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Functional response of the Long-eared Owl (*Asio otus*) to changing prey numbers: a 20-year study

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The diet of the Long-eared Owl (*Asio otus*) was investigated in central Slovenia from 1982 to 2001. The Common vole (*Microtus arvalis*) was the most frequent prey species (55% of all items by number), with a yearly proportion in the diet from 17% to 85%. This frequency of the Common vole reflected its abundance in spring on the meadows, showing a type II functional response — as prey density increased, consumption rate of the owl increased at a decelerating rate, until a plateau was reached. Peak proportions were recorded every 5 to 6 years. The next two most frequent prey species were Wood mouse (*Apodemus sylvaticus*; 14%) and Field vole (*Microtus agrestis*; 12%). The Field vole, Common pine vole (*Pitymys subterraneus*) and Water vole (*Arvicola terrestris*) were found to be a sporadically important alternative prey. The results are discussed in the light of the optimal foraging theory, which predicts that diet depends on the absolute abundance of the high rank food, that low-ranked prey are dropped from the diet as the abundance of high-ranked prey increases, and that predators do not exhibit "partial preferences", i.e. prey species is either included in the diet or completely excluded. Only the first two predictions were confirmed unequivocally. A method of prey ranking, based on its importance for the predator, using optimal foraging theory predictions, is presented. Accordingly, the Common vole was the only main prey species for the Long-eared Owl. Wood mouse was considered as the only important alternative prey, and Field vole, Common pine vole and Water vole as sporadically important alternative prey species. All others were alternative prey of low importance.

1. Introduction

Studies on the diet of the Long-eared Owl (*Asio otus*) are usually based on a prey spectrum derived from pellets collected over one to a few years. The core findings in these papers are: open meadows are the main hunting habitat (Getz 1961, Marti 1976, Tome 1991) and *Microtus* voles are the most frequently preyed species (summarized in Czarnecki 1956, Marti 1976, Mikkola 1984, Cramp 1985). Their proportion in the diet reflects closely their abundance in the field (Korpimäki 1992a).

In northern Europe, the change in vole population density occurs in a well-known cyclic pattern, with peaks every 3–5 years (Korpimäki 1992b). In recent years in southern Finland this kind of fluctuation appears to be levelling-off (Solonen & Karhunen 2002). In central and western Europe, vole populations are more stable

(Korpimäki & Norrdahl 1991), with cycle periods between two and 10 years (Mackin-Rogalska & Nabaglo 1990). From southern Europe there has been only one report presenting vole fluctuation over a three-year period (Tome 1994). Very little is known about owl-vole relations in this part of the Europe.

To explore the diet of the vole specialist under all conditions of available food, investigation over a complete cycle is necessary and, in order to confirm a pattern in feeding regime, the time series must be even longer. The majority of the articles on the Long-eared Owl present its diet over a time period shorter than one vole cycle, and reports on the feeding pattern are scarce. The longest period of systematic diet analysis published so far is 12 years (Smettan 1987), with three more presenting the diet over 10 and 11 year periods (Zimmerman 1963, Wendland 1984, Korpimäki 1992b).

In this paper I report on the diet of the Long-eared Owl from central Slovenia (southern Europe) over a 20 year period, which is sufficient to allow the effect of any vole related pattern on the feeding regime to be observed. Using prey abundance as a measure of prey profitability for the predator, the results are discussed in the context of the predictions of the optimal foraging theory (hereafter OFT; summarized in Pyke 1977, 1984). This states that (1) diet of the predator depends only on the absolute abundance of high rank food, (2) increase in abundance of high ranked prey causes low ranked prey to be dropped from the diet. Since not all prey species show all-or-none behaviour response, the third prediction, (3) that food type is either included or completely excluded from the diet, has been rejected in many studies (summarized in Pyke 1984) and a gradual response suggested instead (Pyke 1984). If the results of the present long-term study support the predictions, then changes in abundance of the main prey in the field must be reflected in the owl's diet, and the proportion of this prey in the diet must correlate negatively with the breadth of the food niche. The prediction of a gradual response will be supported if there is at least one abundant, but poorly represented species in the diet exhibiting a significant positive correlation with food niche breadth. In the paper I also suggest a method of prey species ranking according to their importance for the predator, using the first two predictions of the OFT.

