Diet and breeding performance of Ural Owls *Strix uralensis* under fluctuating food conditions

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Food samples from 91 nests of Ural Owls *Strix uralensis* were collected in the Kauhava region, western Finland, during 1973–85, and in the Keuruu region, central Finland, during 1965-85. The most important prey group by number was *Microtus* voles (*M. agrestis* and *M. epiroticus*, 35 % of prey items), followed by the Water Vole (22 %), Bank Vole (12 %), shrews (10 %) and birds (9 %). The proportions of *Microtus* and Bank Voles in the diet correlated positively with the abundance of these voles in spring trappings. The diet width was negatively related to the spring trap index of *Microtus* voles. The percentage of Water Voles in the food varied irregularly, but the proportions of shrews, birds and frogs seemed to vary inversely with the numbers of *Microtus* spp. in the diet.

The Ural Owl is a food generalist, but its diet is only partly explained by opportunistic foraging. *Microtus* voles are the preferred prey. The year-to-year variation of the diet seemed to be in agreement with the optimal foraging theory in the sense that the diet width tended to increase as the abundance of the preferred prey decreased.

The mean clutch size and number of fledglings in successful nests were positively correlated with the spring trap index of *Microtus* voles. This is consistent with the hypothesis that long-lived species adjust their reproductive efforts to fluctuating food conditions.

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Introduction

The Ural Owl *Strix uralensis* breeds in Eurasian boreal forests, being a resident and long-lived K-strategist (e.g. Korpimäki 1986a). The resident habit has possibly evolved to ensure access to nest-holes, which are in short supply (Lundberg 1979).

The diet of the Ural Owl has been extensively studied in Finland (summarized by Mikkola 1983, Korpimäki 1986a) and in Sweden (Lundberg 1981). Data have also been gathered in Norway (Mysterud & Hagen 1969) and in Germany (Schäfer & Finckenstein 1935, Uttendörfer 1952). They show that Ural Owls use voles as their staple food. In Fennoscandia voles show 3–5-year population cycles, with most pronounced fluctuations in the north (e.g. Kalela 1962, Hansson & Henttonen 1985). Thus, during one cycle, Ural Owls experience one or two years which offer good food conditions for breeding, and one or two poor years. In order to maximize the number of surviving young produced in a life-time (Williams 1966), Ural Owls should adjust their reproductive efforts to fluctuating food conditions (e.g. Hirschfield & Tinkle 1975). For example, only 24 % of the females in a South Finnish population laid eggs in low vole years, while 76 % laid in peak years. The mean clutch size was 3.5 in good years, but only 2.3 in poor ones (Pietiäinen et al. 1986).

Although much field work has been done on the Ural Owl, so far the links between the diet and the small mammals available, and between the breeding performance and small mammal numbers have not been studied on the basis of simultaneous collection of food samples and trapping of small mammals in the same area. Here we report the results of one such study in western and central Finland.

Material and methods

The study was carried out in the Kauhava region (ca. 63°N, 23°E) in western Finland and in the Keuruu region (ca. 62°15'N, 24°30'E) in central Finland. In the former area the proportions of the most important habitats are: forest (mainly pine-dominated) 46 %, agricultural land 28 % and marshland 20 %. Water bodies are few. In the latter area the proportions of forests (71 %, mainly spruce-dominated) and water bodies (11 %) are higher, but the proportions of agricultural land, marshland and inhabited areas are much lower. The two areas also differ with respect to snow conditions. The maximum snow depth in central Finland is 55–65 cm and the duration of the snow cover 150–160 days, while the corresponding figures for western Finland are 30–40 cm and 130–140 days (Solantie 1975, 1977).

In the Kauhava region (Kauhava, Lappajärvi, Evijärvi, Kortesjärvi, Ylihärmä, Alahärmä) food samples were collected in 1973, 1975–83 and 1985 (a total of 32 samples), while in the Keuruu region (Keuruu, Virrat, Vilppula) they were collected in 1977–80 and in 1982–85 (a total of 41 food samples). Mikkola (1969) and Mikkola & Mikkola (1974) have also presented data on 18 food samples collected in the Keuruu region during 1965–70 and this material is included in the present study.

Each food sample consisted of pellets and other prey remains collected from a nest-site and from the ground near the nest after the breeding season. The samples contain mainly the prey items brought by the mates to the nest during the latter part of the nestling period (cf. Lundberg 1976). Earlier, the females remove prey remains from the nests. Some females cleaned their nests until the end of the nestling period, and in these cases the number of prey items in a sample was low.

