Food of the Pygmy Owl *Glaucidium passerinum* in the breeding season

ERKKI KELLOMÄKI

KELLOMÄKI, E. 1977: *Food of the Pygmy Owl* Glaucidium passerinum *in the breeding season.* — Ornis Fennica 54:1—29.

Prey animals (2240 exx.) were sampled at 28 nest sites in southern Finland (62°N, 24°E) in 1962—72. The number of nestlings averaged 5.1 ± 0.3. On average, the diet consisted of shrews (3.5 %), voles (50.0 %), mice (0.5 %), bats (0.1 %), lizards (1.3 %), insects (0.3 %) and birds (44.5 %). The species breeds later than other Finnish owls; probably because the Pygmy Owl feeds extensively on birds, the breeding season is so timed that young birds are plentiful.

When the vole populations were dense (1962, 1965—66, 1969), the proportion of voles in the diet exceeded that of birds. The diversity of the avian prey, and the proportion of birds and young birds increased towards the end of the breeding season, apparently as a result of decreased catchability of small mammals, due to the growth of the plants in the field layer, and increased availability of birds, especially fledglings. Different prey species were exploited at different rates.

The bird and small mammal populations in the surroundings of the nests were studied quantitatively. The diversity of prey birds correlated significantly with the diversity of the surrounding community. Factor analysis revealed that the composition of the bird diet was similar to that of available bird prey. The abundance of birds was more important than that of mammals in explaining the proportions of birds and mammals in the diet.

The owls also hunt in temporarily productive microhabitats. It is suggested that a "searching image" is formed. The Pygmy Owl is not a food specialist, and miscellaneous food items are also used in good vole years; this is because the productivity of the habitats occupied by the species is poor, and the optimum hunting strategy is thus to exploit all the prey available.

E. Kellomäki, Ansiomäentie 10 C 10, SF-13100 Hämeenlinna 10, Finland.

Contents

Introduction

The hunting strategy of the predator influences the evolution of the predator and its prey in various ways. A typical predator tries to obtain maximum advantage from energy consumed, to produce the largest possible number of offspring (SCHOENER 1971). Usually, predators exploit two or more prey species, thus possibly decreasing interspecific competition among the prey. Hence, predation may increase the diversity of biotic communities (e.g. SLOBODKIN 1961, CONNELL 1971, MACARTHUR 1972, ROUGHGARDEN & FELDMAN 1975).

When an abundant prey population decreases, partially owing to predation, the predator may switch to alternative prey populations, which have meanwhile increased. In this way predation may regulate animal populations (e.g. ELTON 1927, MURDOCH 1969). Food specialists, such as vole-eating owls, can emigrate to new breeding areas when vole populations decrease (e.g. v. HAARTMAN et al. 1963—72).

In the pioneering investigations of the food and feeding habits of avian predators (e.g. UTTENDÖRFER 1939, 1952), no detailed attention was paid to the influence on the diet of the availability of the prey, but this factor has been taken into account in more recent studies (e.g. TINBERGEN 1946, HAGEN 1952, 1965, 1969, SOUTHERN 1954, P. SULKAVA 1964, 1972, S. SULKAVA 1964, PASANEN & S. SULKAVA 1971). Few data exist on the diet of the Pygmy Owl *Glaucidium passerinum* during the breeding season, and the most extensive European investigations (MÄRZ 1964, JANSSON 1964, BERGMANN & GANSO 1965, KELLOMÄKI 1969, SCHERZINGER 1970, MIKKOLA & JUSSILA 1974) do not consider the dependence of the choice of prey on the availability of the food.

Owing to its small size, the Pygmy Owl is more suitable than other owls for an investigation of the relation between available and chosen food. Among birds of prey, the hunting area increases with increasing body size (SCHOENER 1968). Thus it is easier to determine the hunting area and to census the prey populations in the case of the Pygmy Owl than in that of larger birds of prey.

In this investigation of the food biology of the Pygmy Owl, attention was concentrated on the following questions. Which are the most abundant prey animals in Finland? Does the diet during the breeding season show annual or seasonal variation? How does the availability of the prey influence the food chosen? Which mechanisms cause the Pygmy Owl to switch to alternative food items, when some prey populations become scarce? And what is the ecological niche of the Pygmy Owl in the northern coniferous (taiga) region, as seen from the point of view of its feeding and breeding biology?

Breeding biology

The Pygmy Owl is the smallest owl in Europe. In Finnish Pygmy Owls the total length is 158—192 mm (both sexes combined; sample size not given; v. HAARTMAN et al. 1963—72); the body weight of the males is 47—62 g ($n=5$), and that of the females 55—70 g ($n=12$).

In Finland the species inhabits large forests. Of the 46 nest sites investigated by KELLOMÄKI (1970), 70 % were more than 1 km away from the nearest house; 67 % were in old spruce forests, and 48 % of the nest holes ($n=44$) were in spruces. Two nests were in nest-boxes.

In Finland, egg-laying begins in mid-April at the earliest (v. HAARTMAN

1963—72). In my data (Table 1) the number of nestlings per brood averaged 5.1±0.3 (Table 2), the range being 3—7. The incubation period lasts 28—30 days (BERGMAN 1939, JANSSON 1964, KELLOMÄKI unpubl.), and the eggs hatch towards the beginning of June. The times of hatching of the first young in five nests in 1970 were: 1, 2, 4, 12 and 15 June.

The nestling period lasts 27—30 days (JANSSON 1964, BERGMANN & GANSO 1965, KELLOMÄKI 1966). Fledging in the latest nests takes place about 15 July. So the Pygmy Owl breeds later than other owl species in southern Finland.

The attacks of a hunting Pygmy Owl are released only by optical stimuli (SCHERZINGER 1970). It makes only surprise attacks; if unsuccessful, it does not pursue the prey further (KELLOMÄKI 1966). The Pygmy Owl collects prey animals in holes in both summer and winter (JANSSON 1964, KELLOMÄKI 1966).

During the incubation and nestling periods, hunting is done almost exclusively by the male, but at the end of the nestling period the female may also take part (SONERUD et al. 1972, JUSSILA & MIKKOLA 1973, KELLOMÄKI unpubl.). The male does not carry prey animals to the nest but gives them to the female some 10—30 m from the nest in the "sojourning sector", which lies in front of the nest-hole (about 60°; SEIERSTAD et al. 1960, KELLOMÄKI unpubl.). The prey animals are given to the female at a height of about 5—10 m, on a branch. The male usually sits on the same branches throughout the incubation period and remains of prey animals are found under these branches. The female plucks some of prey animals within the "sojourning sector". She sanitates the nest hole by carrying out food remains, which are dropped at the foot of the nest tree or elsewhere within the "sojourning sector". At the very end of the nestling period, no sanitation takes place.

TABLE 1. The material used to investigate the food of the Pygmy Owl in the present study. The symbol *B* after the number of prey items indicates that the birds breeding in the surroundings of the nest were censused, while the symbol *M* indicates that small mammals were trapped. The nest was not found in the cases 29—34.

	Site	Prey items
1.	Jalasjärvi 1962	208
2.	Jalasjärvi 1963	51
3.	Eräjärvi 1964	23
4.	Virrat Sipilä 1965	31
5.	Keuruu Rautovuori 1966	16
6.	Suodenniemi 1966	90
7.	Virrat Killi 1966	40
8.	Keuruu Raiski 1967	29
9.	Lappi Tl 1967	42
10.	Virrat Killi 1967	3
11.	Keuruu Raiski I 1968	19 *B*
12.	Keuruu Raiski II 1968	70 *B*
13.	Kauhava 1969	226 *BM*
14.	Keuruu Raiski 1969	20 *BM*
15.	Nokia Toritunjärvi 1969	56
16.	Nokia Korpijärvi 1969	53
17.	Kalvola 1970	221 *BM*
18.	Keuruu Raiski I 1970	106 *BM*
19.	Keuruu Raiski II 1970	28 *BM*
20.	Keuruu Raiski III 1970	89 *BM*
21.	Keuruu Asunta 1970	158 *BM*
22.	Orivesi 1970	173
23.	Pohjaslahti Monoskylä 1970	147 *BM*
24.	Pohjaslahti Lauttajärvi 1970	44 *B*
25.	Virrat Lakeisneva 1970	115 *BM*
26.	Isokyrö 1971	13 *BM*
27.	Virrat Lakeisneva 1971	92 *BM*
28.	Virrat Liedenpohja 1971	77 *BM*
29.	Keuruu Raiski 1971	— *BM*
30.	Keuruu Asunta 1971	— *BM*
31.	Pohjaslahti Monoskylä 1971	— *M*
32.	Keuruu Raiski 1972	— *BM*
33.	Pohjaslahti Monoskylä 1972	— *BM*
34.	Virrat Lakeisneva 1972	— *BM*
	Total prey items	2 240

TABLE 2. The numbers of visits when prey remains were gathered (1), the number of nestlings (2), prey animals per nestling (3) and the composition of food (4: M = mammals, B = birds, in %) at some nest sites of the Pygmy Owl (see Table 1 for the names of sites).

