Diet of breeding Tengmalm's Owls *Aegolius funereus*: long-term changes and year-to-year variation under cyclic food conditions

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The diet of breeding Tengmalm's Owls *Aegolius funereus* was studied in the Kauhava region, western Finland, using two methods: identification of prey animals cached in the nest-holes (a total of 4366 prey items in 1973–86) and found in the pellets and other prey remains collected from the nest-holes (12540 in 1966–86). *Microtus* voles (*M. agrestis* and *M. epiroticus*) were the most abundant prey group in the caches (45% of the number of prey), followed by bank voles (32%), shrews (15%) and birds (5%). Shrews amounted to 33% of prey items in the pellets, followed by *Microtus* spp. (27%), bank voles (24%) and birds (12%).

During 1966–86, the percentages of water shrew, water vole, house mouse, brown rat and insects in the diet seemed to increase, whereas the percentages of field and bank voles seemed to decrease. These long-term changes were probably caused by habitat changes in the study area.

The proportion of *Microtus* voles (preferred prey) in the diet correlated positively with the abundance of these voles in spring trappings. The percentages of shrews and birds in the diet varied inversely with the numbers of *Microtus* spp. in the food. This supported the prediction of the optimal foraging theory in the sense that the diet composition depended only on the density of preferred prey.

Adult males are resident in the study area. Their preferred prey showed 3–4-year population cycles, but the populations of alternative prey (bank vole, common shrew and birds) did not show marked year-to-year fluctuations. Thus, resident males can survive by switching to alternative prey in low vole years.

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Introduction

Tengmalm's Owl *Aegolius funereus* usually uses low-perched sit-and-wait hunting technique, which seems to be an adaptation to foraging in woodland (Norberg 1970, Sonerud et al. 1986, pers. obs.). Extensive studies in North and Central Europe (summarized by Korpimäki 1981, 1986a; see also Jäderholm 1987) show that Tengmalm's Owl uses voles, especially *Microtus* and *Clethrionomys* species, as its staple food. The populations of these voles are relatively stable in Central Europe, but show 3–5-year cycles in Fennoscandia, with most pronounced fluctuations in the north (e.g. Kalela 1962, Hansson & Henttonen 1985). The population fluctuations of voles in Fennoscandia largely affect the breeding density and breeding performance of Tengmalm's Owl: densities of breeding pairs are low and clutch sizes and numbers of young produced are small in poor vole years, but they are much better in good vole years (e.g. Linkola & Myllymäki 1969, Korpimäki 1981, 1985a, 1987a, 1987b).

Regional and year-to-year changes of vole populations affect the diet composition of Tengmalm's Owl. The diet is more varied in Central Europe than in North Europe (Korpimäki 1986a). In peak years the diet consists mainly of *Microtus* and *Clethrionomys* voles, but in low years the proportions of shrews and birds increase strongly (Sulkava & Sulkava 1971, Korpimäki 1981). The proportion of *Microtus* voles in the diet seems to fluctuate in accord with the abundance of these voles in the field (Korpimäki 1981). However, the results from the year-to-year variation in the dict were based on relatively short-term data. Thus, my intention in this paper is to study long-term changes and year-to-year variation in the diet composition of breeding Tengmalm's Owls in relation to the population fluctuations of voles. The study is based on data collected over 21 years (1966–86) in western Finland.

Material and methods

The study was carried out in the Kauhava region (ca. 63°N, 23°E), western Finland. The study area is 1300 km^2. The proportions of the most important habitats are: woodland (mainly pine-dominated) 46%, farmland 28% and marshland 20%. Further details are given in other papers (Korpimäki 1981, 1986b, 1987a, 1987c).

The diet composition of Tengmalm's Owls was studied by two methods: identification of prey items (i) cached in the nests and (ii) found in the pellets and other prey remains collected from the nest-holes. Nest-holes of Tengmalm's Owl regularly contain a store of prey animals, especially during the egg- laying, incubation and hatching periods (Korpimäki 1981, 1987d). These prey items were identified on visits to all the nests of the population (a total of 407 nests) in 1973–86 (the number of prey items totalled 4366) (Table 1). To avoid counting any individual in a food store twice, the tails of small mammals and the claws of birds were cut off; Tengmalm's Owls always begin to eat their prey from the head (Scherzinger 1971, Korpimäki 1981, 1987d).

A layer of pellets and other prey remains accumulates on the bottom of the nest-hole during the nestling period (Sulkava & Sulkava 1971). Each food sample consists of pellets and other prey remains collected from a nest-hole. The number of nests where food samples were collected totalled 133 in 1966–86 (Table 1). In poor owl years, such as 1968, 1972, 1975, 1981 and 1984, the food samples were collected from a majority of the nests of the population, whereas in other years the collection nests were randomly chosen.