2. Methods and material

The study was conducted at Ljubljansko barje (46°00'N, 14°30'E), central Slovenia, from 1982 to 2001. The area is about 160 km^2 and lies 287 to 290 m above sea level (for a detailed description see Tome, 1991). Pellets were collected from roosting places and also, during the breeding season, from and under the nests. These collections were made at five localities where the owls are most common. Meadows predominate in all five (about 70%), the rest being fields (about 20%) and patchily distributed forests (about 10%). The closest locations are 5 km apart, the most distant 20 km. Sampling took place all year round, except in 1982, 1983 and 1987 when pellets were collected only during the winter.

The species of small mammal remains from the pellets were identified according to Kryštufek (1985). Not all mice from the genus *Apodemus* could be keyed to a species — they were divided into Wood mouse (*Apodemus sylvaticus*) and Yellow-necked mouse (*A. flavicollis*) according to the relative proportion of identified individuals in particular samples. Birds and insects were not identified beyond the class level. The biomass of mammals was calculated using average masses of species, obtained from skull measurements (Tome 2000) or from the literature (Tome 1991). Average mass for birds was obtained from humerus measurements (Yalden 1977). For the study of year-to-year variation, prey species with less than 1% occurrence were pooled into two categories — shrews and other mammals. Food niche breadth (hereafter FNB) was calculated according to Levins (1968), using the equation

$$FNB = (\Sigma p_i^2)^{-1} \quad (1)$$

where p_i is the proportion of the species i in the diet. In calculations birds and insects were regarded as two taxons. The importance of a prey species for the Long-eared Owl was determined using the Spearman correlation coefficient between yearly proportions in the diet by number

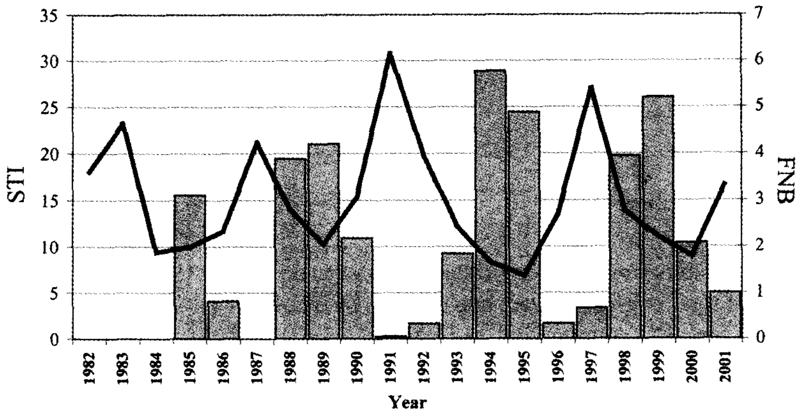

Fig. 1. Variation in the relative abundance of Common vole in the field (STI = snap-trap index; bars) and variation in food niche breadth (FNB = food niche breadth; line) of the Long-eared Owls from Ljubljansko barje. Snap-trap data for 1982, 1983, 1984 and 1987 are missing.

and FNB. P values were corrected with the sequential Bonferroni technique (Rice 1989).

Year-to-year relative abundance of small mammals on the meadows was estimated by snap trapping in May and early June. Traps were placed 5 m apart, in lines of 30, and left for one night, each year on the same trapping area. They were set on small mammal runs or in front of entrances to small mammal subterranean quarters. From 1985 to 2001, 3335 trap nights were accumulated — data for 1987 are missing. A snap-trap index (hereafter STI = no. of animals caught per 100 traps per year) was used to determine differences in density between years. The traps were efficient in trapping voles and mice, but were too robust for shrews.

3. Results

On Ljubljansko barje Common vole (*Microtus arvalis*) was the dominant small-mammal species on the meadows, as demonstrated by the fact that they comprised 398 (94%) out of 424 animals trapped in the period 1985–2001. Its relative abundance (STI) fluctuated from 0.26 in 1991 to 28.9 in 1994 (Fig. 1). The ratio of the minimum to maximum value exceeds 100. Of other small mammals, 11 were Wood mice (*Apodemus sylvaticus*), six Field voles *(Microtus agrestis)*, six Moles (*Talpa europaea*), two Common shrews (*Sorex araneus*) and one Miller's water shrew (*Neomys anomalus*).

