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Vole-induced regular fluctuations in the Estonian owl populations

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Estonia has been considered to hold non-cyclic vole populations, which should be revealed in owl productivity or movements. I asked (1) whether owl and vole populations fluctuate regularly in Estonia, (2) are the fluctuations in Estonia synchronous to those in its neighbouring areas, (3) do Estonian and northern owl populations exchange individuals? I found significant periodicity in owl reproduction, which was linked to vole abundance, suggesting that Estonia belongs to the transition zone between cyclic and non-cyclic vole populations. The migration intensities of nomadic owl species were positively correlated with each other, and in the long-eared owl related to its productivity. Having found that owl productivity fluctuates independently in Estonia and southern Finland, and owls do not move freely between the countries, I discussed possible causes for this.

1. Introduction

There is plenty of evidence on how fluctuations in the numbers or productivity of vole-eating birds are linked to the abundance of the voles (e.g., Korpimäki 1992, Newton 1998). Much less is known about spatial organisation of these fluctuations. On one hand, the population changes of many animal species have shown large-scale synchrony (Ranta *et al.* 1995), including evidence of travelling waves in the vole numbers (Ranta & Kaitala 1997). Some owls, like the long-eared owl (*Asio otus*) and Tengmalm's owl (*Aegolius funereus*), can respond to these structured dynamics with shifting their breeding areas, while some other species — e.g., the Ural owl (*Strix uralensis*) and tawny owl (*S. aluco*) — are everywhere tenacious to scarce nest-sites and do not migrate (Lundberg 1979, Korpimäki 1992). On the other hand, vole populations in northern Europe are assumed more or less cyclic while populations that are more southern are largely non-cyclic (Hansson & Henttonen 1988). Hence, the southern owls are mostly resident (Mikkola 1983), and the possible tactics of movements in migratory (nordic) owls are not straightforward.

In this paper, I work with three main questions.

1. Do the populations of voles and their avian predators fluctuate regularly in Estonia? Regarding voles, Hansson and Henttonen (1988)

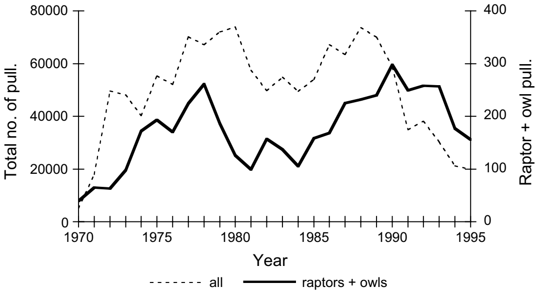

Fig. 1. Total number of nestlings (all birds and raptors + owls) ringed in Estonia, 1970–1995.

on their map answered "no", but more recently Kirk (1990) found regular fluctuations in a bank vole (*Clethrionomys glareolus*) population in North-eastern Estonia. For owls, noncyclic vole populations could mean residency (in the species that shift their breeding areas in more northern areas), and more or less random fluctuations in the productivity (in all vole-eating species). Again, this is not supported by recent (1989–1998) monitoring data, which showed that the numbers of long-eared owls on Estonian sample plots reached minima every three years (four minima detected), while the numbers of typical resident species (tawny and Ural owl) did not change regularly (Lõhmus 1999). However, the latter time-series are short, and the owl productivity and migration have not been analysed.

2. Are the fluctuations in Estonia synchronous to those in its neighbouring areas? There are three possible answers: (a) strictly coinciding dynamics reveal large-scale synchrony and suggest similar factors driving it; (b) lagged dynamics support the travelling waves concept (Ranta & Kaitala 1997); (c) structurally different dynamics indicate local regulation. I will concentrate on comparisons with Finland, which lies less than a hundred kilometres north from Estonia, and is known to have rather regularly fluctuating owl populations (Haapala *et al.* 1998). In the west, Estonian mainland is separated from the nearest one (Sweden) by about 300 kilometres of the Baltic Sea. Data from the southern (Latvia) or eastern areas (West Russia) are nearly missing.
3. Do Estonian and South-Finnish populations of nomadic/migratory owls freely exchange individuals? If nomadic avian predators can synchronise vole populations in large areas (e.g., Norrdahl & Korpimäki 1996), synchrony in voles could be accompanied by free migration of owls. It is known that depending on vole abundance, Finnish Tengmalm's owls move largely all over Fennoscandia (Saurola 1979), but do they track also Estonia, which is so close?

To answer these questions, I check for regular fluctuations in the productivity of the Estonian owl populations; analyse whether or not the observed patterns coincide with the fluctuations in vole populations; explore relationships between the productivity and migration of the nomadic owls, particularly the long-eared owl; and compare Estonian and Finnish data in order to find spatial correlations.

In addition to voles, several other factors can create regular oscillations in bird populations (Newton 1998). Theoretically, via avian prey the owl populations could be influenced by regular outbreaks of some insect species, etc. Therefore, I study comparatively also some other bird species to check for patterns similar to those in owls.