The food samples contain mainly the prey items brought by the mates to the nest during the latter part of the nestling period. Earlier, the females remove prey remains from the nests (Korpimäki 1981 and unpubl.). A majority of the prey is brought by the males because the females take part in feeding, only at a low rate, during less than two weeks at the end of the nestling period (Korpimäki 1981).

The food samples were dried and later 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 counted on the basis of the mandibles. The field voles *Microtus agrestis* and common voles *M. epiroticus* were sometimes difficult to separate, because the joint branch of the mandible was broken. Thus, not all these individuals could be identified to species. The identification of water voles *Arvicola terrestris* and other larger mammals was mostly based on leg bones and reference material in the Zoological Museum, University of Oulu. Birds were mostly identified by comparing the humeri or other larger bones, and beaks and feathers, with reference material. The identification of insects is described elsewhere (Itämies & Korpimäki 1987).

Diet width (diet diversity) was calculated using Levins's (1968) formula (for further details, see Korpimäki & Sulkava 1987). In the calculations, the specific level of prey identification was used as far as possible, because supraspecific levels of prey identification consistently underestimate diet width (Greene & Jaksić 1983).

Abundances of small mammals were measured each spring and autumn with snap-trap captures, covering a total of 25 780 trap nights in 1973–86. Methods are described elsewhere (Korpimäki 1981, 1986c, 1987c).

Results

Diet composition using two methods

Mammals formed the most frequent prey group both in the caches (95.1% of number and 92.2% of weight of prey) and in the pellets (87.4% and 78.0%) (Table 1). The most important prey mammals in the caches were *Microtus* voles; most of them were common voles. The second most abundant cached prey was the bank vole *Clethrionomys glareolus*, followed by shrews (most of them common shrews *Sorex araneus*). Among mammals found in the pellets, shrews were the most frequent prey, followed by *Microtus* voles and bank voles.

Birds amounted to 4.9% of the number and 7.8% of the weight of the cached prey (Table 1). The corresponding proportions in the pellets were 12.3% and 22.0%. The most frequent birds in the food stores were Chaffinch *Fringilla coelebs*, Yellowhammer *Emberiza citrinella*, Song Thrush *Turdus philomelos*, Redwing *T. iliacus* and Willow Warbler

Table 1. Diet composition of breeding Tengmalm's Owls by number and by weight of prey based on the two methods: identification of cached prey (pooled data from 1973–86) and pellets and other prey remains (1966–86). (n) = nestling, (y) = young.