Site	(1)	(2)	(3)	(4) M	B
4	..	5	6.2	..	..
5	..	4	4.0	..	..
10	..	7	5.7	..	..
12	6	4	17.5	18.6	78.6
13	4	7	32.3	77.9	22.1
15	1	6	9.3	51.8	48.2
16	1	5	10.6	54.7	45.3
17	4	7	31.6	62.4	37.1
18	5	4	26.5	28.3	69.8
19	2	4	7.0	60.7	28.6
20	2	5	17.8	50.5	49.4
21	5	5	31.6	49.4	48.1
23	9	3	47.0	26.5	69.4
25	4	4	28.8	12.2	85.2
27	2	6	15.3	21.7	71.7
28	3	6	12.8	61.0	37.7
$\bar{x}$	3.7	5.1	18.3	44.3	53.2
S.D.	2.3	1.3	11.1	20.4	19.9

Material and methods

Study area and material

The food remains studied (2240 prey animals) were gathered during the breeding period at 28 nest sites in southern Finland in 1962—72 (Table 1). The main study area comprises the communes of Virrat, Keuruu and Pohjaslahti (about 62°N, 24°E). Food remains were sampled at 16 nest sites in these communes.

In studies on the food of birds of prey, the method generally used is sampling of the food remains (e.g. UTTENDÖRFER 1939, TINBERGEN 1946) and its effectivity depends on the number of times the remains are sampled (TINBERGEN 1946, P. SULKAVA 1972). In this study, a positive and significant correlation ($r=0.83$, $P<0.001$, $n=13$) was found between the numbers of sampling visits and the numbers of prey animals per nestling. (For data, see Table 2. Observation points 4, 5 and 10 were excluded, because of lack of knowledge of sampling visits.) The proportion of birds and mammals does not depend on the number of sampling visits (the correlation coefficients calculated from the data given in Table 2 were not significant).

Direct observation (JANSSON 1964) was not used owing to its laboriousness and the difficulty of determining the prey animals without taking them from the female. This method would also have disturbed the breeding too much.

Determination of prey animals

Birds. Birds were determined by comparing their remains with reference material from museum collections. It was impossible to distinguish between *Phylloscopus trochilus* and *Ph. collybita,* so these two species are treated jointly *(Phylloscopus* sp.). The bones of birds in pellets are usually broken into small pieces; hence, the number of birds could be determined only by using a few bones which had remained unbroken, mostly humeri and metacarpals. The numbers of avian prey estimated from feathers were significantly larger than those estimated from bones (Table 3; if the two methods were equally effective, the probability of always getting a better result when feathers were used would be $0.5^{15} = 0.00003$). The numbers used in this study are based on feathers.

Mammals. Mammals were determined from jawbones with the aid of measurements given by SIIVONEN (1967) and reference material from mammal collections. The pellets of Pygmy Owl nestlings contain fewer jawbones than bones of feet (KELLOMÄKI 1969), because the female often eats the head of prey animals before feeding the young. The species composition of the headless voles was considered to correspond to that of the jawbones found at the nest site. This method probably did not bias the actual ratios of vole species, as only two species were usually involved, viz. *Microtus agrestis* and *Clethrionomys glareolus.* At site 13, however, there were also individuals of *Microtus arvalis.*

Abundance of available prey

Birds were censused twice at each of 20 nest sites (only once at site 26), in one or more study plots, totalling 1058 ha. The plots were selected so that the main vegetation types of the territory were included. However, since the direct observations (up to 500 m from the nest) of hunting Pygmy Owls were few, the boundaries of the hunting territories could not be determined, and the vegetation of the census plots may not always correspond to that of the actual hunting area. As not more than two censuses were made at each site, the numbers have probably been underestimated. ENEMAR (1959) suggested that about 60 % of the birds present are observed during one census. The efficiency of my censuses was thus presumably higher, perhaps roughly 80 %, which may be considered sufficient for the present purpose.

The small mammal populations were snap-trapped at 18 sites (Table 1). In May-June, two trap lines, 10 m apart, were set in suitable vegetation types. In both lines, traps baited with fresh cheese were placed at intervals of about 10 m, preferably in places where voles were to be expected. The total number of traps was usually 100. Trapping was normally performed during a period of 5 days, and traps were checked once a day. The total number of trap-nights was 12 420.

Results

General

Different prey groups and the most abundant prey species. The food of Finnish Pygmy Owls consists of shrews Soricidae, voles Cricetidae, mice Muridae, bats Vespertilionidae, lizards Lacertidae, insects Insecta and birds Aves. The proportions of different species and groups by numbers and by weight are given in Table 4. The most abundant shrew species was *Sorex araneus.* Shrews occurred rather regularly among the prey animals, their constancy (proportion of nest sites where this prey group occurred) being 67 %. Voles formed the most abundant food item group; their constancy was also high, 92 %. The numbers of *Clethrionomys glareolus* exceeded those of *Microtus agrestis,* but the two voles made similar contributions to the prey biomass. Mice occurred only in small numbers and irregularly (constancy 10 %). Only one bat species, *Myotis daubentoni,* was found (site 22). Small mammals were the main group in the diet of the Pygmy Owl, 54 % by number and 60 % by weight.

Both lizards *(Lacerta vivipara)* and insects (all of them *Coleoptera)* were consumed, but their proportions in the diet were small. The avian prey comprised 37 species. They formed 44.5 % of the prey by number and 39.4 % by weight, and were found at all the nest sites. The most abundant species were *Fringilla coelebs, Phylloscopus* sp., *Carduelis spinus* and *Erithacus rubecula.*

TABLE 3. The numbers of avian prey estimated from (A) feathers, (B) bones. See Table 1 for the names of sites.

Site	Prey items A	Prey items B	B/A %
12	55	12	21
13	49	14	28
15	27	8	29
16	24	7	29
17	82	30	36
18	74	21	28
19	8	2	25
20	44	10	22
21	74	30	40
22	43	27	62
23	102	11	10
24	30	8	26
25	100	22	22
27	67	20	29
28	30	4	13
$\bar{x}$	53.9	15.1	28
S.D.	28.4	9.3	3

The average number of mammals at a nest site was 48.1, while the average for birds was 49.4. The difference is not significant (*U* test of Mann-Whitney).

Weight groups. The weights of the individual prey animals averaged 20.6 g. Animals belonging to the weight group of 20.0—29.9 g constituted half of the total numbers and biomass of the prey (Table 5), the next largest group being 30.0—39.9 g. The heaviest prey animals were *Dendrocopos major, Turdus philomelos* and *Turdus iliacus.* The weight groups of the smallest and largest animals were of slight importance.

Annual variation in food composition. The composition of the food varied markedly from year to year (Table 6). However, only single nests

TABLE 4. The diet of the Pygmy Owl at 28 nest sites in southern Finland, 1962—72. Weights of mammals from SIIVONEN (1967), of birds from v. HAARTMAN et al. (1963—72). Weights estimated to 5 g for lizards, and to 1 g for insects. Weight used for unidentified birds (Aves sp.) 20 g. Constancy = proportion of nest sites where the prey animal occurred.

Prey species	Weight	Numbers of prey		Prey biomass		Constancy
	g	*n*	%	g	%	%
Sorex araneus	10	29	1.3	290	0.6	39
S. caecutiens	6	5	0.2	30	0.1	10
S. minutus	4	19	0.9	76	0.2	39
S. minutissimus	2	1	0.0	2	0.0	3
Sorex sp.	7	25	1.1	175	0.4	32
Soricidae, total		79	3.5	573	1.2	67
Clethrionomys glareolus	20	631	28.2	12 620	27.4	85
Microtus agrestis	30	442	19.7	13 260	28.8	71
M. arvalis	25	46	2.1	1 150	2.5	3
Cricetidae, total		1 119	50.0	27 030	58.7	92
Micromys minutus	8	5	0.2	40	0.1	7
Mus musculus	15	5	0.2	75	0.2	10
Muridae, total		10	0.5	115	0.3	10
Vespertilionidae, total	10	2	0.1	20	0.0	3
Mammalia, total		1 210	54.0	27 738	60.2	92
Reptilia, total	5	28	1.3	140	0.3	39
Insecta, total	1	6	0.3	6	0.0	17
Apus apus	42	2	0.1	84	0.2	7
Dendrocopos major	60	2	0.1	120	0.3	7
Jynx torquilla	37	5	0.2	185	0.4	17
Alauda arvensis	37	3	0.1	111	0.2	10
Hirundo rustica	19	4	0.2	76	0.2	14
Parus major	20	18	0.8	360	0.8	57
P. ater	9	4	0.2	36	0.1	14
P. cristatus	12	22	1.0	264	0.6	50
P. montanus	11	40	1.8	440	1.0	67
Aegithalos caudatus	8	1	0.0	8	0.0	3
Certhia familiaris	9	14	0.6	126	0.3	32
Troglodytes troglodytes	10	2	0.1	20	0.0	7
Turdus philomelos	60	2	0.1	120	0.3	7
T. iliacus	50	3	0.1	150	0.3	7
Oenanthe oenanthe	23	2	0.1	46	0.1	7
Saxicola rubetra	17	6	0.3	102	0.2	17
Phoenicurus phoenicurus	16	11	0.5	176	0.4	28
Erithacus rubecula	17	84	3.8	1 428	3.1	67
Sylvia borin	20	6	0.3	120	0.3	14
S. communis	15	1	0.0	15	0.0	3
Phylloscopus sp.	9	99	4.4	891	1.9	64
Regulus regulus	6	21	0.9	126	0.3	57
Muscicapa striata	16	29	1.3	464	1.0	39
Ficedula hypoleuca	13	40	1.8	520	1.1	67
Anthus pratensis	18	1	0.0	18	0.0	3
A. trivialis	22	60	2.7	1 320	2.9	71
Motacilla alba	21	12	0.5	252	0.6	28
M. flava	19	1	0.0	19	0.0	3
Carduelis spinus	13	97	4.3	1 261	2.7	82
C. flammea	14	22	1.0	308	0.7	32
Pyrrhula pyrrhula	34	17	0.8	578	1.3	35
Loxia curvirostra	41	13	0.6	533	1.2	32

Cont. on p. 7

Cont. from p. 6

Prey species	Weight g	Numbers of prey n	 %	Prey biomass g	 %	Constancy %
Fringilla coelebs	23	179	8.0	4 117	8.9	89
F. montifringilla	23	10	0.5	230	0.5	14
Emberiza citrinella	32	20	0.9	640	1.4	46
E. hortulana	24	1	0.0	24	0.1	3
Passer domesticus	32	3	0.1	96	0.2	7
Aves sp.	20	139	6.2	2 780	6.0	89
Aves, total		996	44.5	18 164	39.5	100.0
All total		2 240	100.1	46 048	100.0	

were investigated in each of the years 1962—65. Thus, annual differences between these years may be spurious.