2. Material and methods

2.1. Estimation of productivity

I used the number of ringed nestlings as an index of productivity. Ringing totals were derived from annual reports of Matsalu Ringing Centre, 1970–1995. The data on old "Moscow" rings, were included according to Kastepõld and Kastepõld (1991). In general, the period started with sharp increase in ringing activity, followed by a period of intensive ringing (1972–1990, with a temporary decrease in the early 1980s), and a dramatic decrease since then (Fig. 1). However, the Estonian raptor and owl monitorings have markedly developed in the 1990s (Lõhmus 1999), and although not emphasising on ringing, they seem to compensate the latest decrease in general ringing activity. Therefore, only 1970 was excluded from further analyses because of low ringing totals. In addition to owls, I will present the grand total of all ringed nestlings of vole-specialised raptors and owls, including *Buteo buteo, Circus cyaneus, C. pygargus, Falco tinnunculus, Asio otus, A. flammeus, Aegolius funereus, Strix aluco* and *S. uralensis*.

Among owls, only the tawny owl and long-eared owl were ringed abundantly enough to allow these data to be included in the analyses. Therefore, I also added local data on the Ural owl. The study plot (100 km^{-2}) was situated near Laeva (58°28´N, 26°18´E) in East-central Estonia.

Natural landscapes dominate in the plot: forests cover 53%, mires and flood-plain meadows 33%. In 1991–1998, the owls' territories were mapped, potential nest sites were carefully searched for and systematically checked, and the number of fledged young was determined. The amount of fieldwork was similar in all years, reaching about 300 hours per season. I failed to determine the reproductive success on two or three territories (out of nine to fourteen territories), in different years.

In order to compare fluctuations in the reproductive success of the tawny and long-eared owls with other bird species, which could indicate causes of the fluctuations, I used available long-term data from Estonia. Four long-lived (two large birds and two medium-sized common raptors) and four short-lived species (two thrush-sized passerines and two small hole-nesting passerines; Table 1) were considered. All studies on non-passerines cover Estonia in total, those on passerines, however, were conducted near Viljandi, South-central Estonia (35 kilometres west from the Ural owl plot). The ringing totals of the goshawk and buzzard increased significantly during the study period ($r_s = 0.427$, $n = 25$, $t = 2.27$, $p = 0.033$, and $r_s = 0.579$, $n = 25$, $t = 3.41$, $p = 0.002$, respectively), probably due to increase in their numbers (at least in the buzzard; *see* Lõhmus *et al.* 1998). Therefore for these species, I used standardised residuals of linear regression as indices of the relative productivity.

2.2. Detection of owl migration

Three coastal ringing stations have regularly caught owls in Estonia: Kabli (58°00´N, 24°25´E) and Lao (58°14´N, 24°07´E) in South-western Estonia, and Sõrve on Saaremaa Island (57°55´N, 22°02´E). Kabli has worked since 1969, Lao in 1981–1992 and since 1994, Sõrve in 1978–1990. In this paper, the ringing totals up to 1997 were used, including 382 Tengmalm's owls, 188 long-eared owls, 2 short-eared owls and 187 other owls (tawny, Ural and pygmy owls). Hereafter, I will use a common term "nomadic owls" for the first three species, because they shift their breeding areas in the north (Korpimäki 1992).

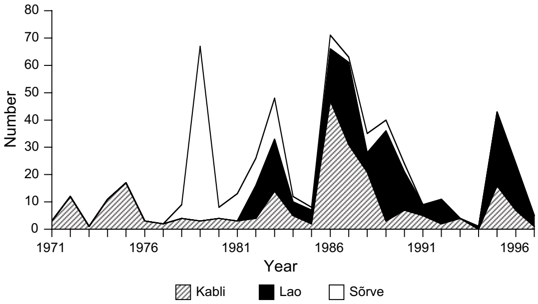

Fig. 2. Autumn numbers of ringed nomadic owls at three ringing stations in Estonia: Kabli (1971–1996), Lao (1982–1992, 1994–1996) and Sõrve (1978–1990).

The migrants were mist-netted in Sõrve (the total length of the nets 130–195 metres annually), while in both Kabli and Lao mainly one large Helgoland-type trap was used. In Sõrve, the share of long-eared owls could have been underestimated because this species is not so easily mist-netted. In Kabli in 1969–1970, another type of a trap was used (Vilbaste 1972); however, no owls were caught in both years. Therefore the data from these years have been excluded. The same reason applies for the first year (1981) in Lao.

Annual trapping efforts were rather stable. Trapping began in summer and ended in late October or the first decade of November. Only in the first years in Sõrve (1978–81) and Lao (1982–1983) the start was exceptionally late (in September or even in early October).