Prey species or group	Weight (g)	Source	Caches			Pellets		
			N	Number %	Weight %	N	Number %	Weight %
Sorex araneus	7.5	1	634	14.5	5.7	3971	31.7	13.7
S. isodon	10.5	2	3	0.1	0.0	–	–	–
S. caecutiens	5.5	2	2	0.1	0.0	–	–	–
S. minutus	3.5	1	24	0.6	0.1	136	1.1	0.2
Neomys fodiens	14.5	1	4	0.1	0.1	47	0.4	0.3
Sorex spp.	7	1	–	–	–	1	0.0	0.0
Shrews total			667	15.3	5.9	4155	33.1	14.2
Sciurus vulgaris	295	2	1	0.0	0.4	3	0.0	0.4
Myopus schisticolor	27.5	2	1	0.0	0.0	–	–	–
Clethr. glareolus	16.5	1	1389	31.8	27.3	3030	24.2	23.0
Arvic. terrestris (y)	65	1	7	0.2	0.5	27	0.2	0.8
Microtus agrestis	25	1	898	20.6	26.8	668	5.3	7.7
M. epiroticus	23.5	1	1023	23.4	28.7	1410	11.2	15.2
Microtus spp.	24.5	1	28	0.6	0.8	1287	10.3	14.5
Microtus spp. total			1949	44.6	56.3	3365	26.8	37.4
Voles total			3346	76.6	84.2	6422	51.2	61.2
Rattus norvegicus (y)	45	1	3	0.1	0.2	8	0.1	0.2
Micromys minutus	8	1	102	2.3	1.0	177	1.4	0.7
Mus musculus	15	1	34	0.8	0.6	195	1.6	1.3
Murids total			139	3.2	1.7	380	3.0	2.2
Mammals total			4153	95.1	92.2	10960	87.4	78.0
Bonasa bonasia (y)	30	1	1	0.0	0.0	–	–	–
Aegolius funereus (n)	102	1	5	0.1	0.6	71	0.6	3.3
Dendrocopos major	88	3	–	–	–	1	0.0	0.0
Jynx torquilla	37	3	–	–	–	1	0.0	0.0
Apus apus	37	3	–	–	–	9	0.1	0.2
Hirundo rustica	19	3	2	0.1	0.1	34	0.3	0.3
Parus major	20	3	4	0.1	0.1	34	0.3	0.3
P. cristatus	12	3	–	–	–	14	0.1	0.1
P. montanus	11	3	3	0.1	0.0	30	0.2	0.2
Parus spp.	14	3	–	–	–	37	0.3	0.2
Certhia familiaris	9	3	1	0.0	0.0	–	–	–
Turdus viscivorus	115	3	–	–	–	3	0.0	0.2
T. pilaris	106	3	2	0.1	0.3	52	0.4	2.5
T. philomelos	67	3	20	0.5	1.6	25	0.2	0.8
T. iliacus	58	3	17	0.4	1.2	129	1.0	3.4
Turdus spp. (n)	20	1	17	0.4	0.4	–	–	–
Saxicola rubetra	16.5	3	–	–	–	4	0.0	0.0
Erithacus rubecula	16.5	3	5	0.1	0.1	3	0.0	0.0
E. rubecula (n)	10	1	4	0.1	0.1	–	–	–
Phylloscopus trochilus	10	3	10	0.2	0.1	–	–	–
P. collybita	8	3	1	0.0	0.0	–	–	–
Phylloscopus spp.	9	3	–	–	–	118	0.9	0.5
Regulus regulus	5.5	3	2	0.1	0.0	3	0.0	0.0
Muscicapa striata	15.5	3	–	–	–	2	0.0	0.0
Ficedula hypoleuca	12.5	3	–	–	–	12	0.1	0.1
Anthus trivialis	22	3	1	0.0	0.0	16	0.1	0.2
A. pratensis	18	3	3	0.1	0.1	–	–	–
Motacilla alba	20.5	3	–	–	–	2	0.0	0.0
Garr. glandarius (n)	20	3	1	0.0	0.0	–	–	–
Sturnus vulgaris	74	3	1	0.0	0.1	1	0.0	0.0
Carduelis chloris	29	3	–	–	–	2	0.0	0.0

Prey species or group	Weight (g)	Source	Caches			Pellets		
			N	Number %	Weight %	N	Number %	Weight %
C. flammea	14	3	2	0.1	0.0	11	0.1	0.1
C. spinus	12.5	3	1	0.0	0.0	8	0.1	0.1
Pyrrhyla pyrrhyla	34	3	4	0.1	0.2	36	0.3	0.6
Loxia pytyopsittacus	56	3	–	–	–	1	0.0	0.0
Loxia spp.	41	3	1	0.0	0.1	–	–	–
Fring. montifringilla	22	3	4	0.1	0.1	4	0.0	0.0
F. coelebs	22	3	69	1.6	1.8	733	5.9	7.2
F. coelebs (n)	5	1	4	0.1	0.0	–	–	–
Emberiza citrinella	32	3	21	0.5	0.8	30	0.2	0.4
E. citrinella (n)	10	3	5	0.1	0.1	–	–	–
E. schoeniclus	18	3	–	–	–	1	0.0	0.0
E. rustica	19	3	1	0.0	0.0	–	–	–
Passer domesticus	32	3	1	0.0	0.0	1	0.0	0.0
Thrush-size	77	3	–	–	–	8	0.1	0.3
Chaffinch-size	22	3	–	–	–	38	0.3	0.4
Tit-size	20	3	–	–	–	70	0.6	0.5
Birds total			213	4.9	7.8	1544	12.3	22.0
Insects	0.2	4	–	–	–	36	0.3	0.0
No. of prey items			4366			12540		
No. of nests			407			133		

Sources: 1) Korpimäki (1981), 2) Siivonen (1974), 3) v. Haartman et al. (1963–72), and 4) Itämies & Korpimäki (1987).

Phylloscopus trochilus. The same species were also most abundant in the pellets. Pellets also contained some insects, mainly coleopterans.

The mean weight of the cached prey was 19.2 g. Cached birds were heavier than mammals (30.8 vs. 18.6 g). The weight of prey animals identified in the pellets averaged 17.4 g (birds 31.1 g, mammals 15.5 g). The weights of prey items ranged from 0.2 g (insects) to 295 g (red squirrel *Sciurus vulgaris*) (Table 1).