The proportions of birds in the diet were at their lowest in 1962, 1966 and 1969. The proportions of voles seem to fluctuate inversely with the proportions of birds, because birds and small mammals together constitute nearly 100 % of the diet. In 1967—68, when birds were most abundant among the prey, *Clethrionomys glareolus* was found in least numbers. This vole species did not show such clear variation in its occurrence as was found in birds. The proportion of *Microtus agrestis* varied greatly. In 1969, individuals of *Microtus arvalis* were found at one nest site. They have been treated jointly with *M. agrestis,* because these two congeners are ecologically similar. The proportion of *Microtus* sp. in the diet of Pygmy Owls seems to fluctuate inversely, with the proportions of birds. The proportions of *Sorex* were at their highest in 1963, but after 1964 it was found in small numbers only. Mice were found only in 1966 and 1969.

Individuals of *Lacerta vivipara* were found in the diet of the Pygmy Owl in 1963, 1967 and 1970—71, i.e. in years with higher bird numbers. Insects were found in the food only in 1968 and 1970.

Diet in different phases of the breeding season. The composition of the food was studied at five nest sites (12, 17, 21, 23 and 25; see Table 1) in three phases of the breeding season: (I) incubation (in May), (II) the first half of the nestling period (about 1—15 June), and (III) the latter half of the nestling period (about 16—30 June). The division of the nestling period into two parts is justified by the much greater weight increase of the nestlings during the first half (KELLOMÄKI unpubl.).

Towards the end of the breeding season, the proportion of birds increased while the proportion of mammals decreased correspondingly (Table 7). The numbers of birds differed almost significantly between phases I and II ($P<0.1$, χ^2 test), and highly significantly between phases II and III ($P<0.001$).

TABLE 5. Weight distribution of the prey animals ($n=2240$, 46 048 g).

Weight (g)	Proportion (%) by number	 weight
<10.0	10.2	3.6
10.0—19.9	17.7	11.9
20.0—29.9	49.3	50.0
30.0—39.9	21.9	32.3
>40.0	1.0	2.2
Total	100.1	100.0

TABLE 6. The proportion (%) of the most important prey animals by number in the food of the Pygmy Owl in 1962—71. Annual differences have been compared with the χ^2 test; significant differences between the columns are shown (* = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$). The avian prey could not be determined to species in 1963 owing to the poor condition of the feathers.

	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971
Sorex araneus	2.4	15.7	0	0	0	0	2.3	1.7	0.5	1.7
Soricidae, total	4.8 ***	43.1	17.4	3.2	3.4	0	5.6	3.7 **	1.1 **	3.9
Clethr. glareolus	47.6 ***	17.6 *	39.1 *	45.2	28.8 **	9.5	7.9 ***	31.8 *	25.6	29.7
Microtus agrestis	31.3	0	0	25.8 *	47.9 ***	8.1	1.1	33.8 ***	18.6 **	9.3
Cricetidae, total	78.8 ***	17.6 *	39.1 *	71.0	76.7 ***	17.6	9.0 ***	65.6 ***	44.2	39.0
Muridae, total	0	0	0	0	0.7	0	0	0	0.8	0
Mammalia, total	83.7 ***	60.8	56.5	74.2	80.8 ***	17.6	14.6 ***	69.3	46.4	42.9
Reptilia, total	0	2.0	0	0	0	1.4	0	0	1.8	3.9
Insecta, total	0	0	0	0	0	0	2.3	0	0.4	0
Parus montanus	0	..	0	0	1.4	1.4	3.4	1.4	2.2	2.8
Erithacus rubecula	0	..	0	0	1.4	4.1	1.1	3.7	5.3	4.4
Phylloscopus sp.	2.4	..	0	0	0	2.7	18.0	3.9	5.3	2.8
Ficedula hypoleuca	1.9	..	4.4	0	0.7	5.4	4.5	0.9	1.6	3.3
Anthus trivialis	1.9	..	4.4	0	1.4	4.1	2.3	2.0	3.2	3.3
Carduelis spinus	1.0	..	4.4	3.2	0.7	5.4	5.6	2.0	5.8	7.1
Fringilla coelebs	2.4	..	4.4	3.2	3.4 *	10.8	10.1	5.1 *	10.1	12.6
Aves, total	16.4 ***	37.3	43.5	25.8	19.2 ***	81.1	83.2 ***	30.7 ***	51.5	53.3
All total	100.1	100.1	100.0	100.0	100.0	100.1	100.0	100.0	100.1	100.1
Prey items/nests	208/1	51/1	23/1	31/1	146/3	74/3	89/2	355/4	1081/9	182/3

The occurrence of different birds in the diet was fairly constant. Six species were studied in detail, *Parus montanus, Erithacus rubecula, Phylloscopus* sp., *Anthus trivialis, Carduelis spinus* and *Fringilla coelebs*. Only one significant difference could be shown in their occurrence as food items in different phases of the breeding season. *Fringilla coelebs* was utilized more during phase III than phase I, but as almost 20 comparisons were made, about one significant result may be expected to occur by chance.

The proportion of nestlings and fledglings increased among the avian prey from phase I to III. The proportion of young birds also increased dur-

TABLE 7. Proportions of prey animal groups in the diet of the Pygmy Owl in different phases of the breeding season at 5 nests (12, 17, 21, 23, 25; see Table 1 for names of the nests) in 1968 and 1970. Phase I = incubation, phase II = first half of nestling period, phase III = latter half of nestling period.

Prey group	Phase I *n*	Phase I %	Phase II *n*	Phase II %	Phase III *n*	Phase III %	Total *n*	Total %
Birds	60	42.0	168	50.6	205	72.4	424	55.9
Mammals	75	52.4	162	48.8	70	24.7	316	41.7
Other	8	5.6	2	0.6	8	2.8	18	2.4
Total	143	100.0	332	100.0	283	99.9	758	100.0

ing the breeding season, from 3.1 % (phase I) to 17.6 % (II) and 30.6 % (III). Both increases are significant ($P<0.05$, $P<0.02$, respectively; Mann-Whitney U test).

The diversity of the avian prey was estimated with the Shannon-Wiener index H′ (Krebs 1972) for each nest site and phase separately (sites 12, 17, 21, 23 and 25, see Table 1). The averages of I (1.77) and II (2.28) differed almost significantly ($P<0.06$), but the average of III (2.20) did not differ from either I or II (paired-sample t test).

Table 9. Correlation coefficients (r) between chosen and available mammal prey. A. Based on the number of trapped individuals per 100 trap-nights, B. as A but multiplied by biomass. In all comparisons, the variable "chosen" has been the percentage of small mammals in the diet. All the sites (12) have been included where mammals were trapped and the nest found (see Table 1). None of the correlation coefficients is significant.

Species	Correlation A	Correlation B
Sorex araneus	0.08	0.03
Soricidae, total	—0.40	—0.30
Clethrionomys glareolus	0.39	0.37
Cricetidae, total	0.30	0.21

Choice and availability of mammalian prey

The correlation between the choice and availability of mammalian prey was investigated by two methods. The proportions of prey chosen were compared with (1) the proportions and (2) the densities (ind./100 trap-nights) of prey available. Both methods gave the same results, thus the comparisons are presented by method (1) only (Tables 8 and 10). I have not studied species which were observed at less than two sites in both the actual prey and the trapped material.

Table 8. Dependence of the selection of mammalian prey on the availability of the species. Only those nest sites have been included where individuals of the prey species were both chosen by the owls and trapped by the investigator. The percentages do not total 100 %, for different sites were studied for different species. The representation of the species in the diet has been studied with the χ^2 test (number of individuals chosen compared with number of individuals trapped, with the null hypothesis that the proportion of the species should be equal in the two cases). If the percentage is higher in the first column, the species is over-represented in the diet, i.e. the Pygmy Owl hunts this species more than its frequency in the environment suggests. The higher percentage has been italicized if the difference is statistically significant.