Although year-to-year variation in the abundance of the nomadic owls is evident from ringing totals (Fig. 2), the years differ in the number of active stations. To reduce the latter effect, I pooled the data by (a) standardising the ringing totals by station, and (b) taking the averages from the standardised values for each year. So the resulting standardised value for 1971–1977 represents only the Kabli results, in 1978–1981 it is an average of the Kabli and Sõrve data, etc. As will be shown in Results, the numbers of the long-eared and Tengmalm's owls are well correlated, there-

Table 1. Data for comparative analysis of the reproductive success of different bird species.

Species	Variable[1]	Study years	Source
Ciconia ciconia	1	1968–80, 1985–95	H. Veromann (unpubl. Ph.D. thesis), M. Ots (unpubl. diploma thesis)
Aquila chrysaetos	1	1975–95	Randla & Tammur 1996; A. Lõhmus, unpubl.
Accipiter gentilis, *Buteo buteo*	2	1971–95	Annual reports of Matsalu Ringing Centre
Turdus iliacus	3	1969–93	Edula 1997
Sturnus vulgaris	4	1971–87	Edula 1999 and pers. comm.
Ficedula hypoleuca, Parus major[2]	4	1968–87	Edula 1999 and pers. comm.

[1] Variables: 1 = fledglings per occupied nest (pair), 2 = total number of annually ringed nestlings (residuals of linear regression), 3 = relative frequency of successful breedings, 4 = fledglings per clutch.
[2] First clutch.

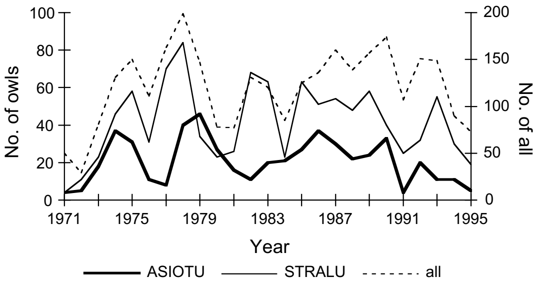

Fig. 3. Variation in the annual number of ringed nestlings of the long-eared owl (ASIOTU), tawny owl (STRALU) and all the vole-eating raptors and owls.

fore the suspected systematic underestimation of long-eared owls in Sõrve should not change the general pattern of the nomad abundance.

2.3. Measuring vole abundance

There have been no special studies on long-term dynamics of voles in Estonia (except Kirk 1990, which covers a local population of the bank voles), and I had to rely on more circumstantial data.

First, I checked the abundance of voles in the food of owls during breeding season, because several studies on owl diets showed that it can reflect the vole dynamics (e. g., Korpimäki 1988, Korpimäki *et al.* 1990). Two Estonian data sets were available, both based on the analysis of pellets and prey remains. The analyses followed standard methods (e.g., Marti 1987) and reference collections were used for identification of bone fragments.

Rein Kalda (unpublished diploma thesis, University of Tartu) has analysed the food of the tawny and long-eared owls in 1976–1979. In both species, over ten nest-sites were studied, often for several years. Most sites were sparsely situated on the agricultural landscapes of northern and western Estonia. Annual sample sizes were 348–672 prey individuals of the tawny owl, and 364–506 individuals of the long-eared owl. Kalda also studied the food of the kestrel (n = 237–471), which I also use because of the additional data from 1970 (Kalda & Leht 1978). Feeding habits and food composition of the kestrel are highly similar to that of the long-eared owl (Korpimäki 1987).

My own analyses concentrate on the food of the Ural owl nestlings in Laeva in 1991–1998. Comparative results on long-eared owl were obtained from three years (1990, 1991 and 1996) when one nest site was found in Laeva. In 1990–1992, I gathered pellets in a roosting site of the tawny owl near Põlva, South-eastern Estonia.

Second, on one meadow in the Ural owl plot small mammals were trapped with snap traps in the autumns of 1991–1995. Every autumn the traps were distributed in three-trap clusters, randomly all over the meadow (each cluster at least 10 metres from the others), for two nights. Vole abundance is expressed as the "vole index" (the number of voles per hundred trap-nights). The samples are local and small (79–114 trap nights per autumn) but they still can serve as an additional tool for detecting the variation in vole numbers.

2.4. Finnish and Latvian data

I compared the Estonian data with the productivity estimates from Finland and migration data from Latvia.

The productivity cycles in owls in southern Finland were reconstructed according to the published data on (1) the totals of ringed nestlings in 1969–1984 (Saurola 1978, 1979, 1985); (2) the numbers of active nests and occupied territories of Tengmalm's and the long-eared owls in 1975–1997 (Solonen 1984, Haapala *et al.* 1998, P. Saurola, pers. comm.). I classified the years as follows:

- — minima: 1971, 1975, 1978, 1981, 1984, 1987, 1990, 1993, 1996;
- — maxima: 1969, 1973, 1977, 1980, 1983, 1986, 1988, 1991, 1994, 1997;
- — intermediate: 1970, 1972, 1974, 1976, 1979, 1982, 1985, 1989, 1992, and 1995.