The samples were dried and later all bones, feathers and scales were separated. Hairs of large samples were dissolved in sodium hydroxide (according to Degn 1978). Small mammal species were determined according to Siivonen (1974). The numbers of individuals were mostly counted on the basis of the mandibles, but in some cases the numbers of femurs, tibiae or sacral bones of voles, mice or shrews were larger than those of the mandibles. The bones were determined by comparison with reference material in the Zoological Museum, University of Oulu. The Field Voles *Microtus agrestis* and Common Voles *M. epiroticus* were sometimes difficult to separate, mainly because the joint branch of the mandible was broken. Thus, not all these individuals could be identified to species. The identification of Water Voles and larger mammals was mostly based on leg bones and reference material. Separation of the young of the two hare species (*Lepus timidus* and *L. europaeus*) was impossible.

Birds were mostly identified by comparing the humeri or other larger bones, and beaks and feathers, with reference material. Lizards and frogs were identified with the aid of various major bones.

Diet width (diet diversity) was calculated using Levins's (1968) formula:

$$DW = 1 / \Sigma p_i^2,$$

where p_i is the proportion of the prey taxon i in the diet. This index renders values ranging from 1 to n, where n is the number of taxa in the diet. In the calculations of diet width indices for the two study areas, the specific level of prey identification was used as far as possible; supraspecific levels of prey identification consistently underestimate diet width (Greene & Jaksić 1983).

In the Kauhava region, the abundances of small mammals were assessed each spring and autumn by snap-trapping. The trap nights in 1973–85 totalled 24440. The methods have been described in other papers (Korpimäki 1981, 1986b, 1987a).

The aspects of the breeding performance examined were the number of breeding pairs, clutch size and the number of fledglings. Data on breeding performance were also collected in some other communes of South Ostrobothnia (Seinäjoki, Nurmo, Peräseinäjoki and Lapua), western Finland, during 1973–85.

Results

Diet composition

The diet of the Ural Owl comprised mammals, birds, frogs and lizards (Table 1). Mammals formed the most abundant prey group, 86% by number of prey and 87% by weight. Among mammals, the most important prey by number was *Microtus* voles (*Microtus agrestis* and *M. epiroticus*, 35%); 96% of them were Field Voles. The second most frequent prey was the Water Vole *Arvicola terrestris* (22% by number), followed by Bank Vole *Clethrionomys glareolus* (12%) and shrews (10%, most of them Common Shrews *Sorex araneus*). Mammal prey also included young hares *Lepus* spp., sciurids (Red Squirrel *Sciurus vulgaris* and Flying Squirrel *Pteromys volans*), Brown Rats *Rattus norvegicus*, mice (House Mouse *Mus musculus* and Harvest Mouse *Micromys minutus*), small mustelids (Stoat *Mustela erminea* and Least Weasel *Mustela nivalis*), and Northern Bats *Eptesicus nilssoni*.

Table 1. Composition of the diet of the Ural Owl by number and by weight in the Kauhava region (pooled data from 1973, 1975–83 and 1985) and the Keuruu region (1965–70, 1977 and 1982–85) in the breeding season.

