and the average fledging success either ($r_S = 0.41$, $P > 0.05$, $n = 15$). The number of young fledged correlated, however, positively with the number of small voles and Water Voles found in the nests studied ($r = 0.38$, $P < 0.01$, $df = 49$, and $r = 0.45$, $P < 0.001$, $df = 49$; respectively).

Significant relationships between the clutch size or fledgling production of owls and the vole abundance or weather variables studied emerged only when the data of the poor vole years were excluded. Then there was a significant negative relationship between the average clutch size and the frost see-saw effect ($r_S = -0.78$, $P < 0.01$, $n = 10$). The clutch size could also be predicted from a linear combination of the autumn vole density and the intensity of the frost see-saw (backward stepwise multiple regression analysis; $F_{2,6} = 6.79$, $P < 0.05$, $R^2 = 0.69$). There was a significant negative relationship between the average fledgling production and the intensity of the frost see-saw ($r_S = -0.75$, $P < 0.05$, $n = 10$) as well. It was the only one of the food and weather variables studied that was entered into the model in a backward stepwise multiple regression analysis ($F_{1,7} = 5.06$, $P = 0.06$, $R^2 = 0.42$). The average number of fledglings per nesting attempt was, however, largely determined by the clutch size ($r_S = 0.86$, $P < 0.001$, $n = 15$).

4. Discussion

4.1. Winter weather and the abundance of voles

The present study did not reveal any definite trends in the winter weather variables studied. This may be largely due to the short study period and the normal well-known wide fluctuations in weather conditions. The weather parameters rather suggest that winters were generally at their mildest in the middle of the study period. The mildness of winters was suspected to be negatively related to the abundance of voles. In accordance with this, vole abundance was at its lowest also in the middle of the study period. This held true on the basis of both the vole trap indices and the prey remains found in the nest samples.

The present results show that the abundance of voles has not only fluctuated but also generally declined during the study period. This observation was reinforced directly both by the vole trapping and by the prey remains found in the nests of owls, as well as indirectly by the relationships between winter weather, vole abundance, and the breeding of owls. The decline of voles might be connected to recent climate change trends but the short time period of the study does not allow a more detailed analysis of the topic.

Earlier, (in the 1950–1960's) in the inner part of southern Finland (Tavastia), the fluctuations of Field Voles, the most common prey species of Tawny Owls, followed approximately a four-year rhythm, including increase, peak, decrease, and intermediate years (Linkola & Myllymäki 1969). The increase and peak years seemed to correspond to the good vole years, and the decrease and intermediate years to the poor vole years of the present study. There was usually continuous snow cover (of 20–60 cm) during about 3–5 months, and the temperature was mainly below 0 °C during the whole winter. In Fennoscandia, the snow cover period and cyclicity indices of microtines are positively related to the latitude as well as to the annual period and especially to the maximum depth of the snow cover (Hansson & Henttonen 1985). Populations of small voles are relatively stable in Central Europe but show 3–5-year cycles in Fennoscandia with most pronounced variations in the north (Kalela 1962, Hansson & Henttonen 1985).

4.2. The response of owls to the variations in vole abundance

Tawny Owls responded to changing vole densities by varying their diet. The earlier studies concerning the diet of Tawny Owls in Finland (Linkola & Myllymäki 1969, Itämies & Mikkola 1972, Mikkola 1983) also suggest similarly flexible food habits for the species. The Tawny Owl, as with some other predators, might have a stabilising role in microtine cycles in the Fennoscandian taiga, especially in areas with thin snow cover (Erlinge *et al.* 1983, Korpimäki 1985). The possibilities of resident owls to prey upon microtines in winter increase with decreasing snow cover (cf. also Jędrzejewski *et al.* 1994).

In the present study area, the habitats and habitat distribution of the owls studied remained relatively unchanged during the study period. No pronounced large-scale habitat changes occurred that might be responsible for the general decline of voles in the diet of owls. For example, the decrease in the number of cattle farms and grassy ditches as well as in the area of hay fields, all providing good shelter for voles, may have concerned at most a few single owl territories. Such changes, including wood cutting, reforestation, and sinking water tables, were suggested to have caused the decline of voles and toads in the diet of Tawny Owls in Berlin, Germany (Wendland 1984). A similar decrease of small voles in the diet of Tengmalm's Owls in western Finland was suggested to be caused by habitat changes (Korpimäki 1988).

Small voles are probably the most suitable prey for Tawny Owls as well as for many other predatory species. When there are plenty of small voles available, they are usually easily caught by predators. Some larger prey (e.g., Water Voles, birds) may be important alternatives but the biomass does not indicate unambiguously the profitability of the prey. Larger prey may be more difficult to catch and handle, and more remains may be left unused of larger prey than of smaller ones (cf., e.g., Newton 1986). Therefore small voles may be more important prey for Tawny Owls than suggested by their total mass in the diet.

4.3. Effects of variable food conditions on the breeding of owls

Changing food conditions were expected to affect the breeding of Tawny Owls relatively little. However, some relationships emerged that probably indicated directly, or indirectly (through weather factors), the effects of the prevailing vole abundance.