Species	Sites	Prey chosen *n*	Prey chosen %	Prey trapped *n*	Prey trapped %
Sorex araneus	6	12	2.4 ***	20	*33.3*
S. minutus	4	6	1.5 ***	8	*16.3*
Clethr. glareolus	11	330	*56.9* **	44	40.0
Microtus agrestis	2	49	32.9	12	24.5

Shrews were found to be chosen in smaller and *Clethrionomys glareolus* in greater numbers than was to be expected from their availability (Table 8). As to *Microtus agrestis*, the difference between its choice and availability was not significant. The effect of the density of a given prey species on its preference was studied with correlation analysis (Table 9), but no significant correlations were found. This lack of correlation between the proportion of a prey species in the diet and its availability implies that the diet of Pygmy Owls tends to be fairly constant (see e.g. Järvinen 1974). The effect of the weight of the prey on prey selection was examined by dividing small mammals into three weight groups: (1) under 10 g (*Sorex caecutiens, S. minutus, S. minutissimus* and *Micromys minutus*), (2) 10—20 g (*Sorex araneus, Clethrionomys glareolus*

TABLE 10. Effect of prey weight on prey selection at the 12 sites where both small mammals were trapped and the nest was found (see Table 1). The χ^2 test was used to compare the diet with the trapping results (prey density = ind./100 trapnights). See Table 8 for further explanation.

Weight groups	Prey chosen		Prey trapped		Prey density	
g	*n*	%	*n*	%	$\bar{x}$	%
<10	16	2.6 ***	14	*12.7*	0.21	16.7
10—20	377	60.1 **	84	*76.4*	0.94	74.6
>20	234	*37.3* ***	12	10.9	0.11	8.7
Total	627	100.0	110	100.0	1.26	100.0

and *Mus musculus)* and (3) over 20 g *(Microtus agrestis* and *M. arvalis)* (Table 10). Groups 1 and 2 were chosen less, and group 3 more often than expected. About 60 % of the food chosen and 70 % of the food available belonged to weight group 2.

Choice and availability of avian prey

Species. The dependence of the choice of avian prey on its availability was first studied for those bird species which were both caught by the owls and observed in the censuses at five or more sites (Table 11). *Parus montanus, Erithacus rubecula,* and *Carduelis spinus* were chosen more, and *Phylloscopus* sp. less often than expected. Other species, such as *Fringilla coelebs* and *Anthus trivialis* were used as food in relation to their availability (Fig. 1). When densities were compared instead of numbers, the results were similar.

The effect of the density of a given prey species on its preference was studied by correlation analysis (Table 12), but only one significant correlation was found. The data for the separate species are perhaps too meagre to warrant definite conclusions, but when the total bird densities (as such or weighted by the biomasses) are compared with prey choice, significant positive correlations emerge. In other words, the preference for bird prey increases with increasing bird densities. The dependence of the choice of avian prey on its availability was examined further by comparing the average proportions of single species in the diet and in the available prey. A significant positive correlation was obtained ($r = 0.77$, $n = 18$, $P < 0.001$).

Weight groups. When the correlation between chosen and available prey was examined according to weight groups (Table 13), the Pygmy Owl was found to avoid extreme weight groups (5.0—9.9 and >40.0 g), and prefer middle groups (especially 10.0—14.9, 15.0—19.9 and 30.0—39.9 g). About 50 % of the chosen and 45 % of the available prey birds belonged to the weight group 15.0—29.9 g. The result was similar,

TABLE 11. Dependence of selection of avian prey on the availability of different species. Only those nest sites have been included where individuals of the prey species were both chosen by owls and censused by the investigator. For other explanations, see Table 8.

Species	Sites	Prey chosen		Prey censused	
		n	%	*n*	%
Parus major	7	8	2.0	20	2.9
P. cristatus	5	8	3.5	7	2.3
P. montanus	11	31	*5.5* ***	15	2.1
Certhia familiaris	5	8	2.6	16	2.5
Erithacus rubecula	10	58	*9.7* ***	45	5.1
Phylloscopus sp.	13	79	10.8 ***	242	*22.0*
Regulus regulus	6	9	2.6	24	4.1
Muscicapa striata	9	26	4.5	18	3.0
Ficedula hypoleuca	11	27	4.3	34	3.5
Anthus trivialis	11	42	6.2	53	5.2
Carduelis spinus	10	59	*9.7* **	61	6.1
Pyrrhula pyrrhula	5	7	3.0	7	1.4
Loxia curvirostra	8	11	2.6	33	4.1
Fringilla coelebs	13	143	19.8	219	22.7

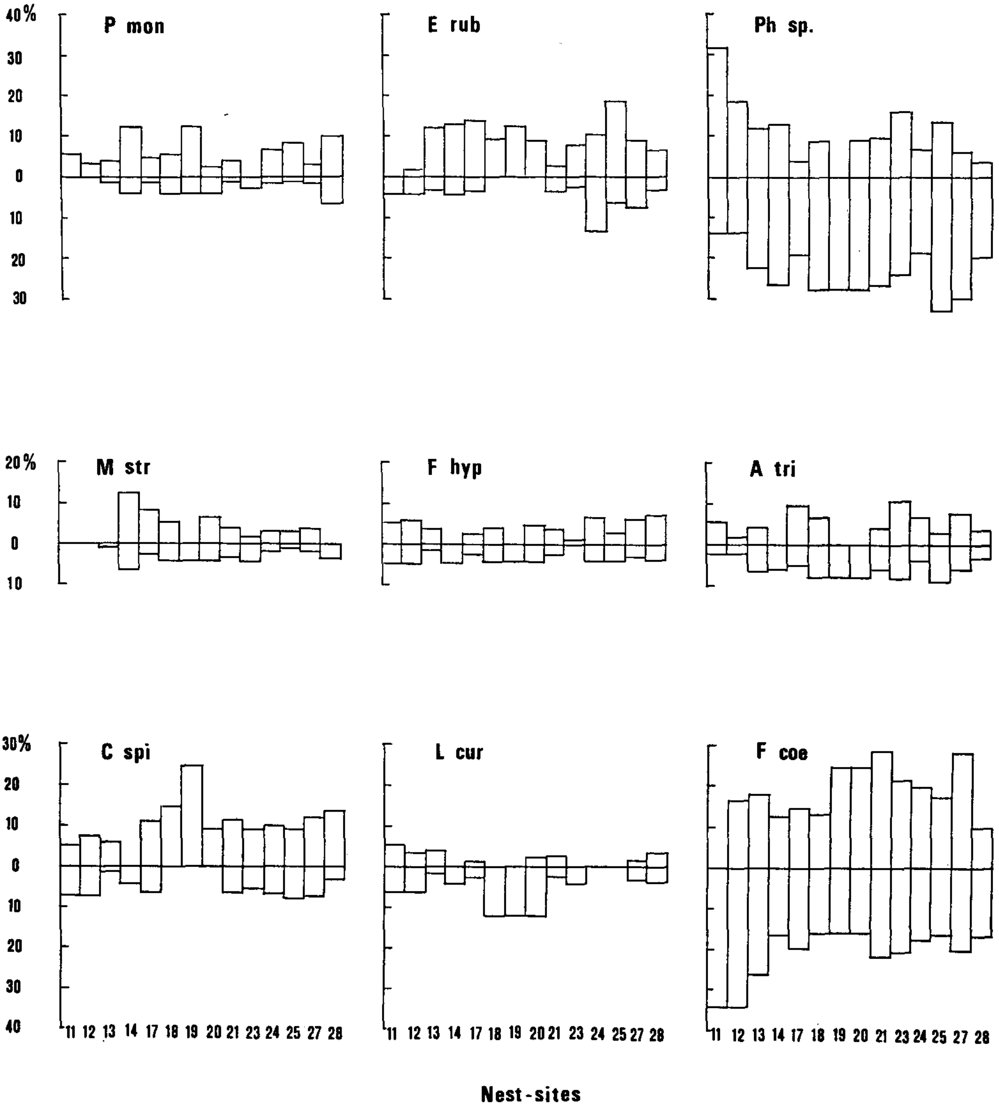

FIG. 1. The choice and the availability of nine prey birds of the Pygmy Owl at 14 nest sites. P mon = *Parus montanus*, E rub = *Erithacus rubecula*, Ph sp. = *Phylloscopus* sp., M str = *Muscicapa striata*, F hyp = *Ficedula hypoleuca*, A tri = *Anthus trivialis*, C spi = *Carduelis spinus*, L cur = *Loxia curvirostra*, F coe = *Fringilla coelebs*. The horizontal axis gives the nest sites studied (11, 12, . . ., 28; cf. Table 1). The vertical axis gives the percentages of the bird species in the chosen (above) and available (below) prey.

TABLE 12. Correlation coefficients (*r*) between chosen and available avian prey. A. Based on the density of censused birds (pairs/km^2), B. as A but multiplied by biomass. In all comparisons, the variable "chosen" has been the percentage of birds in the diet. The sites included (14) are all those where birds were censused and the nest found (see Table 1), except site 26 (birds censused only once).

Species	Correlation A	B
Parus major	—0.19	—0.17
P. montanus	0.48	0.32
Erithacus rubecula	0.21	0.25
Phylloscopus sp.	—0.06	—0.07
Muscicapa striata	0.61*	0.27
Ficedula hypoleuca	0.27	0.27
Anthus trivialis	0.13	0.11
Carduelis spinus	—0.25	—0.27
Loxia curvirostra	—0.22	—0.23
Fringilla coelebs	—0.13	—0.15
Aves total	0.59*	0.69 **

when the availability of the prey birds was expressed by using percentages calculated on the basis of their densities.

Ecological groups. The hunting habits of the Pygmy Owl were examined by comparing the chosen and available prey in different ecological groups, distinguished according to the nest sites of the prey birds (Table 14). Tree-nesters, ground-nesting forest birds, ground-nesters of open terrain and house-nesters were not chosen in unexpected numbers, but hole-nesters were hunted more often than was expected from their availability.