There were large differences between the diets determined by the two methods. The proportions of *Microtus* voles and bank voles were higher and the percentages of shrews and birds were lower in the caches than in the pellets (Table 1). The reason is that the two diets reflect the food composition in different phases of the breeding season. Prey caches were found in the nests during the egg-laying, incubation and hatching periods, and at the early stages of the nestling period (Korpimäki 1981, 1987d), whereas pellets and other prey remains accumulated in the nest-holes only in the latter part of the nestling period (Korpimäki 1981). Marked changes in the food composition of Tengmalm's Owl occur in the course of the breeding season: the proportions of *Microtus* voles and bank voles decrease and the proportions of shrews and birds increase (Korpimäki 1986b).

Table 2. Spearman rank correlation (r_s) between the percentages of different important prey species or species groups in the cached prey and in the pellets in 1973–86. df = 12 in each case.

Prey species or group	r_s	P<
Sorex araneus	0.64	0.05
Shrews total	0.65	0.05
Clethrionomys glareolus	0.56	0.05
Microtus agrestis	0.66	0.05
M. epiroticus	0.73	0.01
Microtus spp. total	0.86	0.001
Murids	0.86	0.001
Birds	0.68	0.01

The percentages of shrews, bank voles, *Microtus* voles, mice and birds in the cached prey correlated positively with the percentages of these prey groups in the pellets during 1973–86 (Table 2). This shows that the year-to-year variation of the most important

Table 3. The proportions (%) of the most important species or groups by number of prey in the diet of Tengmalm's Owl based on the identification of the cached prey during 1973–86. The group "other mammals" includes water voles, one red squirrel and one wood lemming. P = number of prey items, N = number of nests where cached prey items were identified.

Year	Shrews	Bank vole	*Microtus* spp.	Murids	Other mammals	Mammals total	Birds	P	N
1973	44.5	28.1	25.8	1.6	–	100.0	–	128	18
1974	22.8	53.7	20.1	0.7	0.3	97.6	2.4	294	13
1975	24.6	16.4	–	–	–	41.0	59.0	61	3
1976	11.1	34.9	38.4	5.2	–	89.5	10.5	172	19
1977	4.2	17.8	75.4	1.4	–	98.9	1.2	779	63
1978	30.5	38.4	17.9	5.3	–	92.1	8.0	151	14
1979	20.8	55.3	12.7	7.5	–	96.3	3.8	347	37
1980	26.2	31.6	15.0	5.6	–	78.4	21.6	301	24
1981	46.0	30.0	6.0	–	–	82.0	18.0	50	10
1982	11.9	32.6	41.7	11.3	0.3	97.9	2.1	328	34
1983	23.8	39.3	25.9	0.4	2.5	92.1	7.9	239	27
1984	60.2	24.8	3.5	–	–	88.5	11.5	113	10
1985	11.2	43.7	42.4	1.8	–	99.1	0.9	439	47
1986	4.5	21.3	72.2	1.9	0.1	99.9	0.1	964	88

Table 4. The proportions (%) of the most important species or groups by number of prey in the diet of Tengmalm's Owl based on the identification of prey animals found in the pellets and other prey remains during 1966–86. The group "other mammals" includes water voles and red squirrels. P = number of prey items, N = number of nests where food samples were collected.

Year	Shrews	Bank vole	*Microtus* spp.	Murids	Other mammals	Birds	Insects	P	N	Diet width
1966	13.8	44.8	32.8	0.6	–	8.1	–	174	3	3.65
1967	34.8	28.0	15.5	0.6	–	21.1	–	161	4	4.50
1968	67.7	3.2	7.7	–	–	21.3	–	155	1	2.08
1969	25.9	29.1	40.0	3.1	–	1.9	–	320	4	4.91
1970	4.1	18.8	71.0	5.5	–	0.7	–	293	5	4.38
1971	14.8	29.6	25.4	0.6	0.3	29.3	–	311	6	6.48
1972	16.4	36.3	39.0	–	–	8.2	–	146	1	4.73
1973	37.1	31.4	15.9	4.2	0.5	11.0	–	574	6	4.16
1974	34.5	38.6	11.7	0.3	0.3	14.7	–	892	7	3.63
1975	65.2	2.9	8.8	1.5	–	21.7	–	69	2	2.36
1976	13.5	33.5	20.9	5.1	0.2	26.8	–	474	7	5.91
1977	19.1	26.3	42.0	2.0	0.1	10.6	–	1488	12	5.73
1978	25.2	28.4	15.4	5.0	0.3	25.6	–	602	7	6.34
1979	44.9	27.4	13.4	5.0	0.1	9.3	–	1030	8	3.58
1980	32.5	12.8	10.3	6.0	–	36.4	1.9	514	10	6.07
1981	55.2	9.3	10.6	0.8	1.0	19.8	3.3	611	5	3.16
1982	43.8	23.3	22.5	4.8	0.3	5.2	0.1	1487	9	4.01
1983	38.3	22.7	10.1	2.4	1.0	25.5	–	506	9	4.72
1984	77.8	5.1	6.1	0.4	0.2	10.4	–	527	6	1.96
1985	28.1	24.2	42.9	2.6	0.1	2.1	–	1304	11	4.99
1986	16.9	16.7	60.8	3.7	–	1.4	0.6	902	10	4.95