The numbers of ringed Tengmalm's and the long-eared owls in 1969–1987 in Pape, extreme South-western Latvia, were used according to Rute and Baumanis (1986), Baumanis *et al.* (1987a, 1987b, 1988) and Celminš *et al.* (1990). More recent data (1988–90, 1993–94, and 1996–97) were provided by Agu Leivits (pers. comm.). The distances from Pape to the Estonian stations Sõrve, Kabli and Lao are 200, 290, and 300 kilometres, respectively.

2. 5. Statistical methods

Cyclicity in the numbers of the ringed nestlings and nomads was explored with periodograms. The hypothesis that the time-series follow white-noise series was analysed with the Kolmogorov-Smirnov test, which fitted the exponential distribution to periodogram values. For ANOVA, the homogeneity of variances was checked with Levene's test. The analyses were performed with the STATISTICA 4.5 software.

3. Results

3.1. Fluctuations in reproductive success

The annual numbers of the ringed tawny and long-eared owls' nestlings fluctuated markedly and with a significant synchrony (Fig. 3; $r_s = 0.424$, $n = 25$, $t = 2.24$, $p = 0.0352$). The fluctuations were not random, revealing four year periods in tawny owls

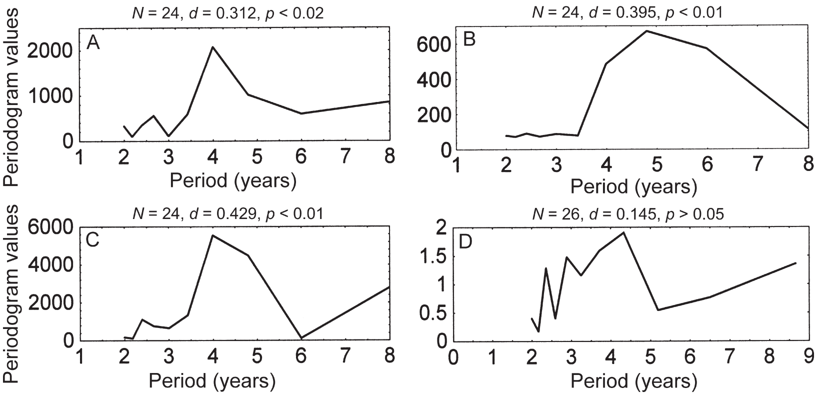

Fig. 4. Periodograms of the ringing totals of (a) tawny owl, (b) long-eared owl, (c) nestlings of all the vole-eating raptors and owls, 1972–1995; (d) standardised number of the nomadic owls in ringing stations, 1972–1997. Data from 1971 was excluded because of the odd number of observations. The results of Kolmogorov-Smirnov test, which fitted exponential distribution to periodogram values, are presented at the top of each graph.

and less clear, four to six year periods in the long-eared owl (Fig. 4A and B). The numbers of all vole-eating raptors and owls showed periodicity of four to five years in 1972–1995 (Fig. 4C).

In the 1990s, there were three years (1992, 1995 and 1998) when only few, if any, Ural owls started to breed in Laeva (Fig. 5). These years overlap with minima in the numbers of the Estonian long-eared owls (Lõhmus 1999). Indeed, the data in Figs. 5 and 6 and Lõhmus (1999) show that the dynamics of the long-eared owl are revealed both in the number of breeders ($r_s = 0.82$, $n = 8$, $t = 3.45$, $p = 0.014$) and the productivity ($r_s = 0.78$, $n = 8$, $t = 3.04$, $p = 0.023$) of the Ural owl in Laeva.

The productivity of the other bird species revealed no pronounced periodicity and did not correlate with the productivity of the tawny and long-eared owls, except nearly significant positive correlation between the buzzard and tawny owl ($r_s = 0.387$, $n = 25$, $t = 2.01$, $p = 0.056$).

3.2. The importance of voles

The share of voles in the diet of all the studied avian predators changed in a similar way (Figs. 6 and 7). Between 1976–1979, voles were most abundant in the breeding season of 1978 and most scarce in 1977 (Fig. 7). Judging by the food composition of the kestrel, 1970 was among the best vole years of the decade. In the 1990s, owls took voles most frequently in 1990, 1993 and 1996, and most rarely in 1992 and 1998. In the diet of the long-eared owl, the vole abundance in 1990 (89%, $n = 57$) and 1996 (91%, $n = 69$) did not differ (Z-test: $p >> 0.05$). As 1995 was probably the poorest vole year of the period (*see* below),

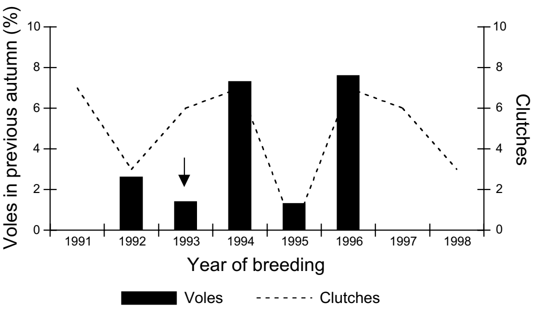

Fig. 5. Relationship between the number of breeding Ural owls (clutches) in a given year and the abundance of the *Microtus* voles in autumn of the previous year. The exceptionally low trapping result in autumn 1992, which contrasted with high number of breeding owls in spring 1993, is indicated with an arrow.