Diversity of chosen and available prey birds. Since the diversity of the chosen avian prey was at its highest during the first half of the nestling period (p. 9), the values for phase II were used when the material could be divided into different phases. Otherwise the diversity of the total avian prey was used. The diversities of the chosen and available avian prey showed a significant correlation ($r=0.67$, $P<0.01$, $n=13$); in other words, about 45 % of variation in the diversity of the diet could be explained by the diversity of the bird community in the hunting area of the owl.

Factor analysis of the composition of chosen and available prey

Material and methods. Factor analysis can be used (1) in summarizing the information given by the basic variables and (2) in revealing hidden functional connections between the basic variables (THURSTONE 1961). All the 43 prey species which were observed in the diet at least twice were used as variables. Correspondingly, the variables used for the available prey were the 35 species trapped or observed in the censuses at least twice. Birds and mammals were treated separately.

Factor analysis is begun by determining the correlation coefficients between the variables (in this investigation between the abundance of different prey species in the diet and in the censuses). An attempt is then made to explain, or summarize, the correlations between the variables with certain

TABLE 13. Effect of prey weight on bird prey selection at the 14 sites where birds were censused and the nest found (see Tables 1 and 12; site 26 excluded here, too). χ^2 test used to compare diet with results of census.

Weigth group g	Prey chosen *n*	%	Prey censused Pairs *n*	%	Pairs/km^2 $\bar{x}$	%
5— 9.9	104	15.8 ***	316	*28.6*	47.5	30.1
10—14.9	172	*26.1* ***	131	11.8	21.1	13.4
15—19.9	107	*16.2* ***	117	10.6	18.8	12.0
20—29.9	221	33.5	376	34.0	48.4	30.7
30—39.9	37	*5.6* ***	24	2.2	2.5	1.6
>40	18	2.7 ***	142	*12.8*	19.3	12.2
Total	659	99.9	1106	100.0	157.5	100.0

TABLE 14. Effect of ecological group of prey on prey selection at 14 sites where birds were censused and the nest found (see Table 1; site 26 excluded). χ^2 test used to compare diet with censuses.

Ecological groups	Prey chosen		Prey censused			
			Pairs		Pairs/km^2	
	n	%	*n*	%	$\bar{x}$	%
Tree-nesters	288	43.8	517	46.7	66.0	41.8
Hole-nesters	138	*20.9* *	186	16.8	28.8	18.2
Ground-nesting forest birds	212	32.1	378	34.2	59.7	37.9
Ground-nesters of open terrain and house-nesters	21	3.2	25	2.3	3.2	2.0
Total	659	100.0	1106	100.0	157.5	99.9

basic components, factors, which can be more easily understood than the extensive correlation matrix. The correlation matrix is analysed with standard computer library programs (the so-called polar axis method with rectangular Varimax rotation was used). The factors are so estimated that the first factor explains the maximum amount of total variation, the second factor explains as much as possible of the remaining variation and so on. In the present study it was necessary that the factors could be reasonably interpreted. Hence, in most cases, fewer factors were used than could validly (MÄKELÄ 1968, ROOS 1971) have been taken into account. As a result, the proportion of total variance explained by the factor solutions was rather low.

As the biomass of prey animals may influence the choice of prey by the Pygmy Owl, factor analyses were also applied to figures weighted by the biomasses. However, the results were quite similar to those obtained with unweighted data and are not given here.

Factor solutions. The factor solutions are presented in Tables 15 and 16. In the interpretation, factor loads below 0.30 were excluded and regarded as zero loads (MARKKANEN 1964; the load varies from —1 to +1 and indicates the influence of the factor).

The mammalian prey chosen yielded a two-factor solution (Table 15; 53 % of total variance explained). The first factor (F_1) comprises forest mammals: shrews and *Clethrionomys glareolus.* These animals form the basic mammalian diet of the Pygmy Owl in bad vole years. The second factor (F_2) is called the factor of field mammals, because *Microtus agrestis* and different mice *(Mus, Micromys)* have high loads. This species combination characterizes years of rodent peaks.

The avian prey chosen yielded a three-factor solution (Table 16; 44 % of total variance explained). The most

TABLE 15. Factor analysis of the mammalian prey of the Pygmy Owl. The table gives the factor loads of the variables (prey species). The loads have been calculated from correlation coefficients between variables by factoring. Loads exceeding 0.3 italicized.

Variables	Prey chosen F_1	F_2	Prey trapped G_1	G_2
Sorex araneus	*0.931*	0.021	0.232	*—0.424*
S. caecutiens	*0.842*	0.200	—	—
S. minutus	*0.887*	0.001	0.223	0.278
Sorex sp.	*0.443*	—0.297	—	—
Clethr. glareolus	*0.474*	*0.806*	0.113	0.297
Microtus agrestis	0.292	*0.859*	*0.498*	0.067
Micromys minutus	0.066	*0.607*	—	—
Mus musculus	0.188	*0.666*	—	—
Variance explained (%)	29.2	23.8	9.1	8.8
	53.0		17.9	

TABLE 16. Factor analysis of the avian prey of the Pygmy Owl. The table gives the factor loads of the variables (prey species). The loads have been calculated from correlation coefficients between variables by factoring. Loads exceeding 0.3 italicized.

Variables	Prey chosen			Prey censused		
	F_1	F_2	F_3	G_1	G_2	G_3
Apus apus	—0.063	*0.686*	—0.099	—	—	—
Dendrocopos major	—0.144	*0.621*	0.250	—0.143	—0.121	*0.592*
Jynx torquilla	0.119	*0.791*	0.215	0.041	*0.740*	—0.061
Alauda arvensis	0.274	0.188	—0.243	*0.526*	—0.179	*0.429*
Hirundo rustica	—0.028	0.436	0.059	*0.887*	—0.205	0.099
Parus major	—0.137	*0.348*	*0.324*	0.225	*0.771*	0.017
P. ater	0.164	0.030	*0.730*	—	—	—
P. cristatus	*0.373*	0.068	*0.347*	—0.245	—0.113	*0.814*
P. montanus	*0.501*	0.272	*0.591*	0.238	0.126	*0.514*
Certhia familiaris	*0.473*	*0.414*	—0.233	*0.409*	*0.638*	*0.330*
Troglodytes troglodytes	—0.079	0.158	—0.247	—0.036	0.131	—0.024
Turdus philomelos	—0.099	*0.469*	0.023	*0.424*	—0.098	—0.221
T. iliacus	0.150	*0.410*	*0.605*	0.006	*0.400*	—0.238
Oenanthe oenanthe	*0.320*	—0.066	—0.169	—	—	—
Saxicola rubetra	—0.064	—0.161	—0.090	*0.463*	—0.263	*—0.404*
Phoenicurus phoenicurus	—0.063	—0.006	*0.342*	*0.385*	*—0.666*	0.152
Erithacus rubecula	*0.743*	0.081	*0.490*	*0.742*	0.271	—0.026
Sylvia borin	*0.718*	—0.190	—0.023	0.007	0.176	*—0.310*
S. curruca	—	—	—	*0.720*	0.124	*—0.478*
Phylloscopus sp.	*0.628*	*0.403*	0.281	*0.921*	—0.099	0.283
Regulus regulus	*0.310*	—0.075	0.085	*0.312*	*0.551*	*0.371*
Muscicapa striata	*0.752*	0.062	0.225	0.205	0.177	*0.631*
Ficedula hypoleuca	*0.415*	*0.359*	*0.479*	*0.562*	*0.522*	0.047
F. parva	—	—	—	0.003	*0.807*	—0.089
Prunella modularis	—	—	—	—0.280	—0.096	0.020
Anthus trivialis	*0.881*	—0.077	—0.005	*0.864*	—0.133	0.298
Motacilla alba	*0.326*	—0.260	0.295	0.156	0.134	*—0.463*
Carduelis spinus	*0.855*	0.263	0.235	*0.859*	0.234	—0.161
C. flammea	*0.391*	*0.472*	0.074	*0.502*	—0.112	*—0.378*
Pyrrhula pyrrhula	*0.345*	0.079	*0.528*	0.054	*0.340*	—0.145
Loxia curvirostra	0.144	*0.630*	—0.106	0.181	—0.210	*0.805*
Fringilla coelebs	*0.778*	*0.355*	0.172	*0.846*	0.117	—0.031
F. montifringilla	—0.003	*0.459*	*0.644*	—0.044	*0.874*	0.073
Emberiza citrinella	*0.799*	—0.087	0.292	*—0.430*	—0.224	*—0.313*
Passer domesticus	0.195	*0.452*	*—0.355*	—	—	—
Aves sp.	*0.530*	0.001	—0.245	—	—	—
Variance explained %	20.3	12.7	11.2	22.9	15.7	13.1
		44.1			51.8	

important prey birds (about 70 $^{0}/_{0}$ of prey individuals) of the Pygmy Owl have high loads on the first factor (F_1), called the factor of forest birds, because common forest birds (*Anthus trivialis, Carduelis spinus, Fringilla coelebs, Muscicapa striata, Erithacus rubecula* and *Phylloscopus* sp.) have the highest loads. However, birds breeding in open habitats, such as *Emberiza citrinella, Motacilla alba* and *Oenanthe oenanthe,* also have high loads.