More nestings of owls occurred in good vole years after mild winters. Abundance alone does not therefore indicate the availability of voles. In mild and wet winters owls probably manage better in catching small voles, when their hollows are frequently filled by water and they are forced to move more on the ground. Correspondingly, Water Voles may be better and earlier available when springs are less snowy. The over-wintering of owls may then be more successful and less constraining than in hard and snowy winters.

In good vole years there was a significant negative relationship between the average clutch size and the number of days when the temperature fell below freezing. This suggests that the latter variable was negatively correlated with the abundance of voles. In poor vole years, voles obviously were very scarce even without the effect of the frost see-saw. Probably due to the availability of alternative prey, vole abundance had no pronounced direct effect on the fledgling production of nesting Tawny Owls. The final breeding success was in any case largely determined already by the clutch size.

Though the breeding success per nesting attempt varied annually relatively little, there were large variations in the offspring production of the owl population (cf. Wendland 1984). When the availability of voles is low, or the breeding conditions are bad, generally only the most suitable territories are occupied by breeding birds that, in turn, represent the most capable individuals of the population (cf. Pietiäinen 1989, Solonen *et al.* 1991). In such cases the average values of breeding parameters per nesting attempt vary considerably less than in good vole years when higher numbers of various kinds of individuals and territories are engaged in breeding.

4.4. Methodological aspects

The present study included both local and larger scale data. The weather factors are known to be large scale ones and their effects are commonly wide-ranging and general. However, to find clearer relationships between the intensity of the frost see-saw effect, vole abundance, and the breeding of owls, the frequency of the temperature falling below the freezing point might have to be measured more exactly than on only a daily basis.

The data on voles and owls may be suitable for generalisations and may indicate larger-scale phenomena, but there may be also considerable local variation. The present spring vole index was clearly near the observation limit of the method but, however, seemed to agree rather well with reality. Although for practical reasons not measured before May, it also seemed to indicate well the vole abundance of early spring before the breeding season of owls.

In addition to temporal fluctuations and changes, the number and quality of prey items found in the nests studied probably varied considerably also due to local variations. The small number of samples might have not been quite representative for the periods of time examined. For a more comprehensive and detailed approach, a larger and spatially more representative set of nest samples is needed.

Acknowledgements: Hannu Pietiäinen read a draft of the manuscript and made valuable suggestions. Comments by Harri Hakkarainen, Jukka Jokimäki and Jari Valkama were also useful. Kimmo af Ursin's enthusiasm was indispensable during the field work. Marcus Walsh kindly checked the English.

Selostus: **Lehtopöllö selviytyy hyvin ravintotilanteen vaihteluista levinneisyytensä pohjoisrajoilla**

Tutkimme talviolojen, myyrien runsauden sekä lehtopöllön ravinnon ja pesimämenestyksen välisiä suhteita Etelä-Suomessa Uudellamaalla vuosina 1986–2000 kootun aineiston valossa. Talvien sääoloissa ei havaittu merkitseviä suuntauksia, vaikka talvien vähittäinen leudontuminen vaikuttaa ilmeiseltä. Pöllöjen pääravinnon, pikkumyyrien määrä vaihteli kolmivuotisjaksoittain, mutta myyrien runsauden yleinen taso näyttää viime aikoina laskeneen. Niinpä myös pikkumyyrien osuus pöllöjen ravinnossa oli tutkimuksen alkuvuosina merkitsevästi suurempi kuin myöhemmin. Vastaavasti, kun myyriä oli niukasti, vaihtoehtoisten saaliskohteiden osuus pöllöjen ravinnossa oli suuri. Pöllöjen pesintöjen määrä voitiin arvioida keväisen myyrätilanteen perusteella. Keskimäärin uusmaalaiset lehtopöllöt munivat ja tuottivat poikasia hieman, mutta ei merkitsevästi enemmän "hyvinä" kuin "huonoina" myyrävuosina. Lähemmin tutkitun paikallisen populaation pesimätuloksessa ero oli kuitenkin tilastollisesti merkitsevä. Pesään tuotujen myyrien ja pesästä lähteneiden poikasten määrien välillä oli positiivinen riippuvuus. Pesyekoon ja poikastuoton sekä myyrien määrän ja tarkasteltujen säämuuttujien välillä todettiin merkitseviä yhteyksiä vain "hyvien" myyrävuosien aineistossa. Pöllöjen keskimääräisen pesyekoon ja "pakkassahavaikutuksen" eli sellaisten päivien, jolloin lämpötila ainakin kerran laski pakkasen puolelle, lukumäärän välillä oli merkitsevä käänteinen riippuvuus. Myyriä on ilmeisesti keväällä sitä vähemmän, mitä enemmän tuollaisia päiviä talven aikana on. Tilanne oli samankaltainen myös pöllöjen poikastuoton suhteen, vaikka se määräytyykin paljolti jo pesyekoon perusteella.

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