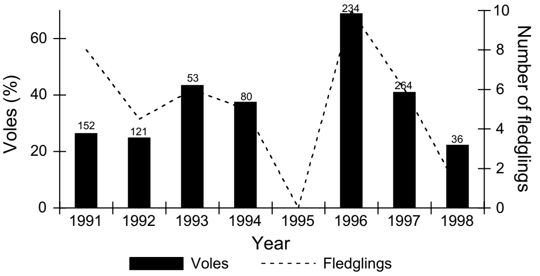

Fig. 6. Variation in the total number of the fledged Ural owl young and the relative abundance of the *Microtus* and *Clethrionomys* voles in the food of the nestlings. The numbers above the bars are those of determined prey individuals. In 1995, no owls started to breed and no food samples were collected.

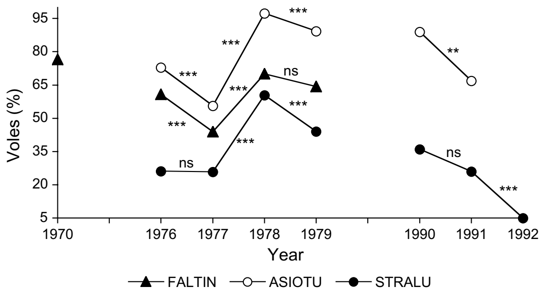

Fig. 7. Variation in the relative abundance of the *Microtus* and *Clethrionomys* voles in the food of the kestrel (FALTIN), long-eared owl (ASIOTU) and tawny owl (STRALU) in Saue (1970s) and eastern Estonia (1990–92). Year-to-year differences (according to Bonferroni *Z*-test): ns = $p > 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. The voles were much more abundant in the food of both owls in 1979 than in 1976 ($p < 0.001$); the difference was not significant in the kestrel. Vole abundance in the food of the kestrel in 1970 was significantly higher than in any other year (compared with 1976 and 1977: $p < 0.001$, with 1978: $p < 0.05$, with 1979: $p < 0.01$).

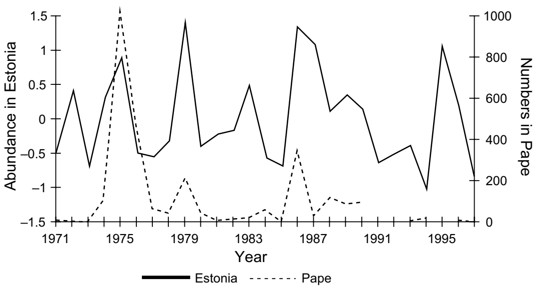

Fig. 8. Variation in the autumn abundance of the ringed nomadic owls in Estonia (standardised average values from three ringing stations) and Pape (absolute numbers).

the time-series analysis indicated a clear three-year periodicity in the 1990s.

In the Ural owl, the numbers of breeders were at their lowest every three years (1992, 1995, 1998), and were usually related to the vole index in the previous autumn, although with one exception (Fig. 5). The total number of fledged nestlings was positively correlated with the vole abundance in their diet (Fig. 6; $r_s = 0.775$, $n = 7$, $t = 2.74$, $p = 0.041$). There are no food data from 1995 because no owls bred, but two facts suggest that the vole densities of the study period were at their lowest in spring 1995: (1) the vole index in autumn 1994 was very low (Fig. 5), and (2) only in this year's winter and spring owls were often observed to hunt also at daytime (which indicates severe food shortage; *see* Newton 1998). If 1995 had been considered the year with the poorest vole numbers in spring, the time-series presented in Fig. 6 would have correlated much stronger ($r_s = 0.85$, $n = 8$, $t = 3.96$, $p = 0.0075$).

3.3. Autumn migration

In Estonia, peaks in the autumn abundance of nomadic owls were detected mostly every 3–4 years: 1972, 1975, 1979, 1983 and 1986; some increase also in 1989 and 1993 (Fig. 8). However, the variation between 1986 and 1995 shows no clear pattern, and the time-series in general does not differ significantly from white noise series (Fig. 4D).

There was a significant positive correlation between the nomad abundance in Kabli and Lao ($r_s = 0.615$, $n = 15$, $t = 2.81$, $p = 0.0147$), but no such correlations were found between Kabli and Sõrve ($r_s = –0.031$, $n = 13$, $t = –0.10$, $p = 0.921$), and Lao and Sõrve ($r_s = 0.266$, $n = 9$, $t = 0.73$, $p = 0.489$). The total nomad abundance in Estonia was positively correlated with both the numbers of Tengmalm's ($r_s = 0.466$, $n = 24$, $t = 2.47$, $p = 0.022$) and the long-eared owls ($r_s = 0.447$, $n = 24$, $t = 2.34$, $p = 0.029$), and the total number of nomads in Pape ($r_s = 0.460$, $n = 24$, $t = 2.43$, $p = 0.024$; *see* also Fig. 8).