Species living both in forests and in open habitats characterize the second factor (F_2), called the factor of edge species, because many species are most abundant in the ecotone between forests and fields. Hole-nesters *(Jynx torquilla, Apus apus* and *Dendrocopos major)* have the highest loads. The heaviest prey animals of the Pygmy Owl have high loads on this factor *(Dendrocopos major, Turdus philomelos, T. iliacus* and *Apus apus).*

Factor F_3, "birds of spruce forest", shares some species with F_2: *Fringilla montifringilla, Turdus iliacus, Ficedula hypoleuca, Passer domesticus* and *Parus major.* Among the birds with their highest loads on this factor are many species of old spruce forests, such as *Parus ater, Fringilla montifringilla, Parus montanus, Pyrrhula pyrrhula* and *Turdus iliacus,* but also species of other habitats *(Phoenicurus phoenicurus* and *Ficedula hypoleuca).*

It was wished to compare these factor solutions with those based on the analysis of prey available. Only four small mammal species *(Sorex araneus, S. minutus, Clethrionomys glareolus* and *Microtus agrestis)* were trapped, and direct comparison of the two-factor solution (only about 18 % of total variance explained) is thus difficult. The low degree of variance explained suggests that the total trapping time (12 420 trap-nights) was too small for comparison with factor analysis. However, the factors could be interpreted in the same way as in the analysis of prey chosen: *Microtus agrestis* formed factor G_1, "field mammals", while *Sorex araneus* formed factor G_2, "forest mammals". Thus, the same species, *Microtus agrestis* and *Sorex araneus,* have the highest loads on the factors of both the prey chosen and the prey available.

The consistence of this factor solution with that based on prey chosen was tested with the consistence coefficient (φ; HARMAN 1960), defined as

$$\varphi_{pq} = \frac{\Sigma a_{jp} \cdot a_{jq}}{\sqrt{(\Sigma a_{jp}^2)\,(\Sigma a_{jq}^2)}}$$

where a_{jr} = the load of variable j ($j = 1, \ldots n$) on factor r and n = number of variables.

The consistence coefficient was 0.01 for the "forest mammals" (F_1, G_2) factors and 0.74 for "field mammals" (F_2, G_1). The coefficients were calculated by using the four common species in the chosen and available prey. Thus, the structure of the correlation matrix for the mammal prey chosen by the Pygmy Owl differed considerably from that based on snap-trapping.

When the bird census results were analysed, a three-factor solution (52 % of total variance explained) was obtained. Factor G_1, "forest birds", includes the most abundant bird species of the available prey (e.g. *Phylloscopus* sp., *Anthus trivialis, Fringilla coelebs,* and *Erithacus rubecula).* These form about 70 % of the prey individuals available. Most species which have high loads on G_1 breed in forest habitats. The species which had the highest loads on the factor "forest birds" in both analyses (chosen and available prey) included *Carduelis spinus, Anthus trivialis, Fringilla coelebs* and *Erithacus rubecula.* The consistence coefficient between the two factors was 0.62.

Hole-nesting species, such as *Ficedula parva, Ficedula hypoleuca, Parus major, Jynx torquilla* and *Phoenicurus phoenicurus,* have high loads on the second factor (G_2), the factor of hole-nesters. Most other species of this factor are typical of spruce forests. Several species *(Fringilla montifringilla, Parus major, Jynx torquilla* and *Certhia familiaris)* have high loads on G_2 and F_2 ($\varphi = 0.41$).

The third factor, G_3, is difficult to interpret, because many loads are negative, and the variables represent birds breeding both in forests (*Parus cristatus, Loxia curvirostra, Muscicapa striata, Dendrocopos major* and *Parus montanus*) and in open terrain (*Alauda arvensis, Motacilla alba, Saxicola rubetra* and *Emberiza citrinella*). The highest loads belong to species breeding in spruce forests. On the other hand, many of the species of G_3 breed in the edge zone of forests and fields, and the factor was named accordingly (factor of edge species). The consistence coefficients showed that the organization of the second and third factors differed in the factor solutions of chosen and available prey. φ was very low, 0.10, for F_3 and G_3 but $\varphi = 0.34$ for F_2 and G_3, and $\varphi = 0.44$ for F_3 and G_2.

Thus, the prey chosen by the Pygmy Owl tallied fairly well with the composition of the available prey revealed by censuses of the avifauna of the nest sites.

Influence of alternative food

General. The dependence of the choice of prey on its availability has so far been treated separately for mammals and birds. Since the diet of the Pygmy Owl consisted of mammals and birds in equal proportions, I shall now study the influence of the availability of alternative food items on the choice of prey. The material used is that sampled at the 12 nest sites where the most thorough investigations were made (see Table 1). At these sites the average proportion of birds among the prey was 47.9 % and that of mammals 49.6 %. These means did not differ significantly (Mann-Whitney U test). The material derived from these 12 nest sites is representative of the total material, in which the averages are 49.4 % for birds and 48.1 % for mammals (28 sites).

Regression analysis. The influence of alternative food upon the choice of the prey of the Pygmy Owl was studied with regression analysis. It was assumed that the choice of prey can be influenced by the availabilities (densities) of birds and small mammals separately. Thus, the dependent variables were the proportions of birds and mammals in the diet, and the independent variables were the densities of birds and small mammals in the vicinity of the nest sites. The independent variables were not correlated ($r = 0.04$). Hence the correlation coefficients are, at the same time, partial correlation coefficients, from which the amount of variance explained can be estimated directly (MÄKELÄ 1968).

The data are shown graphically in Fig. 2. In addition to using untransformed variables, I also studied models in which the dependent variable was logarithmically transformed (base e) and/or the independent variables were logarithmic or inverse (1/density). The relative importance of the independent variables in the models was estimated with standardized regression coefficients (see EZEKIEL & FOX 1959, MÄKELÄ 1968).

The proportion of mammals in the diet was best explained by a model in which the independent variables were the density of birds and the logarithm of mammal density (73 % of total variance explained). The equation of the model was

$$P_M = 0.51 \ln M - 0.66 B + 46.82,$$

where P_M = proportion of mammals in the diet, M = density of mammals and B = density of birds. The model is statistically significant (F test, $P < 0.01$). The density of birds was more important than the logarithmic density of the mammals in the model (significance levels $P < 0.01$ and $P < 0.05$,

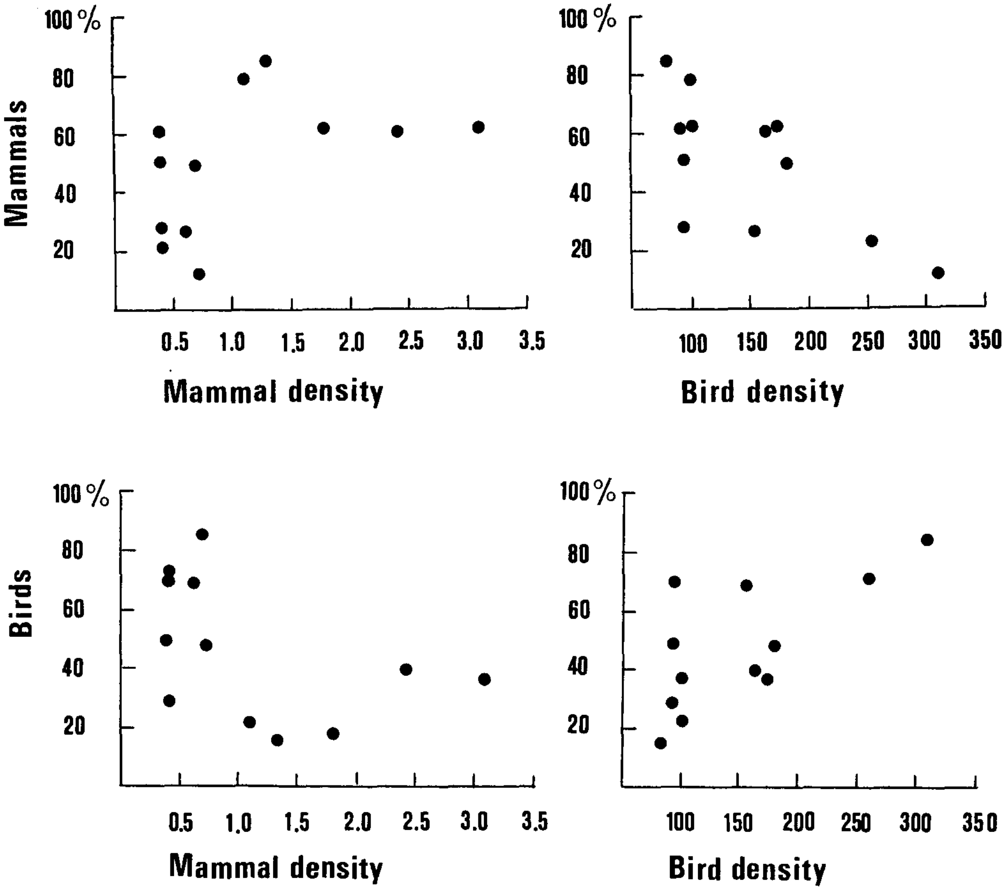

FIG. 2. Influence of the availability of the alternative prey items on the choice of the prey of the Pygmy Owl at 12 nest sites. Bird density: pairs/km^2; mammal density: ind./100 trap-nights.

respectively), perhaps because the non-linear dependence of P_M upon M was not adequately taken into account.