Prey species or group	Weight(g)	Source	Kauhava region			Keuruu region		
			n	Number %	Weight %	n	Number %	Weight %
Erinaceus europaeus	652	1	1	0.1	0.6	–	–	–
Sorex araneus	7.5	2	156	9.6	1.0	300	6.9	0.7
S. caecutiens	5	1	10	0.6	0.0	15	0.3	0.0
S. minutus	3.5	2	13	0.8	0.0	21	0.5	0.0
S. minutissimus	2.5	1	5	0.3	0.0	6	0.1	0.0
Neomys fodiens	15	1	10	0.6	0.1	32	0.7	0.2
Soricidae total			194	11.9	1.8	374	8.6	0.9
Eptesicus nilssoni	11	3	–	–	–	2	0.0	0.0
Sciurus vulgaris	285	1	8	0.5	1.9	66	1.5	6.1
Pteromys volans	133	3	2	0.1	0.2	19	0.4	0.8
Clethrionomys glareolus	17	2	185	11.4	2.6	536	12.3	2.8
Arvicola terrestris	177	1	313	19.3	46.6	1015	23.2	57.8
Microtus agrestis	25	2	229	14.1	4.8	947	21.7	7.6
M. epiroticus	24	2	25	1.5	0.5	25	0.6	0.2
Microtus spp.	25	2	251	15.5	5.2	604	13.8	4.7
Microtus spp. total			505	31.1	10.5	1576	36.1	12.6
Clethrionomys /Microtus	23	2	41	2.5	0.8	39	0.9	0.3
Rattus norvegicus	257	1	35	2.2	7.6	37	0.8	3.1
Micromys minutus	8	2	3	0.2	0.0	10	0.2	0.0
Mus musculus	15	2	7	0.4	0.1	24	0.5	0.1
Mustela erminea	185	1	3	0.2	0.5	2	0.0	0.1
M. nivalis	42	1	12	0.7	0.4	17	0.4	0.2
Lepus spp.	173	4	70	4.3	10.2	60	1.4	3.3
Mammalia total			1378	84.8	83.6	3777	86.4	88.2
Anseriformes	300	5	2	0.1	0.5	2	0.0	0.2
Galliformes	370	5	19	1.2	5.9	22	0.5	2.6
Charadriiformes	188	5	4	0.3	0.6	–	–	–
Falconiformes	200	5	1	0.1	0.2	–	–	–
Strigiformes	122	2	6	0.4	0.6	8	0.2	0.3
Piciformes	73	5	5	0.3	0.3	7	0.2	0.2
Cuculus canorus	107	5	1	0.1	0.1	–	–	–
Caprimulgus europaeus	80	5	1	0.1	0.1	–	–	–
Columbiformes	475	5	3	0.2	1.2	2	0.0	0.3
Passeriformes								
Corvidae	156	5	7	0.4	0.9	15	0.3	0.8
Thrush-size	74	5	37	2.3	2.3	176	4.0	4.2
Chaffinch-size	22	5	47	2.9	0.9	127	2.9	0.9
Flycatcher-size	12	5	8	0.5	0.1	11	0.3	0.0
Warbler-size	8.5	5	19	1.2	0.1	23	0.5	0.1
Aves spp.			1	0.1	0.1	–	–	–
Aves total			161	9.9	13.9	393	9.0	9.5
Amphibia	36	5	85	5.2	2.6	199	4.6	2.3
Reptilia	3	6	–	–	–	1	0.0	0.0
No. of prey items			1625			4370		
No. of nests			32			59		

Sources: 1) Zoological museum, University of Oulu, 2) Korpimäki (1981), 3) Siivonen (1974), 4) Mikola's (1985) curve for the tibia length and body weight of hares, 5) Glutz von Blotzheim & Bauer (1980), and 6) Avery (1971).

Birds formed 9% of the prey by number and 11% by weight (Table 1). The most important bird group by number was passerines, among which thrush- and chaffinch-sized species were most abundant. Bird prey also included anatids, tetraonids, waders, owls, woodpeckers, and doves (Table 1). Frogs (the only species *Rana temporaria*) were regularly taken (5% by number), but lizards (*Lacerta vivipara*) were only occasionally caught. The diet composition in the Kauhava and Keuruu regions was almost the same (Table 1).

The mean weight of the prey animals was 71.7 g, birds being heavier than mammals (83.4 vs. 72.5 g). The weights ranged from 2.5 g (Pygmy Shrew *Sorex minutissimus*) to 652 g (Hedgehog *Erinaceus europaeus*) (Table 1). In the diet composition by weight, the Water Vole was the most important prey (55%), followed by *Microtus* voles (12%), the Brown Rat (5%) and hares (5%).

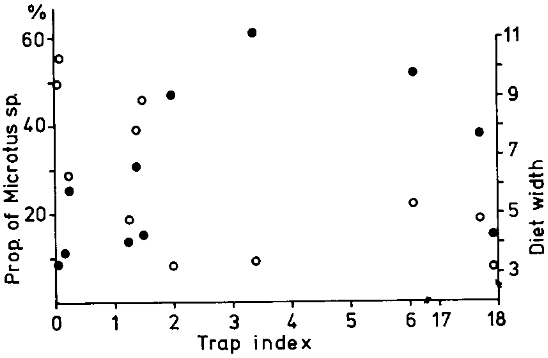

Fig. 1. The correlation between the spring trap index (ind./100 trap nights) of *Microtus* voles and the proportion of these voles in the diet (dots, Spearman rank correlation, r_s= –0.73, P=0.01) in the Kauhava region during 1973, 1975–83 and 1985, and between the spring trap index of *Microtus* voles and the diet width indices (circles, r_s= –0.73, P=0.01) in the Kauhava region during 1973, 1975–83 and 1985.