prey groups in the diets determined by the two methods was similar, although cached prey items were collected from all the nests of the population, whereas pellets and other prey remains only from some of the nests (Tables 3 and 4). In the following, only the diet composition determined by pellet analyses was used because it was based on larger samples of prey animals.

Table 5. Significance of long-term changes in the diet composition of Tengmalm's Owl during 1966–86 using Spearman rank correlation. Basic data in Table 4. df = 19 in each case, ns = not significant.

Prey species or group	r_s	P<
Sorex araneus	0.31	ns
S. minutus	0.02	ns
Neomys fodiens	0.43	0.05
Clethrionomys glareolus	–0.44	0.05
Arvicola terrestris	0.45	0.05
Microtus agrestis	–0.41	0.10
M. epiroticus	0.05	ns
Micromys minutus	0.29	ns
Mus musculus	0.39	0.10
Rattus norvegicus	0.62	0.01
Mammals total	–0.02	ns
Aegolius funereus nestlings	0.16	ns
Hirundo rustica	0.53	0.05
Parus major	0.14	ns
P. cristatus	–0.06	ns
P. montanus	–0.15	ns
Turdus pilaris	–0.13	ns
T. philomelos	0.15	ns
T. iliacus	0.27	ns
Phylloscopus spp.	–0.10	ns
Ficedula hypoleuca	0.42	0.10
Anthus trivialis	0.40	0.10
Pyrrhyla pyrrhyla	0.08	ns
Fringilla coelebs	0.04	ns
Emberiza citrinella	0.03	ns
Birds total	–0.05	ns
Insects	0.60	0.01
Diet width	0.15	ns

Long-term changes

During 1966–86, the percentages of the water shrew *Neomys fodiens*, water vole, brown rat *Rattus norvegicus*, Swallow *Hirundo rustica* and insects in the diet of Tengmalm's Owl increased, whereas the percentage of bank voles decreased significantly (Table 5). The increasing trend of the Swallow is uncertain, however, as one pair of Tengmalm's Owl in 1980 took 68 % of all Swallows (n = 34) observed in the diet, but there were no pairs specializing in water shrews, water voles, brown rats and insects. In addition, during the same study period, the percentages of the house mouse *Mus musculus*, Pied Flycatcher *Ficedula hypoleuca* and Tree Pipit *Anthus trivialis* in the diet tended to increase, and the percentage of field voles tended to decrease, but

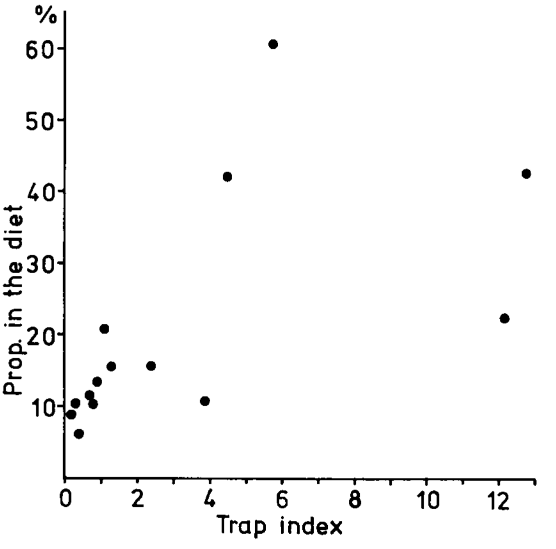

Fig. 1. The correlation between the spring trap index (ind./100 trap nights) of *Microtus* voles and the proportion of these voles in the diet of Tengmalm's Owl in the Kauhava region during 1973–86. Spearman rank correlation: r_s = 0.86, P < 0.001.

these changes were only indicative. In contrast, the percentages of other prey species or groups mentioned in Table 5 were constant. Diet width did not change during the 21 years.