The annual number of migrating Tengmalm's owl was positively correlated with that of the long-eared owl in both Estonia and Pape (Fig. 9). One of the two short-eared owls was caught in 1995 (a peak migration year), the other in 1985 (poor migration year). In Estonia, the total numbers of other owls (the tawny, Ural and pygmy owl) were not correlated with the abundance of nomads ($r_s = 0.298$, $n = 27$, $t = 1.56$, $p = 0.131$). Moreover, 51 out of 106 Ural owls ever caught at the Estonian stations were trapped in 1997 (all in Lao) — a year of a minimal nomad migration.

The number of ringed nestlings of the long-eared owl in a given year was positively correlated with the nomad abundance in that year (Fig. 10), but it was not correlated with the nomad abundance in the previous autumn ($r_s = 0.144$, $n = 25$, $t = 0.70$, $p = 0.492$). The number of the

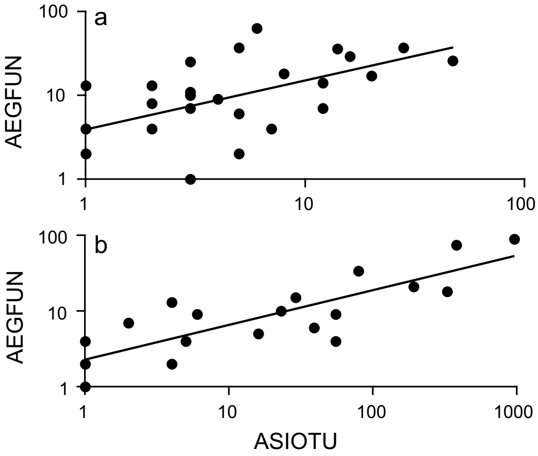

Fig. 9. Relationship between the numbers of the ringed Tengmalm's owls (AEGFUN) and long-eared owls (ASIOTU) in autumn (a) in Estonia in 1971–1997; (b) in Pape in 1969–1987. Both correlations are very significant (Estonia: $r_s = 0.60$, $n = 27$, $t = 3.770$, $p < 0.001$; Pape: $r_s = 0.77$, $n = 25$, $t = 5.72$, $p < 0.00001$). Note the logarithmic scales.

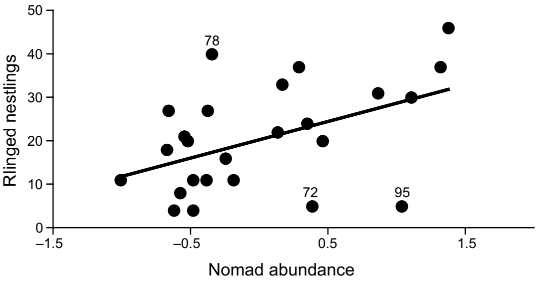

Fig. 10. Relationship between the number of the long-eared owl nestlings ringed in summer and the standardised number of all the nomadic owls caught at the Estonian ringing stations in autumns 1971–1995 ($r_s = 0.443$, $n = 25$, $t = 2.37$, $p = 0.027$). Three most deviating years are indicated with numbers.

tawny owl nestlings in a given year was not correlated with the nomad abundance neither in the same year ($r_s = 0.161$, $n = 25$, $t = 0.78$, $p = 0.443$) nor in the previous autumn ($r_s = -0.031$, $n = 25$, $t = -1.15$, $p = 0.884$).

3.4. Finnish data

Although the South-Finnish owl populations had also apparent 3–4 year periodicity (*see* lists of years in Material and methods), the Estonian and Finnish cycles did not coincide significantly (Table 2). Analyses similar to those in Table 2 were made also for different lags (from one to five years) between Estonian and Finnish data. However, no lags were significant.

Out of 382 Tengmalm's and 188 long-eared owls caught during autumn migration in Estonia only two Tengmalm's owls (0.5%) have been ringed in Finland, both as nestlings. One juvenile was controlled on 18.X.1989 in Lao and one second-year bird on 27.IX.1990 also in Lao. In addition, one Tengmalm's owl, which had been ringed as a nestling in Central Finland in 1974, was found wounded in Virtsu (western Estonia) on 27.IX.1975.

4. Discussion

4.1. Periodic fluctuations in owl productivity

The fluctuations in the numbers of ringed nestlings suggested approximately four-year periods

Table 2. Mean number (± S.D.) of ringed nestlings and intensity of autumn migration in nomadic owls during different phases of Finnish owl cycles. Variation between different phases of Finnish cycles was tested with one-way ANOVA. "All" = all vole-eating raptors and owls.