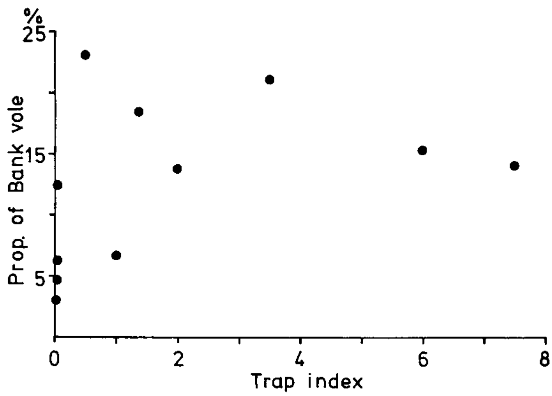

Fig. 2. The correlation between the spring trap index (ind./100 trap nights) of the Bank Vole and the proportion of this vole in the diet in the Kauhava region during 1973, 1975–83 and 1985 (r_s= 0.65, P=0.03).

Yearly variation

In the Kauhava region, the proportion of *Microtus* voles in the diet varied widely (Table 2), being highest in 1973 (61%) and lowest in 1981 (9%). It was positively correlated with the abundance of these voles in the spring trappings during 1973, 1975–83 and 1985 (Fig. 1). A similar relation was also found for the Bank Vole (Fig. 2), but not for the Common Shrew (r_s=0.22, ns). However, the increase of the proportions of *Microtus* and Bank Voles in the diet tended to level off at the highest vole index values (Figs. 1 and 2). This suggests that the correlations may not be linear. The percentage of Bank Voles was largest in 1982 (23%) and smallest in 1981 (3%).

The snap-traps used in the Kauhava region were too small for Water Voles; so data on their population fluctuations are lacking. The proportion of the Water Vole in the diet seemed to vary irregularly, and was not related to the proportion of *Microtus* (r_s = –0.38, ns) or Bank Voles (r_s = –0.18, ns) in the food. Water Voles were taken especially frequently in 1982–83.

The proportions of shrews, birds and frogs seemed to fluctuate inversely with the proportion of *Microtus* voles in the diet, but the correlation was significant only for frogs (r_s = –0.46 for shrews, r_s = –0.55 for birds and r_s = –0.71, p = 0.01 for frogs). Sciurids, mice, rats, small mustelids and hares were evidently taken mainly in poor vole years.

In the Kauhava region, the diet width correlated negatively with the abundance of *Microtus* voles in the spring trappings during 1973, 1975–83 and 1985 (Fig. 1), but not with the abundances of other small mammals (Bank Vole: r_s = 0.24, Common Shrew: r_s = –0.25).

In the Keuruu region, the proportion of *Microtus* voles in the diet varied less than in the Kauhava region, being highest in 1965–66 (59%) and 1985 (47%), and lowest in 1977 (20%, Table 3). In this area the proportion of Bank Voles in the diet was largest in 1965–66 (27%) and smallest in 1967 (3%). The proportion of Water Voles was highest in 1982–83 (as in the Kauhava region), with no correlation with the percentage of *Microtus* voles in the food (r_s = –0.07). The percentages of shrews,

Table 2.The proportions (%) of the most important prey species and groups by number in the diet of the Ural Owl in the Kauhava region during 1973, 1975–83 and 1985.

Prey species or group	1973	1975	1976	1977	1978	1979	1980	1981	1982	1983	1985
Erinaceus europaeus	–	–	–	–	–	–	–	–	–	0.4	–
Soricidae	3.0	9.8	–	3.1	0.7	3.9	5.5	19.4	4.1	8.1	24.9
Sciuridae	–	–	–	–	–	0.9	2.2	1.5	–	0.9	0.2
Clethr. glareolus	21.2	18.5	15.4	14.0	6.3	13.9	6.7	3.0	23.3	4.7	12.4
Arvicola terrestris	–	16.0	–	14.7	28.2	12.6	20.0	13.4	49.3	41.9	9.6
Microtus spp.	60.6	25.9	15.4	48.8	47.2	30.4	11.1	9.0	15.1	13.7	38.1
Clethr./Microtus	12.1	13.6	–	–	–	–	–	–	–	–	4.9
Muridae	3.0	–	–	1.6	2.1	3.9	1.1	22.4	–	4.7	0.6
Mustelidae	–	1.2	–	2.3	1.4	1.7	2.2	–	–	0.4	0.4
Lepus spp.	–	3.7	–	2.3	2.1	14.3	10.0	6.0	1.4	3.8	0.9
Aves	–	7.4	61.6	8.5	11.3	10.9	32.2	17.9	5.5	10.3	4.9
Amphibia	–	3.7	7.7	4.7	0.7	7.4	8.9	7.5	1.4	11.5	3.0
Prey animals	33	81	13	129	142	230	90	67	73	234	533
No. of nests	1	1	1	3	2	5	5	3	1	4	6
Diet width	3.43	6.33	8.88	5.30	3.23	7.88	10.33	9.48	3.10	4.78	4.83