Year-to-year variation

Microtus voles are the preferred prey of Tengmalm's Owls in the study area, as their proportion in the diet is twice as large as their proportion in the field according to the snap-trap captures (Korpimäki 1981). The proportion of these voles in the diet varied widely, being highest in 1970 (71.0%) and 1986 (60.8%), and lowest in 1984 (6.1%) and 1968 (7.7%) (Table 4). It was positively correlated with the abundance of these voles in the spring trappings during 1973–86 (Fig. 1). However, the increase in the percentages of *Microtus* voles in the diet tended to level off at the highest vole index values (Fig. 1).

The percentages of the most important alternative prey (bank voles, shrews and birds) in the food varied largely (Table 4). Bank voles were taken most in 1966 (44.8%) and 1974 (38.6%), and least in 1975 (2.9%) and 1968 (3.2%). The proportion of bank voles in the diet tended to be positively related to the abundance of this vole in the spring trappings during

1973–86 (Spearman rank correlation, $r_s = 0.46$, $P < 0.10$). The percentage of shrews was largest in 1984 (77.8%) and 1968 (67.7%), and smallest in 1970 (4.1%) and 1976 (13.5%). The proportion of the most frequent shrew species (the common shrew) in the food did not correlate with the abundance of this shrew in the spring trappings in 1973–86 ($r_s = 0.39$). The highest numbers of birds were taken in 1980 (36.4%) and 1971 (29.3%), and the lowest ones in 1970 (0.7%) and 1986 (1.4%).

The proportion of bank voles in the diet seemed to correlate positively with the proportion of *Microtus* voles in the diet during 1973–86, but the correlation was only indicative ($r_s = 0.46$, $P < 0.10$). In contrast, the percentages of other most important alternative prey in the diet were negatively related to the percentage of *Microtus* voles in the diet during 1973–86 ($r_s = -0.72$, $P < 0.01$ for shrews, $r_s = -0.52$, $P = 0.05$ for birds). The small proportions of water voles, murids and insects in the diet seemed to vary irregularly, but they were mostly taken in poor vole years.

Discussion

Diet composition

Because two methods were used to study the food of breeding Tengmalm's Owls, the present results reflect the diet composition during the whole breeding season. They support the earlier conclusion that this owl uses *Microtus* and *Clethrionomys* voles as its staple food (see Introduction). Among *Microtus* spp., common voles are clearly more often taken than field voles (see also Korpimäki 1981). Both *Microtus* spp. occupy the open ground, such as farmland and clear-fellings. The common vole favours large cultivated fields with low grass, but the field vole prefers small and abandoned fields with high vegetation cover. Thus, the availability of the common vole is better than that of the field vole, which explains the predominance of the former vole species in the diet of Tengmalm's Owl.

A majority of *Microtus* voles taken by breeding Kestrels and Long-eared Owls *Asio otus* in the study area is common voles (Korpimäki 1985b, 1986d, 1987e), but the situation is reversed in the food of Ural Owls *Strix uralensis* (Korpimäki & Sulkava 1987). Both the Kestrel and Long-eared Owl are open country species, which prefer large field plains as their breeding and hunting habitats (Korpimäki 1987e). In contrast, the Ural Owl mainly occupies large spruce-dominated forest areas, where fields are small (Korpimäki & Sulkava 1987). Present results show that Tengmalm's Owls also often hunt in open habitats.

The bank vole occupies forests and edges of open ground, where Tengmalm's Owl has adapted to hunt (see Introduction), but because *Microtus* spp. are nearly twice as heavy as the bank vole, they are preferred (Korpimäki 1981). Moreover, dense vegetation cover in woodland reduces the availability of bank voles for hunting owls. Tengmalm's Owls start to breed in late March or early April, when the depth of snow layer in the study area is ca. 5–30 cm (Korpimäki 1987a). At that time, *Microtus* spp. are probably easier to catch at their ventilation holes in the snow. After the melting of the snow, the old vegetation cover on the open ground has become compressed, and no new vegetation has grown. Thus, *Microtus* voles are without shelter and vulnerable to avian predation.

In addition to the bank vole, the most important alternative prey groups of Tengmalm's Owl are shrews and birds. Among these, the most common available species, such as the common shrew and Chaffinch (Korpimäki 1981), are also most frequent in the diet.

The mean body weight of Tengmalm's Owl is 161 g for females and 102 g for males (Korpimäki 1981). Thus, adult water voles, brown rats and red squirrels (for weights, see Table 1) are too large a prey, and Tengmalm's Owls can catch only the young of these species.