From 1982 to 2001, 10 991 prey items were extracted from Long-eared Owl pellets (Table 1). The most abundant prey was Common vole, constituting 55% of all items by number and 61% by biomass, followed by Wood mouse (14% by number, 11% by biomass) and Field vole (12% by number, 14% by biomass). The proportion of all other species in the diet was less than 10% by number and less than 5% by biomass. Birds were caught rather infrequently, 264 prey individuals representing 2.4% by number. The mass of individual birds ranged from 12 to 30 g. Insects were preyed only sporadically (less than 0.5% by number; Table 1).

The proportion of the Common vole in the diet varied from 17% to 85% between years (Table 2) and it correlated positively with the abundance of the species on the meadows ($R^2 = 0.603$; $P = 0.0002$; $y = 9.93*\mathrm{Ln}(x) + 37{,}52$; Fig. 2). Common vole was the dominant prey in all but three years, when Field vole, Common pine vole (*Pitymys subterraneus)* and/or Wood mouse were more frequent in the pellets. The proportion of Common vole in the diet changed regularly, although peak years were not perfectly cyclic. There were three peaks and four troughs on every five to six and on every four to six years respectively (Fig. 3). In two years birds almost reached the 10% dominance threshold by number (9.4% in 2001; 9.6% in 1997; Table 2).

FNB varied from 1.37 in 1995 to 6.15 in 1991 (Table 2, Fig. 1). Only the proportion of the Common vole in the diet correlated negatively with FNB (Table 3). Proportions of shrews and birds as collective groups, as well as of Wood mouse correlated significantly and positively with FNB. Apart from Wood mouse and Field vole, the only species to exceed 10% by biomass, in the year when they were preyed upon most, were Common pine vole, and Water vole (*Arvicola terrestris*).

4. Discussion

These results stress the importance of voles in the diet of the Long-eared Owl, and confirm those of other authors (summarized in Czarnecki 1956, Marti 1976, Mikkola 1983, Cramp 1985). The year-to-year proportion of the Common vole in the diet of the Long-eared Owl reflected closely its abundance in the field. The curve indicates a Holling's (1959) "type II" functional response, which is typical for specialist predators (Keith *et al.* 1977, Linden & Wikman 1983). As prey density increased, the proportion in the diet approached a plateau, beyond which any increase was small. This stage was reached already at about 1/3 of the maximal relative abundance of the Common vole in the field. Functional response is more basic than the numerical response, in that it affects survival, reproduction and movement of the predator (Keith *et al.* 1977). So, on Ljubljansko barje, there was probably much support for a numerical response of predators too.

Table 1. Diet composition of Long-eared Owls during 1982–2001 (n = number of prey items; B = biomass of prey items; % = percentage of number and biomass, + = less than 0.1%; M = mean prey mass used for calculating biomass; nm = number of prey items used for calculating prey mean mass, * = mean mass taken from literature).

	n	%	B (g)	%	M (g)	nm
M. agrestis	1343	12.2	38947	13.6	29	740
M. arvalis	6000	54.6	174000	60.7	29	3711
P. subterraneus	703	6.4	11951	4.2	17	328
C. glareolus	272	2.5	5712	2.0	21	158
A. terrestris	190	1.7	8170	2.8	43	116
Arvicolidae	8508	77.4	238780	83.3		
A. flavicollis	161	1.5	5152	1.8	32	50
A. sylvaticus	1533	13.9	32193	11.2	21	751
Mus sp.	2	+	40	+	20	*
M. minutus	304	2.8	2128	0.7	7	303
R. norvegicus	1	+	96	+	96	1
R. rattus	2	+	158	+	79	1
Muridae	2003	18.2	39767	13.9		
S. araneus	56	0.5	504	0.2	9	*
S. minutus	1	+	6	+	6	*
Sorex spp.	1	+	8	+	8	*
N. anomalus	14	0.1	182	0.1	13	*
N. fodiens	3	+	39	+	13	*
Neomys spp.	5	+	65	+	13	*
C. leucodon	39	0.3	429	0.1	11	*
C. suaveolens	25	0.2	225	0.1	9	*
Crocidura spp.	4	+	40	+	10	*
S. etruscus	1	+	3	+	3	*
Soricidae	149	1.4	1501	0.5		
G. glis	1	+	120	+	120	*
M. avellanarius	11	0.1	297	0.1	27	*
T. europaea	17	0.1	1700	0.6	100	*
Mammals	10689	97.3	282165	98.4		
Birds	264	2.4	4488	1.6	17	163
Insects	38	0.3	38	+	1	*
n	10991	100	276208	100		

Table 2. Year-to-year variation in the diet composition of Long-eared Owls during 1982–2001 (numbers represent proportion of prey item numbers; + = less than 0.1%; n = sample size.