Table 3. The proportions (%) of the most important prey species and groups by number in the diet of the Ural Owl in the Keuruu region during 1965–70, 1977 and 1982–85.

Prey species or group	1965–66	1967	1968	1969	1970	1977	1982	1983	1984	1985
Soricidae	0.6	2.7	12.5	11.1	5.2	23.7	2.9	4.6	4.6	15.6
Eptesicus nilssoni	–	–	–	–	–	–	–	–	0.7	–
Sciuridae	1.7	10.8	9.9	6.5	4.3	–	1.0	0.1	–	0.6
Clethrionomys glareolus	26.5	2.7	9.9	23.4	12.2	8.5	7.6	8.8	7.4	11.7
Arvicola terrestris	8.3	8.1	13.2	5.5	2.6	8.5	45.7	40.0	37.7	12.0
Microtus spp.	58.6	37.8	21.7	30.2	21.8	20.3	28.5	32.9	23.3	46.9
Clethrionomys /Microtus	–	–	–	–	–	–	–	–	–	2.9
Muridae	2.8	5.4	3.3	1.3	0.9	1.7	–	1.2	0.8	1.6
Mustelidae	–	2.7	–	0.5	–	–	1.0	0.5	0.7	0.3
Lepus spp.	0.6	2.7	–	0.5	1.7	–	2.9	2.1	1.8	1.0
Aves	1.1	18.9	19.2	11.9	39.9	15.3	4.8	6.4	19.7	3.7
Amphibia	–	2.7	9.2	8.3	8.7	20.3	4.8	3.4	3.5	3.1
Reptilia	–	–	–	0.3	–	–	–	–	–	–
Prey animals	181	37	152	398	115	59	105	1424	284	1145
No. of nests	2	1	4	6	2	1	2	21	5	10
Diet width	2.37	6.15	8.16	5.97	5.79	5.92	3.32	3.67	4.75	3.93

birds and frogs seemed to be negatively related to the proportion of *Microtus* spp. in the diet ($r_s = -0.54$, p = 0.10 for shrews, $r_s = -0.70$, P = 0.02 for birds, and $r_s = -0.94$, P < 0.001 for frogs). The small proportions of sciurids, mice, rats, small mustelids and hares varied irregularly in this area also. The diet width tended to be negatively related to the proportion of *Microtus* voles in the food ($r_s = -0.49$, P = 0.15).

Regional differences in Europe

Several sources of error are involved in comparison of the diet composition between different regions; the data are collected during different periods and the length of these periods varies greatly (Table 4). *Microtus* and *Clethrionomys* voles are important as the prey of Ural Owls all over Europe. The highest proportions of the former have been recorded in North Savo and Germany, and the highest

Table 4. The diet composition (as percentages of total numbers) of the Ural Owl during the breeding season in Europe.

Areas	Kauhava region	Keuruu region	North Savo	Päijät-Häme	Sweden	Norway	Germany
Years	1973–85	1965–85	1976–84	1976–77	1969–78	1949–67	1929–44
Sources	1	1	2	3	4	5	6
Erinaceus europaeus	0.1	–	–	–	–	–	–
Talpidae	–	–	–	5.0	–	–	0.4
Soricidae	11.9	8.6	3.9	4.6	6.7	12.0	7.1
Vespertilionidae	–	0.0	0.1	–	–	–	–
Sciuridae	0.6	1.9	0.2	–	1.1	0.8	0.4
Myopus schisticolor	–	–	–	–	–	0.8	–
Clethrionomys spp.	11.4	12.3	15.3	9.2	11.8	29.3	14.9
Microtus spp.	31.1	36.1	42.7	22.4	30.8	36.8	41.5
Arvicola terrestris	19.3	23.2	33.9	24.4	33.1	0.8	0.4
Ondatra zibethica	–	–	0.1	–	–	–	–
Muridae	2.8	1.5	1.1	5.6	0.6	–	11.7
Sicista betulina	–	–	–	–	–	–	1.8
Small mammal, unidentified	2.5	0.9	–	–	4.0	3.7	–
Mustelidae	0.9	0.4	0.2	0.3	–	0.8	–
Leporidae	4.3	1.4	0.2	–	–	–	0.7
Mammalia total	84.8	86.4	97.7	71.5	88.1	85.0	78.9
Aves	9.9	9.0	2.3	25.1	8.4	15.0	7.4
Amphibia	5.2	4.6	–	1.0	3.4	–	5.3
Reptilia	–	0.0	–	–	–	–	–
Pisces	–	–	–	–	–	–	0.4
Insecta	–	–	–	2.3	–	–	8.1
Prey animals	1625	4370	1739	303	2309	133	282
Diet width	5.65	4.59	3.10	5.28	4.3	03.85	4.38