	Phases of owl cycles in Finland			*F*	*p*
	minimum	intermediate	maximum		
Tawny owl[1)]	43 ±25	40 ±20	42 ±19	0.04	0.96
Long-eared owl[1)]	23 ±12	21 ±14	18 ±11	0.30	0.75
All[1]	131 ±53	117 ±42	114 ±31	0.33	0.72
Migration[2)]	0.1 ±0.6	0.2 ±0.7	–0.2 ±0.7	0.85	0.44

[1)] Total number of ringed nestlings

[2)] (Standardised) number caught in autumn in the 1970s and 1980s. This coincides with the four-year periodicity in the North-Estonian bank vole (Kirk 1990).

Contrarily, the productivity of Ural owls and the number of long-eared owls fluctuated in three-year periods in the 1990s. Compared to earlier decades, this probably indicates a change in the cycle length. In the 1990s, similar three-year periodicity occurred in the productivity of the vole-eating raptors in Estonia (A. Lõhmus & Ü. Väli, unpubl.).

To conclude, periodic component in productivity occurs in several vole-specialists in Estonia, but the numbers fluctuate markedly only in the long-eared owl — a nomadic species.

4.2. Do voles drive the owl productivity in Estonia?

Supported by the data on the Ural owls, my answer is yes. Figs. 5 and 6 illustrate a possible mechanism:

— owls start breeding according to the vole abundance in early spring. This is expectable, because the start is determined by females' body condition (Pietiäinen & Kolunen 1993). After the spring minima (1992, 1995, 1998) the vole numbers probably increase significantly resulting in many breeding owls and their highest productivity in the next year (1993, 1996; also 1990 and 1999?);

— on the third year of the period (1991, 1994, 1997) voles are still abundant in spring and many owls start to breed. However, their breeding success is low, resulting in relatively few fledglings. In autumn, the voles are scarce and the cycle can start again. Probably, these latter points — low breeding success and low vole numbers in the autumn — result from summer declines in vole populations, phenomenon characteristic to cyclic populations (Hansson & Henttonen 1988).

In 1970 — a peak year at least for the buzzards in North-western Estonia — the voles (according to the food of the kestrel) were abundant. In the following year, the vole numbers were at their minimum (Ernits 1972) which was reflected in the ringing totals of the owls. Correlations between the owl productivity and vole abundance are also evident in the tawny and long-eared owls, which had high ringing totals in 1978, a peak year of voles in their diets. The abundance of the bank voles in eastern Estonia between 1981 and 1984 was low in both 1981 and 1984 (Kirk 1993), which is reflected as minima also in the ringing totals.

The impact of vole population dynamics on owls is further supported by comparisons with other bird species. The fluctuations in the owl species productivities were correlated with each other but not with these in other bird species, except perhaps with the one in the common buzzard, which is known to depend partly on voles (Spidsø & Selås 1988). Hence, I argue that periodicity in owl breeding resulted from regular fluctuations in vole populations. Probably, Estonia (like southern Finland; *see* Hansson & Hettonen 1988, Korpimäki 1992) belongs to the transition zone between cyclic and non-cyclic vole populations.

4.3. Productivity and migration

The abundances of the nomadic owl species in autumn were positively correlated with each other, suggesting a common source of variation. Other studies showed that in Tengmalm's owl mostly juveniles migrate (Korpimäki & Hongell 1986, Sykkö & Vikström 1987, Pakkala *et al.* 1994). The Estonian long-eared owls, in turn, are migratory, with less than five per cent of birds remaining to overwinter (*see* Lõhmus *et al.* 1998). In both cases, the most obvious cause behind the variation in migration intensity could be local production of young. It was not possible to get Estonian data on the productivity of Tengmalm's owl, but that of the long-eared owl were indeed positively correlated with the abundance of nomads. However, some other factors can also be involved, as seen from the deviations in Fig. 9. It is particularly difficult to explain high abundance of the nomads in autumn 1995, which by any measures (Figs. 3, 5 and 6; also Lõhmus 1999) was a poor breeding year. Contrarily, the migration "peak" in 1972, could result from a sampling error because the data of that year came from only one station (Kabli), and included no long-eared owls at all.

4.4. Migration between Estonia and Finland

Finnish Tengmalm's owls move largely all over Fennoscandia and sometimes also hundreds of kilometres towards east or south-east (Saurola 1979, Dobrynina 1994, Pakkala *et al.* 1994). If Estonia belonged to the Fennoscandian irruption system, there should be many ring recoveries among caught birds. Leaving out hundreds of owls that are ringed during autumn migration, Heikki Lokki (pers. comm.) has estimated that in Finland about 15% of Tengmalm's and 3% of long-eared owl nestlings are ringed every year. The real proportion of the nomadic owls with Finnish (and any) rings was in our studies thirty times lower, suggesting that there is no free exchange of individuals between Finland and Estonia.

The long-eared is migratory in both Estonia and Finland. The birds ringed in Kabli were found in winter in Germany and the Netherlands (data by Matsalu Ringing Centre), which are also the wintering areas of the Finnish population (*see* Saurola 1983). However, there are no autumn recoveries of the Finnish birds in Estonia, in contrast to five recoveries from the breeding season (data by Helsinki Ringing Centre). Probably the autumn migration of the Finnish long-eared owls is directed towards southern Sweden, but in spring the birds disperse more widely, and regularly settle to breed also in Estonia.