In comparison to the diet of the Kestrel in the same area (Korpimäki 1985b, 1986d), the proportion of insects is very low in the diet of Tengmalm's Owl. Frogs and lizards, which Kestrels take fairly often, lack totally from the food of Tengmalm's Owl. On the other hand, the diet of Tengmalm's Owl included nearly all available mammals and birds of the same size as itself or smaller. So, Tengmalm's Owl has a fairly wide prey spectrum and is not a vole specialist to the same extent as the Long-eared Owl, Short-eared Owl *Asio flammeus* and Hawk Owl *Surnia ulula* in the same study area (for their diets, see Korpimäki 1981: Table 37).

Long-term changes in the diet

Changes in prey choice and/or prey availability may account for the long-term variation in the diet of

Tengmalm's Owl. The former does not seem to be important in this case because the proportions of a majority of the prey species or groups in the food did not change during the 21 years.

Wendland (1984) related the diet variation of the Tawny Owl *Strix aluco* during 21 years in West Berlin to changes in the environment. Marked changes in the nature of the present study area also occurred during the 21 years, and they probably affected the availability of the prey of Tengmalm's Owls. The area of old forest stands decreased and that of clear-fellings and young pine plantations increased. This reduced the availability of the bank vole because its abundance is greater in old forests than in young pine plantations (Korpimäki 1981 and unpubl.) and it is also easier to catch in the former habitat (Sonerud et al. 1986). Moist woodland and marshland were drained extensively. The ditches provide good habitats for the water vole and water shrew, and their proportion in the diet of Tengmalm's Owl increased. The number of abandoned fields decreased and cultivation changed: for example, cattle grazing decreased, and grain and potato fields increased. This impairs the living conditions of the field vole, which is favoured by high vegetation cover. Many fur farms were established, especially during the last ten years. These farms and also rubbish dumps offer good food conditions for house mice and brown rats, which probably caused their increase in the diet of Tengmalm's Owl.

Yearly variation in the diet under cyclic food conditions

The present data show that Tengmalm's Owl reacts opportunistically to the yearly changes in the availability of food (for characteristics of opportunistic foraging, see Wiens & Rotenberry 1979). The data also support the earlier conclusions on the year-to-year variation of the diet composition presented in the Introduction. 1) In peak years the diet consists mainly of *Microtus* and *Clethrionomys* voles. 2) In low years the proportions of shrews and birds are much larger than those of voles. 3) The percentage of *Microtus* voles (preferred prey) in the diet fluctuates in accord with the abundance of these voles in the field.

Present long-term data permit some further conclusions. 1) Although Tengmalm's Owl has adapted to hunt in forests (see Introduction), it seems often to hunt on the open ground and on the edges of woodland, which *Microtus* voles occupy. The reason may be that these voles are more profitable prey than those living in woodland (see above). 2) In the present study area, the bank vole is only an alternative prey for Tengmalm's Owl, because, according to the snap-trap captures, its proportion in the field was nearly twice as large as its proportion in the diet (Korpimäki 1981) and there was no significant correlation between its percentage in the diet and its abundance in the field (present study). This is probably due to the fact that smaller bank voles are not as profitable a prey as *Microtus* voles. 3) Shrews, especially the common shrew, are a more important alternative prey than birds. The probable reasons are that they are more frequent than birds and that the hunting technique used for voles is also suitable for catching shrews. In addition, shrews are much noisier than voles, especially in spring (Heikura 1984, Korpimäki 1986b). Therefore Tengmalm's Owls that locate their prey by hearing, can successfully hunt shrews even in June and July, when the dense vegetation usually protects voles against avian predators. 4) In poor vole years, some male Tengmalm's Owls take plenty of day-active small birds. They are probably old, experienced owls, which have learnt to search for roosting birds or adults and their young from the nests. Familiarity with their territories may improve their success when hunting birds (Korpimäki 1987c). 5) Mice are a regular alternative prey, probably because they are fairly common and the hunting technique used for voles is suitable for catching them. 6) Tengmalm's Owls can occasionally take very large prey (water vole, red squirrel, brown rat, Fieldfare *Turdus pilaris*) or very small prey (insects and pygmy shrew *Sorex minutus*) in comparison with their own body size.

The yearly proportions of *Microtus* voles in the diet correlated positively with their densities in the field, but the densities of the bank vole and common shrew did not correlate with their numbers in the diet. This supported the prediction of the optimal foraging theory in the sense that the diet composition depended only on the density of preferred prey and was independent of the abundance of alternative prey (Schoener 1971, Pulliam 1974, Charnov 1976). When the abundance of *Microtus* voles decreased, Tengmalm's Owls seemed to switch to alternative prey in the following order: bank voles, shrews and birds. It has been suggested that for prey of varying size any preference order should generally correspond only to size order (e.g. Schoener 1971, Pyke et al. 1977). The present data and results from other birds of prey (Kestrel: Korpimäki 1985b, Ural Owl: Korpimäki & Sulkava 1987) suggest that this does not always hold true. In addition to size, many other factors, such as density, behaviour and vegetation cover, may considerably affect the preference order (see also Janes 1985).