Sources: 1) this study, 2) Jäderholm (1987), 3) Kunttu (1978), 4) Lundberg (1981), 5) Mysterud & Hagen (1969), and 6) Schäfer & Finckenstein (1935), Uttendörfer (1952).

proportions of the latter in Norway. The Water Vole is reported to be an important prey species in Finnish and Swedish studies. In all areas Ural Owls also frequently take shrews, but the importance of birds varies widely between areas, the highest numbers having been recorded in Päijät-Häme and Norway, and the lowest in North Savo. However, the food samples from Päijät-Häme were collected in the poor vole years 1976–77, which might be the reason for the low number of voles and high number of birds in the diet. The highest percentages of frogs were recorded in the Kauhava and Keuruu regions, and in Germany. The greatest diet widths were found in the Kauhava region and Päijät-Häme, and the smallest in North Savo and Norway.

Breeding performance in relation to small mammal dynamics

The percentage of nest-boxes used by Ural Owls in South Ostrobothnia (Table 5) did not correlate with the spring trap index of *Microtus* spp. ($r_s = 0.24$), the Bank Vole ($r_s = -0.33$) or the Common Shrew ($r_s = -0.15$) in the Kauhava region during 1975–85. The reason may be the evident increase of the Ural Owl population in this area in 1975–80 through immigration. Despite scanty data, the mean clutch size was positively related to the spring trap index of *Microtus* voles ($r_s = 0.72$, $P = 0.01$), but not to that of the Bank Vole ($r_s = -0.16$) or Common Shrew ($r_s = 0.01$). The mean number of fledglings in successful nests tended to be positively correlated with the spring trap index of *Microtus* voles, but the correlation ($r_s = 0.51$, $P = 0.11$) was not significant.

Discussion

Diet composition

Most of the prey remains originate from the nestling period, when the provision of food is almost exclusively the duty of the male (Lundberg 1980).

Table 5. The population fluctuations and breeding performance of the Ural Owl in South Ostrobothnia, western Finland during 1975–85.

Year	No. of boxes	No. of nests	Percentage used	Clutch size		No. of fledglings in successful nests	
				Mean	n	Mean	n
1975	38	1	2.6	1.0	1	1.0	1
1976	71	2	2.8	1.5	2	1.0	1
1977	85	4	4.7	3.2	4	2.0	4
1978	90	5	5.6	3.0	5	2.2	5
1979	93	8	8.6	2.8	8	2.2	8
1980	90	9	10.0	2.5	8	1.9	7
1981	93	7	7.5	2.2	6	2.2	6
1982	92	8	8.7	3.0	8	3.0	5
1983	77	5	6.5	2.5	4	1.8	4
1984	75	2	2.7	2.0	2	2.0	2
1985	75	11	14.7	3.5	11	2.9	11

Thus, the data reflect mainly the food brought to the nest by the male.

Ural Owls have a fairly wide prey spectrum, compared with, for instance, the most frequent owl species, Tengmalm's Owl *Aegolius funereus*, which concentrates entirely on small mammals and birds even in poor vole years (Korpimäki 1981). In other studies also, the Ural Owl has been considered to be a food generalist (e.g. Lundberg 1976, 1981, Mikkola 1983, Korpimäki 1986a).

The mean body weight of the Ural Owl is 871g for females and 720g for males (Mikkola 1983). The mean prey weight in this study is 71.7g, which is slightly smaller than that recorded in other Finnish studies (78.1g, Korpimäki 1986a). The reason may be that we used a clearly smaller mean weight for young hares (173g, earlier 2000g, see Table 1). The prey weight of a larger sympatric *Strix* species, the Great Grey Owl *S. nebulosa*, averages only 38.4g (Korpimäki 1986a), the prey of the Ural Owl thus being about twice as heavy.