	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
M. agrestis	35.6	23.1	15.6	11.3	18.4	16.1	13.1	13.0	17.9	11.5	5.8	5.0	4.0	3.3	10.6	22.5	20.7	9.9	12.5	11.3
M. arvalis	22.6	16.5	70.7	67.6	62.0	38.7	56.4	67.8	51.9	21.2	41.8	61.3	76.5	85.2	58.8	28.4	55.2	64.4	73.2	50.6
P. subterraneus	31.0	11.2	1.0	9.8	9.5	3.2	10.9	6.9	8.3	10.2	8.9	6.9	1.3	1.2	4.5	2.0	2.3	1.7	2.1	4.9
C. glareolus	1.9	5.2	4.9	2.3	1.1	+	3.1	2.5	1.2	3.8	3.4	3.0	1.0	0.9	3.0	3.9	2.8	0.6	1.6	2.3
A. terrestris	0.5	+	+	+	+	3.2	1.8	+	0.5	5.7	1.7	3.2	0.2	0.3	1.0	3.3	1.3	1.0	1.0	2.3
A. flavicollis	1.9	5.9	+	0.8	+	+	2.4	+	2.6	1.9	2.4	0.9	0.6	0.7	1.0	1.1	1.2	1.3	2.1	+
A. sylvaticus	4.3	28.4	7.8	5.3	3.4	22.6	8.8	7.0	12.2	28.3	24.3	15.8	12.9	6.3	8.5	19.4	10.1	16.0	5.3	14.3
M. minutus	+	+	+	+	+	3.2	+	0.9	3.0	7.5	6.9	1.3	1.5	0.6	1.0	5.9	3.8	3.8	0.4	0.4
Shrews	1.3	1.5	+	1.5	1.7	6.5	1.7	0.9	0.8	3.0	1.6	0.9	0.2	0.6	4.5	2.4	0.9	0.6	0.7	2.6
Other mammals	+	0.7	+	1.5	2.2	+	0.6	+	0.3	0.9	0.2	0.2	0.2	+	+	0.4	0.1	+	+	0.8
Birds	0.9	7.5	+	+	1.1	6.5	0.6	1.0	1.1	4.8	3.1	1.4	1.2	0.9	6.5	9.6	1.6	0.6	1.0	9.4
Insects	+	+	+	+	0.6	+	0.7	0.1	0.1	1.1	+	0.3	0.4	0.1	0.5	1.1	+	0.2	+	1.1
FNB	3.61	4.64	1.88	1.99	2.34	4.23	2.79	2.05	3.07	6.15	3.95	2.44	1.65	1.37	2.68	5.40	2.76	2.21	1.79	3.32
n	213	134	102	133	179	31	845	686	915	999	1007	1267	519	688	199	542	1039	526	702	265

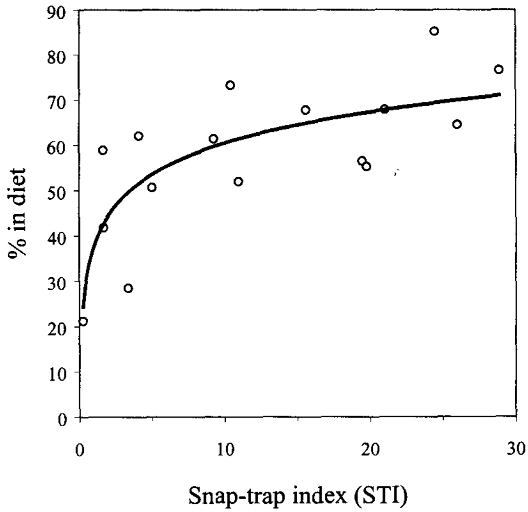

Fig. 2. Functional response of Long-eared Owls to changes in relative abundance of Common vole in the field. Each point represents one of the years from 1984 to 2001 (data for 1987 are missing).