Habitat quality of birds should be considered in terms of its variability in time and space (May 1974, Southwood 1977). The variability in time includes two important characteristics; the length and predictability of the favourable period, which permits breeding, and the length and predictability of the unfavourable period (Southwood 1977). In the present study area, *Microtus* voles show 3–4-year population cycles (Korpimäki 1986c), which means that the quality of the habitat usually varies through time in a fairly predictable manner. Thus, adult male Tengmalm's Owls that are resident in this area (Korpimäki & Hongell 1986, Korpimäki 1987c, Korpimäki et al. 1987) experience one to two years that are good for breeding, and one to two poor years during a vole cycle. In contrast, the populations of the bank vole and common shrew do not show marked year-to-year variations, but have a seasonally fluctuating pattern with low numbers in spring and high numbers in autumn (Korpimäki 1986c). In addition, the populations of birds are probably more stable between years than those of *Microtus* spp. Thus, resident males can switch to prey on bank voles, common shrews and birds in poor years of *Microtus* voles and are able to survive, sometimes even to breed, using alternative prey.

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Selostus: **Helmipöllön ravinnon pitkäaikaismuutokset ja vuosittainen vaihtelu syklisissä ravinto-oloissa Etelä-Pohjanmaalla**

Helmipöllön pesimäaikaista ravintoa tutkittiin Etelä-Pohjanmaalla, Kauhavan seudulla, määrittämällä pesäkoloihin kertyneitä varastosaaliita 407 pesältä vuosina 1973–86 (yhteensä 4366 saalista) sekä keräämällä oksennuspalloja ja muita pesäpohjan saalisjätteitä 133 pesältä vuosina 1966–86 (12540 saalista). Pelto- ja kenttämyyrät muodostivat 44.6% varastosaaliiden lukumäärästä ja 56.3% painosta (53.3% niistä kenttämyyriä); metsämyyrän lukumääräosuus oli 31.8%, päästäisten (runsain laji metsäpäästäinen) 15.3% ja lintujen (yleisimmät lajit peippo, keltasirkku ja rastaat) 4.9% (taulukko 1). Oksennuspalloanalyysien mukaan päästäisten osuus oli 33.1% saaliiden lukumäärästä ja 14.2% painosta, pelto- ja kenttämyyrien lukumääräosuus oli 26.8%, metsämyyrän 24.2% ja lintujen 12.3%.

Useimpien saalislajien osuuksissa ravinnossa ei esiintynyt pitkäaikaismuutoksia vuosina 1966–86, mutta vesipäästäisen, vesimyyrän, kotihiiren, rotan ja hyönteisten osuus näytti jonkin verran kasvavan, kun taas pelto- ja metsämyyrien määrä näytti vähenevän (taulukot 4–5). Nämä muutokset johtuivat ilmeisesti helmipöllön elinympäristössä tapahtuneista muutoksista.

Ravinnon koostumuksen vaihtelut olivat samansuuntaiset sekä varastosaaliiden että oksennuspalloanalyysien perusteella määritetyissä ruokavalioissa vuosina 1973–86 (taulukot 2–4). Pelto- ja kenttämyyrät ovat helmipöllön suosituinta saalista ja niiden osuus ravinnossa korreloi positiivisesti niiden tiheyksiin loukkupyynneissä vuosina 1973–86 (kuva 1). Metsämyyrän osuus ravinnossa vaihteli samansuuntaisesti pelto- ja kenttämyyrien kanssa, mutta päästäisten ja lintujen määrä oli suurin silloin kun myyriä otettiin vähän (taulukot 3–4). Ravinnon koostumus oli riippuvainen ainoastaan suosituimman saaliin tiheydestä, mikä oli sopusoinnussa optimaalisen saalistusteorian kanssa.

Tutkimusalueen aikuiset helmipöllökoiraat ovat pesäpaikkauskollisia. Suosituimpien saaliiden kannat vaihtelevat 3–4 vuoden pituisissa jaksoissa, mutta tärkeimpien vaihtoehtosaaliiden (metsämyyrä, metsäpäästäinen ja linnut) vuosittaiset vaihtelut ovat selvästi vähäisempiä. Siten paikkauskolliset koiraat voivat selvitä hengissä (ja toisinaan jopa pesiä) huonoina myyrävuosina turvautumalla vaihtoehtosaaliisiin.

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