As there were clear differences in the habitat composition between the Kauhava and Keuruu regions, the available prey could also be expected to be dissimilar. The higher proportion of water bodies in the Keuruu region may be reflected in the slightly larger percentage of Water Voles in the diet of Ural Owls. In contrast, the larger proportion of agricultural land in the Kauhava region did not result in a higher percentage of *Microtus* voles, and the smaller proportion of forest was not reflected in a lower proportion of e.g. squirrels or Bank Voles in the diet. According to e.g. Jaksić & Braker (1983) and Steenhof & Kochert (1985), several birds of prey feeding mainly on small mammals are opportunistic foragers — as first outlined by Wiens & Rotenberry (1979). The present results suggest, however, that the diet composition of the Ural Owl is not entirely explained by opportunistic foraging. Interspecific competition may also be involved. The food niches of the Ural Owl and Eagle Owl *Bubo bubo* overlap widely (Korpimäki 1981), and the larger species can even feed on the smaller one (Mikkola 1983). In the Keuruu region the Eagle Owl is scarce, but in the Kauhava region its population is dense (Korpimäki 1987b). The presence of Eagle Owls in the Kauhava region seems to result in Ural Owls mainly occupying large spruce-dominated forest areas, where fields are small. These areas are similar to those in the Keuruu region, which accounts for the similarity of the diets of the Ural Owls in the two regions.

Yearly variation in the diet

The Ural Owl usually searches for food at the edges of clearings, agricultural land or marshland (Lundberg 1981). In both the Kauhava and Keuruu regions, *Microtus* voles are the dominant small mammals in these open habitats, but the Bank Vole mainly occupies forests and their edges. The proportions of these voles in the diet correlated positively with their abundances in the field, which is circumstantial evidence that these small voles are the preferred prey of the Ural Owl in these study areas. Although there are no direct data on the population fluctuations of the Water Vole, it seems that its population varied irregularly and partly asynchronously with *Microtus* and Bank Voles (see also Myllymäki 1983). This is supported by the fact that the percentage of Water Voles in the diet did not correlate with the percentages of *Microtus* or Bank Voles. According to Lundberg (1981), the Water Vole was the preferred prey of Ural Owls in Central Sweden. The large percentage of this vole in the diet in 1982-83 indicate that this may be so in Finland, too.

The optimal foraging theory predicts that the diet width of a predator increases, as the abundance of the preferred prey decreases (e.g. Pyke et al. 1977, Pyke 1984). This was observed in the Ural Owl, because, when the abundance of *Microtus* voles decreased, they hunted alternative prey to a greater extent. According to the variation in the diet between years, the order of preference of the most important alternative prey may be: Bank Vole, shrews, birds and frogs. It has been suggested that for prey of varying size any preference order should generally correspond only to the order of size (e.g. Schoener 1971, Pyke et al. 1977). The present results seem to be inconsistent with this suggestion. Many other factors besides size may affect the preference order (e.g. density, behaviour and habitat of the prey species).

Regional trends in diet width

In general, the diet width is dependent on the prey choice and the diversity of the available food (e.g. Järvinen 1977). The width of the diet of the Ural Owl should increase southwards with the rising number of alternative prey animals, as in Tengmalm's Owl (Korpimäki 1986c). However, this was not true here. The diet width was clearly smaller further south, especially in Germany, than in most studies in Finland.

In Fennoscandia, the "cyclicity indices" of the population fluctuations of microtines are more closely related to the snow cover than to the latitude (Hansson & Henttonen 1985). The Kauhava and Keuruu regions, and North Savo are located at about the same latitude, but the duration and depth of the snow cover increases markedly from west to east (Solantie 1975, 1977), which suggests that the amplitude of the vole cycles and the population fluctuations of the Ural Owl should increase in the same direction (as in Tengmalm's Owl, Korpimäki 1986c). Thus, the proportion of the food material collected in good vole years may increase from the Kauhava region through the Keuruu region to North Savo, causing the diet width to decrease in the same direction.

Breeding performance under fluctuating food conditions

Lundberg (1981) suggested that the breeding frequency of the Ural Owl is determined by the abundance of Field and Bank Voles early in spring, at the time of courtship feeding. In this study the abundances of these voles did not correlate with the breeding frequency in South Ostrobothnia, which, however, may be caused by the increase of the Ural Owl population during the study period. The weather in the preceding autumn and winter may also impair the correlation, because warm autumns and mild winters often precede good breeding seasons (Pietiäinen et al. 1986).