When the abundance of Common vole in the field was low, owls increased predation on other prey species, thus expanding FNB. This result confirms the first two predictions of the OFT, that diet depends on the absolute abundance of the high rank food type in the field, and that decreasing food abundance lead to lesser food specialisation (Pyke 1984). Similar conclusions can be found also in many other studies (for birds of prey see Steenhof & Kochert 1981, Linden & Wikman 1983, Korpimäki 1986, 1992b, Silva *et al.* 1995, Restani *et al.* 2000). OFT predictions can be used to rank prey species with regard to their importance for the predator. Accordingly, all prey species with negative correlation between proportion in the diet and FNB can be regarded as main prey, and all species with a positive correlation as alternative prey.

The Common vole was the only main prey for the Long-eared Owl. All other species, on the other hand, showed positive correlation with FNB and were therefore alternative prey. Of these, I distinguished three different types: important alternative prey, sporadically important alternative prey and alternative prey of low importance for the predator. Two of the characteristics of the important alternative prey are (Rapport 1980), that it is available whenever needed (denoted with sig-

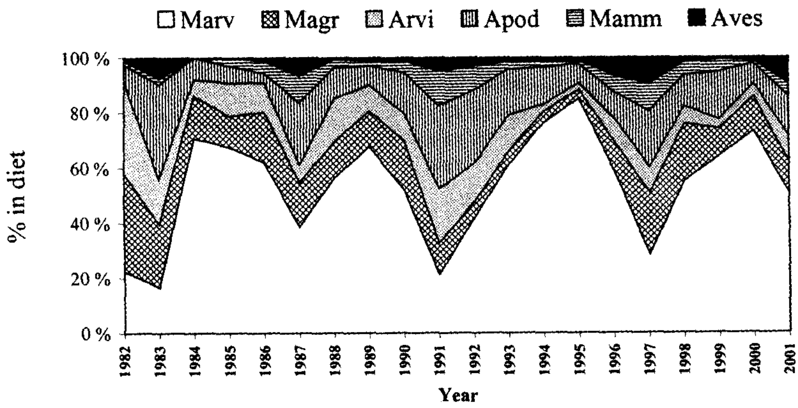

Fig. 3. Annual proportions of major prey species or groups in the diet of Long-eared Owls from Ljubljansko barje by number (Marv = M. arvalis, Magr = M. agrestis, Arvi = other voles, Apod = Apodemus spp., Mamm = other mammals, Aves = birds).

nificant positive correlation between proportion in the diet and FNB), and that it substitutes for the main prey in terms of energy yield (denoted with high proportion in the diet by biomass). In my study area only Wood mouse had both characteristics. Its proportion by number correlated significantly with FNB and it reached over 10% by biomass in the diet. Hence Wood mouse was the only important alternative prey, when considering the diet on the year scale.

In a particular year an overall low value alternative prey species can still be important for the predator, as exemplified by the Field vole, Common pine vole and Water vole in this study. They all exceed 10% by biomass in the diet in at least one of the years. Although insignificant correlation coefficients prevent them from qualifying as important alternative prey, they were crucial for the owls in some of the years and can therefore be considered as sporadically important alternative prey.

Table 3. Spearman rank correlations (r_s) between year-to-year FNB indices and proportions of selected prey items/groups in the diet of Long-eared Owls (n = 20). P values corrected with sequential Bonferroni technique (Rice 1989; ns — not significant; * < 0.05; ** < 0.01).

	r_s	P
M. agrestis	0.500	ns
M. arvalis	–0.982	**
P. subterraneus	0.533	ns
C. glareolus	0.429	ns
A. terrestris	0.580	ns
A. flavicollis	0.404	ns
A. sylvaticus	0.668	*
M. minutus	0.354	ns
Shrews	0.718	**
Other mammals	0.358	ns
Birds	0.667	*
Insects	0.177	ns