The proportion of birds in the diet was best explained when the independent variables were the bird density and the inverse value of the mammal density (68 % of total variance explained). When ln M was used, the percentage was nearly the same (67.5 %). The equation of the model was

$$P_B = 0.68\,B + 0.45\,1/M + 0.75,$$

where P_B = proportion of birds in the diet; the other symbols are the same as in the former equation. The model is statistically significant (F test, $P < 0.01$). The density of birds was more important than the inverse value of the mammal density (significance levels $P < 0.01$ and $P < 0.05$, respectively).

As the proportion of mammals in the diet was at its highest during phase I (Table 7) of the breeding season, data on the composition of the diet during

TABLE 17. The composition of the food (%) of the Pygmy Owl in 1969 and 1971 according to (A) the present study, (B) MIKKOLA (1970), (C) MIKKOLA & JUSSILA (1974). The material of MIKKOLA has been collected in both northern and southern Finland and that of MIKKOLA & JUSSILA in southern Finland. The proportions were tested with χ^2.

Prey group	1969 A	 B	1971 A	 C
Soricidae	3.7	1.6	3.9	6.0
Clethr. glareolus	31.8	37.6	*29.7* **	13.9
Microtus agrestis	33.2 ***	16.1	9.3	2.0
Cricetidae	65.6	62.0	*39.0* ***	17.9
Muridae	0	0.8	0	5.0
Mammalia	69.3	63.5	*42.9* *	28.7
Aves	30.7	32.5	53.3 *	*67.3*
Sample size	355	255	182	101

that phase might be expected to give different results. Sufficiently detailed information was available from only 5 nest sites. The correlation coefficient between P_M and M in phase I was 0.57 ($P<0.05$); it increased somewhat when $\sqrt{M}$ was used ($r=0.61$, $P<0.05$). The corresponding correlation coefficient between P_B and B was 0.63 ($P<0.05$). Regression analysis was not performed with these new figures, because it can be concluded from the correlation coefficients that B is more important in this case, too.

Discussion

Comparison with other investigations

Earlier records concerning the food of the Pygmy Owl during the breeding season are scarce in Finland. Our handbooks (HILDÉN & LINKOLA 1962, v. HAARTMAN et al. 1963—72) state that its diet consists of small mammals, birds, lizards and larger insects. More detailed data on the food of the species have been published by KELLOMÄKI (1969), MIKKOLA (1970), JUSSILA & MIKKOLA (1973) and MIKKOLA & JUSSILA (1974). The data on 656 prey animals published earlier by me (KELLOMÄKI 1969) have been included in the present material.

The samples of the diet of the Pygmy Owl obtained by MIKKOLA (1970) contained the same animal groups as in this investigation. The most abundant avian prey was *Phylloscopus* sp. The material of MIKKOLA & JUSSILA (1974) from 1971—73 also contained the same animal groups as in this study.

When results of different studies are compared, it is best to use samples from the same years (Table 17). The results of this investigation and those of MIKKOLA for 1969 differed significantly only in respect of the proportions of *Microtus agrestis,* although two of the nest sites investigated by MIKKOLA were situated in northern Finland and one in southern Finland. On the other hand, my results and those of MIKKOLA & JUSSILA for 1971 differed significantly from one another in all prey animal groups, except shrews (Soricidae), although both materials were sampled in southern Finland.

In Sweden, data on the food of the Pygmy Owl have been published by BERGMAN (1939), CURRY-LINDAHL (1958, 1960), BENGTSSON (1962) and JANSSON (1964). The largest body of data is given by JANSSON (1964). During one breeding season, 215 prey animals were brought to the nest studied by him, 63 % of them mammals and 37 % birds. Only one shrew was definitely observed. Owing to the method used (direct visual observation), the species of the prey animals could not be determined.

In Norway, the Pygmy Owl has been studied by LUND (1951), SEIERSTAD et al. (1960) and SONERUD et al. (1972). In the two first-mentioned studies, the samples were rather small, but in the study of SONERUD et al. (1972) 108 prey animals were sampled at one nest site; 56 % of this material was birds (13 different species), and three mammal species were found.

In Central Europe, records of the diet of the Pygmy Owl have been published by RETTMEYER

TABLE 18. The composition of the food (%) of the Pygmy Owl in different countries. The data are derived from (A) the present study, (B) JANSSON (Sweden; 1964) for 1961, (C) SONERUD et al. (Norway; 1972) for 1971, (D) MÄRZ (FRG; 1964) for 1962—63, (E) KLAUS et al. (GDR; 1965) for 1964, (F) BERGMANN & GANSO (Austria; 1965) for 1961 and (G) SCHERZINGER (Austria; 1970) for 1966—67.

Prey group	A	B	C	D	E	F	G	Average
Mammalia	54.0	63.0	31.9	19.0	54.0	91.0	50.5	52.3
Aves	44.5	37.0	63.8	80.0	46.0	9.0	49.5	46.4
Other	1.5	0	4.3	1.0	0	0	0	1.3
Prey items/nests	2240/28	215/1	108/1	162/5	57/1	32/1	111/2	

(1925), UTTENDÖRFER (1952), MÄRZ (1964), BERGMANN & GANSO (1965), KLAUS et al. (1965), KNOBLOCH (1966) and SCHERZINGER (1970). The papers of RETTMEYER, UTTENDÖRFER and KNOBLOCH include only a few records. MÄRZ (1964) sampled 162 prey animals at five nest sites in the Federal Republic of Germany in 1962—63: they consisted of small mammals (19 %), birds (80 %) and lizards (1 %). The commonest bird species were *Fringilla coelebs* (15 % of birds), *Regulus regulus* (10 %), *Parus ater* (9 %), *Carduelis spinus* (8 %) and *Phylloscopus trochilus* (7 %). KLAUS et al. (1965) found 57 prey animals (54 % mammals, 46 % birds) at one nest site in the German Democratic Republic. The most abundant bird species were *Fringilla coelebs* (13 % of birds), *Ficedula hypoleuca* (9 %) and *Parus major* (7 %). BERGMANN & GANSO (1965) studied the diet of the Pygmy Owl at one nest site in Austria both by sampling food remains and by direct visual observation. Of the 86 prey items identified, 20 % were mammals and 80 % birds. Of the 32 prey animals recorded by direct observation, 9 % were birds and 91 % mammals. SCHERZINGER (1970) gathered food remains and made direct observations at two nests in Austria in 1966—70. Of the 111 prey animals brought to the nests, 49.5 % were birds and 50.5 % mammals. Of the 190 animals identified in food remains, 35 % were birds and 65 % mammals.

It is difficult to compare my results with those obtained in other areas because of differences in method. For example, it is often not stated how many times food remains have been sampled during one breeding season; the prey animals may be determined by different methods and sample sizes may also differ. Moreover, in studies made elsewhere, the availability of the prey has, in effect, been disregarded.

In the various investigations the proportion of mammals in the food of the Pygmy Owl has varied from 19 to 91 % (average 52 %), and that of birds from 9 to 80 % (average 46 %). Other food items (lizards and insects) have constituted about 1 % (Table 18).

Fringilla coelebs is one of the species that occurred, in similar proportions (χ^2 test), in all the four studies presented in Table 19. It is also the most abundant bird species in the diet of the Pygmy Owl. In Austria, *Anthus trivialis* was used more as food than in Finland ($P<0.01$). The proportions of *Parus major* were larger in both Germany and Austria than in Finland ($P<0.01$). *Regulus regulus* constitutes a larger part of the food of the Pygmy Owl in the FRG than in Finland ($P<0.001$). As regards other bird species, either the differences were not significant when tested with χ^2 or comparison was impossible owing to the smallness of the samples from Central Europe.

Parus montanus, Muscicapa striata and *Carduelis flammea* occur abundantly in the diet of the Pygmy Owl in Finland, but were totally lacking in the samples from Central Europe. Of these species, *Parus montanus* and *Muscicapa striata* are common breeding birds

TABLE 19. The most abundant prey birds in the diet of the Pygmy Owl in different countries. The data derived from (A) the present study, (B) MÄRZ (FRG; 1964), (C) KLAUS et al. (GDR; 1965) and (D) BERGMANN & GANSO (Austria; 1965). The figures give the proportions (%) of the bird species in the total bird prey sample. Percentages differing significantly from those of the Finnish sample are printed in italics.

Bird species	A	B	C	D
Fringilla coelebs	18.0	15.4	12.9	11.6
Phylloscopus sp.	9.9	7.7	1.4	2.9
Carduelis spinus	9.7	7.7	0	0
Erithacus rubecula	8.4	3.1	1.4	10.1
Anthus trivialis	6.0	0	2.9	*14.5*
Parus montanus	4.0	0	0	0
Ficedula hypoleuca	4.0	2.3	8.6	0
Muscicapa striata	2.9	0	0	0
Parus cristatus	2.2	1.5	4.3	0
Carduelis flammea	2.2	0	0	0
Regulus regulus	2.1	*10.0*	4.3	5.8
Emberiza citrinella	2.0	3.1	1.4	2.9
Parus major	1.8	*5.4*	*7.1*	2.9
P. ater	0.2	9.2	1.4	17.4
Chloris chloris	0	4.6	0	0
Troglodytes troglodytes	0.1	3.8	1.4	2.9
Prunella modularis	0	2.3	5.7	4.3
Phoenicurus ochruros	0	1.5	5.7	0
Sylvia communis	0.0	0	4.3	1.4
Aegithalos caudatus	0.0	2.3	4.3	0
Parus caeruleus	0	0	4.3	0
Certhia familiaris	0.6	2.3	1.4	5.8
Sample size	996	130	70	69

everywhere in Central Europe, but *Carduelis flammea* breeds only in the Alps. However, the main part of the avian food consists of the same species in Finland and Central Europe.