In this study the abundance of *Microtus* voles was the most important factor affecting clutch size and number of fledglings produced. The abundance of the Bank Vole and Common Shrew was not of similar importance. Before and during egg-laying, in March-April, Water Voles are still living under ground (Gaisler & Zejda 1973) and they are available for Ural Owls only from May onwards. Thus, their abundance should affect only the survival of the young. The egg-production mainly depends on smaller voles. Among these, *Microtus* voles are larger than Bank Voles and probably easier to catch from their ventilation holes in snow. However, even in low vole years some owl pairs can produce a small number of eggs and young on a diet consisting mainly of birds, though most pairs refrain from breeding (Lundberg 1981, Pietiäinen et al. 1986). As Ural Owls generally hunt in daytime as well, especially in the morning (Korpimäki & Huhtala 1986), their daily activity pattern is more suitable for catching birds than that of Tengmalm's Owl (Korpimäki 1981).

The clutch size and number of young produced by Ural Owls varied widely between years and in parallel to the population fluctuations of *Microtus* voles (as in many other vole-eating birds of prey, e.g. Korpimäki 1985). This is in agreement with the hypothesis that long-lived species adjust their reproductive efforts to fluctuating food conditions in order to maximise their life-time reproductive output (e.g. Hirschfield & Tinkle 1975). Moreover, Ural Owls also seem to adjust their egg size to the annual food supply, investing more in their eggs in good years than in poor ones (Pietiäinen et al. 1986).

In variable environments, selection for high reproductive effort should occur in years that are good for juvenile survival, provided that the quality of the year is predictable by the adults (Hirschfield &

Tinkle 1975). Because of the cyclicity of the microtine populations, the food supply during the nestling and post-fledging periods is usually predictable for Ural Owls at the time of egg-laying; only a few of the crashes occur in spring and summer. Thus, a selective advantage could be expected for those Ural Owls that invest most in reproduction in the increase and peak phases of the vole cycle, because the survival of their offspring is probably highest at that time. In contrast, the reproductive effort should be lowest in the decrease and low phases, when the survival of the offspring is probably lowest.

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Selostus: **Viirupöllön ravinto ja pesintä vaihtelevissa ravinto-oloissa Länsi- ja Keski-Suomessa**

Ravintonäytteet kerättiin yhteensä 91 viirupöllön pesältä Länsi-Suomesta (Kauhavan seudulta) vuosina 1973–85 ja Keski-Suomesta (Keuruun seudulta) vuosina 1965–85. Pelto- ja kenttämyyrät muodostivat 34.7% saaliseläinten lukumäärästä; metsämyyrän osuus oli 12.0%, päästäisten 9.5% ja lintujen 9.2%. Kun painot otettiin huomioon, vesimyyrä kohosi tärkeimmäksi saaliiksi (54.7%, taulukko 1). Pelto- ja kenttämyyrien sekä metsämyyrien osuudet ruokavaliossa korreloivat positiivisesti niiden tiheyksiin loukkupyynneissä (kuvat 1 ja 2). Ravintolokero kaventui, kun pelto- ja kenttämyyrien yhteistiheys maastossa kasvoi (kuva 1). Vesimyyrien osuus ravinnossa vaihteli epäsäännöllisesti ja oli erityisen suuri 1982–83. Päästäisiä, lintuja ja sammakoita syötiin paljon silloin, kun pelto- ja kenttämyyriä oli vähän (taulukot 2 ja 3). Sekä keskimääräinen pesyekoko että poikastuotto (taulukko 5) näyttivät korreloivan positiivisesti pelto- ja kenttämyyrien tiheyden kanssa.

Viirupöllö on yleispeto, jonka suosituinta saalista näyttävät olevan pelto- ja kenttämyyrät. Tulokset ovat sopusoinnussa optimaalisen saalistusteorian kanssa, sillä ravintolokero näytti levenevän suosituimman saaliin vähetessä. Koska sekä munaluku että poikastuotto vaihtelivat samansuuntaisesti pelto- ja kenttämyyrien tiheyksien kanssa, tulokset tukevat hypoteesia, jonka mukaan pitkäikäiset lajit sopeuttavat lisääntymispanoksensa vaihteleviin ravinto-oloihin.

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