The proportion of shrews in the diet remained negligible throughout the study period (less than 3% by biomass in the year when they were preyed on most). This includes 1991 when Common vole had the lowest abundance in the field and when shrews exceeded 60% by number in the diet of the Barn owl (*Tyto alba*) from the same location (Tome 1992). Obviously, shrews were abundant, but were largely avoided as a food type for the Long-eared Owl. Their proportion in the diet correlates positively and highly significantly with the FNB, corresponding to the gradual response prediction, i.e. the partial preference response (Pyke 1984). A similar conclusion can be reached for birds, although, for this collective group, the data on abundance in the field is not adequate to certify the statement statistically. But not all alternative prey species of low importance support the gradual response prediction. Ljubljansko barje is an important bird area (IBA), where the natural environment is still well preserved (Polak 2000). The abundance of insects on the study site is therefore probably much higher than is predicted from the diet list. Nevertheless, the proportion of insects in the diet of the Long-eared Owl was low throughout the investigated period, and their correlation with FNB insignificant — insects as a collective group were a completely excluded food type, supporting the all-or-none prediction. So it appears, that neither of the two responses, gradual or all-or-none, can be applied as a general rule for the third prediction. When tests of the OFT are performed therefore, the whole prey list should be taken into account in order to obtain the overall picture.

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Selostus: **Sarvipöllön toiminnallinen vaste saalismäärän vaihteluun: 20-vuotinen tutkimus**

Artikkelin kirjoittaja tutki sarvipöllön ravinnon koostumusta Sloveniassa viidellä tutkimusalueella vuosina 1982–2001. Sarvipöllön oksennuspalloja kerättiin pöllöjen levähdyspaikoilta ja pesäpaikoilta. Runsain saaliseläinlaji sarvipöllön ravinnossa oli kenttämyyrä. Kaikista saalinäytteistä oli kenttämyyriä 55%. Kenttämyyrien osuus saalisnäytteistä vaihteli vuosittain 17–85%. Kenttämyyrän osuus sarvipöllön ravinnossa seurasi kenttämyyrän keväisiä runsaudenvaihteluja tutkimusalueella. Kenttämyyrän runsaus sarvipöllön ravinnossa oli suurimmillaan 5–6 vuoden välein. Seuraavaksi runsaimmat saalislajit sarvipöllön ravinnossa olivat pikkumetsähiiri (14%) ja peltomyyrä (12%). Näistä vain pikkumetsähiirtä pidettiin tärkeänä sarvipöllön vaihtoehtoisena saalislajina. Peltomyyrä, tunnelimyyrä ja vesimyyrä olivat ajoittain tärkeitä saalislajeja. Kirjoittaja pohti tulosten merkitystä optimaalisen saalistusteorian ("Optimal foraging theory"; OFT) viitekehyksessä. OFT-teorian ennusteiden mukaan pedon ruokavalio määräytyy tärkeimmän ravintolajin runsauden mukaan. Lisäksi vähemmän tärkeiden saalislajien osuus ravinnossa vähenee (tai ne voivat jopa jäädä kokonaan pois saalisvalikoimasta), kun tärkeimmän saalislajin runsaus kasvaa. Pedoilla ei teorian mukaan esiinny "osittaista suosimista" ("partial preferences"). Tässä tutkimuksessa vain kaksi ensimmäistä OFT-teorian mukaista hypoteesia täyttyivät kiistattomasti. Kirjoittaja esittää lopuksi OFT-teoriaan perustuvan sarvipöllön saalislajien arvottamismenetelmän, jossa huomioidaan eri saalislajien merkitys saalistajalle.

References

Cramp, S. (ed.) 1985: The birds of the western Palearctic. Vol. 4. — Oxford Univ. Press, New York. 960 pp.

Czarnecki, Z. 1956: Obserwacje nad biologia sowy uszatey (Asio otus otus L.). — Panstwowe Wydawnictwo Naukowe 13: 207–246.

Getz, L. L. 1961: Hunting areas of the Long-eared Owl. — The Wilson Bulletin 73: 79–82.

Holling, C. S. 1959: Some characteristics of simple types of predation and parasitism. — Canadian Entomologist 91: 385–398.

Keith, L. B., Todd, A. W., Brand, C. J., Adamcik, R. S. & Rusch D. H. 1977: An analysis of predation during a cyclic fluctuation of snowshoe hares. — In: Peterle T. J. (ed.), XII International Congress of Game Biologists: 151–175. The Wildlife Society. Atlanta, Georgia. 538 pp.

Korpimäki, E. 1986: Diet variation, hunting habitat and reproductive output of the Kestrel Falco tinnunculus in the light of the optimal diet theory. — Ornis Fenn. 63: 84–90.