In Estonia, the proportion of ringed owlets is very low and the autumn nomads could be all Estonian birds. However, I suspect that it is not the case, because of the high proportion of Tengmalm's owl among the nomads in Estonia (93% in Sõrve, 82% in Lao, and 39% in Kabli). Even without Sõrve's data that could have been biased in a different way (*see* Material and methods), the dominance of Tengmalm's owl in Estonia is remarkable: only 200 kilometres further south, in Pape, they formed 13%, and a hundred more kilometres south — at Courland Spit — about 14% of the migrating nomadic owls (Belopolsky 1975). At the same time, both in Estonia and Latvia the long-eared owl is four to five times as numerous as Tengmalm's owl, and most of the long-eared owl population migrates (Strazds *et al.* 1994, Lõhmus *et al.* 1998), while in Tengmalm's owl at least a large proportion of adults are resident (Korpimäki 1992). Also these species do not differ markedly in productivity (Lõhmus 1999). Thus, there seems to be a "surplus" of migrating Tengmalm's owls in Estonia, and if these birds do not come from Finland, they can only immigrate from Russia.

4. 5. Spatial structure of fluctuations

The productivity of Estonian and Finnish owl populations was neither synchronous nor clearly lagged. This indicates local regulation of cycles.

However, I argue that lags can be found within Estonia. In the dynamics of the bank vole in Palmse (59°30´N; 25°58´E), North-eastern Estonia, the maxima in 1971, 1975, 1979 and 1983 were followed by 1986; and minima in 1968, 1972, 1977, 1981 and 1985 by 1987 (Kirk 1990, Ling 1992). This does not accord with my results: doubled reconstructions (with both vole and predator data) showed maxima in 1970 and 1978, while trapping in Palmse revealed the maxima one year later. Moreover, recent data on the raptors near the same NE-Estonian area indicate a productivity peak in 1997 instead of 1996, which was a good breeding year for raptors in most of Estonia; the same was found about extreme South-eastern Estonia (Lõhmus 1999). In addition, both known historical irruptions of the nomadic owls into these marginal regions of Estonia in the turn of last century deviated from general dynamics (A. Lõhmus, unpubl.). Are the vole fluctuations in northern and South-eastern Estonia lagged by one year?

It is remarkable that migration intensity in the nomads was synchronous not only in Estonia and in Pape, but the peaks of the long-eared owl migration in 1975 and 1979 were detected also in Helgoland, Germany (Schmidt & Vauk 1981). This is unlikely to be caused only by small Estonian population, and could reveal synchrony in larger areas, probably south of Estonia. At least the latest vole maxima in Latvia (1996 and 1999, U. Bergmanis pers. comm.) seem to coincide with the Estonian ones.

4.6. What causes asynchronous dynamics?

Summarising:

1. a hundred kilometres of sea was enough to make the vole-induced parameters in the Estonian and South-Finnish owls populations to fluctuate independently;
2. this was accompanied by the lack of owl migrations between the countries, although locally the numbers of the long-eared owl responded to vole abundance, and its migration intensity was related to productivity. Instead of to the south, the autumn migration of the Fennoscandian nomadic owls is directed towards the east or south-east (Murmansk and Karelia regions; Dobrynina 1994) or north (in South-Finnish Tengmalm's owls; Saurola 1979). Tengmalm's owl could immigrate to Estonia from Russia (*see* above);
3. migration dynamics suggest synchrony with areas south of Estonia;
4. there is some evidence of one-year lags within Estonia, similar to those within Finland (*see* Kaikusalo & Henttonen 1995).

Thus, it seems that geographical similarities in both vole dynamics and owl response do not "cross" the sea. Why? To answer, one must choose between a cause and consequence in the synchrony of cycles.

As a cause, nomadic avian predators could synchronise vole populations in large areas (Norrdahl & Korpimäki 1996). By preventing the movements of predators, sea could create isolated systems of vole regulation. However, it is not clear as to what extent do owls avoid oversea migration. For example, long-eared owls, probably originating from Fennoscandia, reach British Isles over sea (Mikkola 1983, Overskaug & Kristiansen 1994), and Finnish Tengmalm's owls which migrate via the Central Baltic midway can create invasions in Sweden (Alerstam 1993). Thus, the essential assumption of this hypothesis may be not valid.

As consequences of synchrony in vole dynamics (1) the owls cannot be aware of the situation on the other side of the Gulf of Finland. With such restricted perception, deviations from optimal behaviour could be expected (*see* Spencer *et al.* 1996); (2) if the dynamics of neighbouring vole populations are more likely to be synchronous or to have shorter (e. g. one-year) time-lags when not separated by sea, these populations could be more easily tracked by owls. Hence, it could be a better strategy for nomadic predators to migrate via land than to cross the seas.

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