Korpimäki, E. 1992a: Diet composition, prey choice, and breeding success of Long-eared Owls: effects of multiannual fluctuations in food abundance. — Can. J. Zool. 70: 2373–2381.

Korpimäki, E. 1992b: Population dynamics of Fennoscandian owls in relation to wintering conditions and between-year fluctuations of food. — In: Galbraith, C. A., Taylor, I. R. & Percival, S. (eds.), The ecology and conservation of European owls: 1–10. Joint Nature Conservation Comitee, UK.

Korpimäki, E. & Norrdahl, K. 1991: Numerical and functional responses of Kestrels, Short-eared Owls, and Long-eared Owls to vole density. — Ecology. 72: 814–826.

Kryštufek, B. 1985: Mali sesalci. Naša rodna gruda. — Prirodoslovno društvo Slovenije, Ljubljana. 29 pp.

Levins, R. 1968: Evolution in changing environments. — Princeton Univ. Press, Princeton. 120 pp.

Linden, H. & Wikman, M. 1983: Goshawk predation on tetraonids: availability of prey and diet of the predator in the breeding season. — J. Anim. Ecol. 52: 953–968.

Mackin-Rogalska, R. & Nabaglo, L. 1990: Geographical variation in cyclic periodicity and synchrony in the Common vole, Microtus arvalis. — Oikos 59: 343–348.

Marti, C. D. 1976: A review of prey selection by the Long-eared Owl. — The Condor 78: 331–336.

Mikkola, H. 1983: Owls of Europe. — T.& A.D. Poyser, Staffordshire, UK. 397 pp.

Polak, S. (ed.) 2000: Mednarodno pomembna območja za ptice v Sloveniji. — DOPPS. Ljubljana.

Pyke, G. H. 1977: Optimal foraging: a selective review of theory and tests. — Quart. Rev. Biol. 52: 137–154.

Pyke, G. H. 1984: Optimal foraging theory: a critical review. — Ann. Rev. Syst. 15: 523–575.

Rapport, D. J. 1980: Optimal foraging for complementary resources. — Am. Nat. 116: 324–346.

Restani, M., Harmata, A. R. & Madden, E. M. 2000: Numerical and functional responses of migrant Bald eagles exploiting a seasonally concentrated food source. — The Condor 102: 561–568.

Rice, W. R: 1989: Analyzing tables of statistical tests. — Evolution 43: 223–225.

Silva, S. I., Lazo, I., Silva-Aranguiz, E. & Jaksič, F. M. 1995: Numerical and functional response of Burrowing owls to long-term mammal fluctuations in Chile. — J. Raptor Res. 29: 250–255.

Smettan, H. W. 1987: Ergebnisse zwölfjähriger Nahrungskontrollen der Waldohreule (Asio otus L.) im mittlern Neckarland/Baden-Württemberg unter Berücksichtigung jahreszeitlicher Veränderungen und der Populationsdynamik von Kleinsäugern. — Orn. Jh. Bad.-Württ. 3: 1–52.

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

Steenhof, K. & Kochert, M. N. 1981: Dietary responses of three raptor species to changing prey densities in a natural environment. — J. Anim. Ecol. 57: 37–48.

Tome, D. 1991: Diet of the Long-eared Owl (Asio otus) in Yugoslavia. — Ornis Fenn. 68: 114–118.

Tome, D. 1992: Prehrana pegaste sove Tyto alba na Ljubljanskem barju. — Acrocephalus 13: 33–38.

Tome, D. 1994: Diet composition of the Long-eared Owl in central Slovenia: seasonal variation in prey use. — J. Raptor Res. 28: 253–258.

Tome, D. 2000: Estimating individual weight of prey items for calculation of the biomass in the diet of Long-eared Owl (Asio otus): is it worth of extra effort? — Folia. Zool. 49: 205–210.

Wendland, V. 1984: Parallel Verlauf der Fortpflanzungsrate bei Waldohreule (Asio otus) und Mäusebussard (Buteo buteo). — Beitr. Vogelkd. 30: 1–11.

Yalden, D. W. 1977: The identification of remains in owl pellets. — Mammal Society. Berkshire.

Zimmerman, K. 1963: Kleinsäuger in der Beute von Waldohreule bei Berlin. — Beitr. Vogelkd. 9: 59–69.