Variation in food during the breeding season

This study indicated that the use of birds as food increased and that of mammals decreased towards the end of the breeding season. JANSSON (1964) observed that the Pygmy Owl did not bring the first bird prey to its nest until the young were hatching. In his study, the proportion of avian prey also increased towards the end of breeding, but remained below 50 %. According to SONERUD et al. (1972), the proportion of birds in the diet was 26 % before hatching, and 79 % after it, the increase being highly significant ($\chi^2 = 23.6^{***}$). During the latter half of the nestling period (15—29 June), no mammals were brought to the nest studied by them. A similar trend was found by P. SULKAVA (1972) in the diet of *Accipiter nisus:* the proportion of voles decreased in June even in good vole years.

The increase in the proportion of birds towards the end of the breeding season may be caused by a decrease in the availability of small mammals due to the growth of the plants in the field layer, especially *Vaccinium myrtillus,* in early June, and/or by a real preference for bird food. This preference could be due to the fairly good availability of nestlings and young fledglings. SOUTHERN (1954) observed that the proportions of *Talpa europaea* and *Oryctolagus cuniculus* reached their peaks in the diet of *Strix aluco* when the young prey animals were most plentiful. On the other hand, the vegetation became denser at the same time, making it more difficult for the owls to hunt voles and mice. In forest habitats, *Strix aluco* caught smaller prey animals than in open habitats, a fact interpreted by SOUTHERN (1954) as the result of more difficult hunting conditions in forests due to denser ground vegetation. According to P. SULKAVA (1972), the abundance of voles in the spring diet of *Accipiter nisus* was caused by the lack of shelter in the sparse vegetation at that time. SPARROWE (1972) has shown experimentally that the number of hunting attempts of *Falco sparverius* decreased with increasing density of vegetation.

It seems that the timing of breeding of the Pygmy Owl has evolved to permit extensive exploitation of avian prey, if the availability of mammalian prey decreases owing to denser vegetation or a sudden crash in small mammal populations. HAGEN (1969) has shown that the timing of breeding of *Falco columbarius,* as well as its diet, were determined by the time of the nestling period of its prey animals, which coincided with the greatest need of nourishment of the falcon young. LACK (1954, 1968) has given numerous examples to support his general idea that the egg-laying of birds is so timed that the young are being raised when their food is most plentiful. Thus, the food available determines both the timing of breeding and the diet.

In this investigation, young birds constituted 18 % of the total avian prey during phase II and 31 % during phase III. SONERUD et al. (1972) and MIKKOLA & JUSSILA (1974) have also observed that the Pygmy Owl hunts young birds more at the end of the nestling period. In the studies of BERGMANN & GANSO (1965) and LUND (1951), the proportions of nestlings caught during the whole breeding period were 61 % and 38 %, respectively. In the prey of *Accipiter nisus,* nestlings and fledglings form about 50—70 % the avian food, and their proportion increases during the season (P. SULKAVA 1972). Among the prey brought to the young of *Accipiter gentilis,* about 75 % were young animals, mostly tetraonids (S. SULKAVA 1964).

Annual variation in the diet

According to my investigation, the proportion of voles in the diet of the Pygmy Owl varied annually, being at its largest in 1962, 1966 and 1969. Thus, a cycle of 3—4 years was found in their abundance. The proportion of birds varied inversely with that of voles. In their study of the diet of the Pygmy Owl, MIKKOLA & JUSSILA (1974) found that during the period 1971—73, voles were most abundant in 1973. The proportions of voles and other mammals in the diet of *Aegolius funereus* (P. SULKAVA & S. SULKAVA 1971) and *Accipiter nisus* (P. SULKAVA 1972) varied similarly.

In southern Finland, the peak vole years of the 1960s were 1962, 1966 and 1969 (ARTIMO 1963, P. SULKAVA & S. SULKAVA 1967, LINKOLA & MYLLYMÄKI 1969). In the snap-trapping performed during this study in 1969—71, the proportions of voles in the total catches decreased significantly (χ^2 tests) from 85.7 % (1969) to 45.5 % (1970) and 18.2 % (1971). Thus, the abundance of voles in the food of the Pygmy Owl seems to fluctuate with their abundance in the terrain. This hypothesis is supported by the results of MIKKOLA (1970) and MIKKOLA & JUSSILA (1974).

In Finland, only a few investigations have been made of the influence of prey animal populations upon the diet of predators. SUOMUS (1952) observed that the proportion of *Clethrionomys glareolus* correlated with the density of available vole populations in the diet of *Buteo buteo.* S. SULKAVA (1964) showed that fluctuations in squirrel and tetraonid densities were clearly reflected in the diet of *Accipiter gentilis.* PASANEN & S. SULKAVA (1971) were able to show that the proportions of small mammals in the diet of *Buteo lagopus* depended on their abundance. The peak years of *Clethrionomys glareolus* are reflected in the food of *Accipiter nisus* (P. SULKAVA 1972). In Norway, HAGEN (1965) found that the diet of *Asio otus* changed in parallel with the abundance of small mammals.

The hunting mechanism of the Pygmy Owl

Density-dependent choice. According to the present study, the Pygmy Owl showed a density-dependent choice of birds and small mammals, their proportions increasing with increasing availability. Thus, the hunting mechanism of the species is similar to that of many other vertebrates investigated earlier, e.g. *Turdus philomelos* (CAIN & SHEPPARD 1954). The exploitation of avian food by the Pygmy Owl in relation to its availability (Fig. 2) resembles the S-formed functional response curve presented by HOLLING (1965). However, it should be pointed out that low densities of available bird prey could not be studied by me.

The use of occasionally productive microhabitats. ROYAMA's theory (1970) of the use of occasionally productive microhabitats for maximizing the choice of available prey fits some of my results fairly well. This owl species seems to be inclined to take mixed food even in the years when small mammals are abundant. Apparently, both adult and young birds are always profitably utilized by the Pygmy Owl, because they are easily caught. MACARTHUR & PIANKA (1966) suggested that a predator prefers to continue its pursuit instead of choosing a new prey animal only if during the pursuit it is not able to find and catch a better prey. This kind of behaviour indicates that the predator must have insight into its potential food resources (RAPPORT 1971).

The use of small mammals by the Pygmy Owl in spring, before the growth of the field layer, is comparable to the use of occasionally productive microhabitats. Another occasionally productive food source becomes available after the hatching and fledging of the bird prey. Thus, the succession of prey animals (ROYAMA 1970) seems to influence the composition of the diet of the Pygmy Owl, as well.

The use of alternative prey. Regression analysis (p. 16) suggested that the availability of birds explains the proportions of both birds and small mammals in the diet of the Pygmy Owl better than the availability of mammals. This result appears to disagree with the positive correlation between the clutch size of the Pygmy Owl and the proportion of mammals in its diet ($r=0.64^*$, data from Table 2), and the negative correlation between the clutch size and the proportion of birds ($r=-0.59^*$). LINKOLA & MYLLYMÄKI (1969) have also shown that the clutch sizes of many Finnish raptors are determined by the availability of small mammals before egg-laying.

This inconsistency is resolved when it is noted that, as $P_M \approx 100\text{-}P_B$ (the proportion of insects and lizards is ± 0), the results in both models are very probably best "explained" by either *B* or *M* (for the symbols, see p. 16). The influence of mammal densities on the choice of mammals is evidently more complicated than the influence of bird densities on the choice of birds. Though the data are meagre, Fig. 2 suggests that during higher mammal densities the Pygmy Owl is not so efficient a hunter as when lower mammal densities prevail. The decrease in hunting efficiency is not equally clear in the case of birds.

"Searching image". When the density of a prey population reaches a definite level, the predator forms a specific searching image of the prey and begins to exploit the prey more frequently and efficiently (TINBERGEN 1960). The searching image can be formed, because the predator learns to use a certain prey or a certain hunting habitat or both (CROZE 1970).

The Pygmy Owl has earlier been observed to have learnt a definite hunting habit on several occasions. One individual brought its young ten nestlings of *Jynx torquilla* in succession (SONERUD et al. 1972), and in winter, a Pygmy Owl stored 20 specimens of *Carduelis flammea* in a nest-box (KELLOMÄKI unpubl.). Similar reports have been published on other Finnish birds of prey. S. SULKAVA (1964) observed that *Accipiter gentilis* brought several equally sized tetraonid fledglings to its nest, and assumed that they all came from the same brood. Apparently a searching image had also been formed when 26 hedgehogs *Erinaceus europaeus* were found among 80 prey animals at a nest site of *Bubo bubo* (S. SULKAVA 1966); the hedgehog is otherwise seldom found among the prey remains of this species. In passerines, there is much evidence of the formation of a searching image (e.g. TINBERGEN 1960, CROZE 1970, ALLEN 1974). MUELLER (1971) made similar records of diurnal raptors.

Utilization of the diversity of available prey. The Pygmy Owl exploits the available prey efficiently and widely. The composition of the bird prey chosen was in fairly good accord with the composition of available prey populations as determined by bird censuses. A significant positive correlation was found between the diversities of chosen and available prey birds. This meets the criterion of an efficient choice of prey presented by ROYAMA (1970) on the basis of a mathematical model. According to MACARTHUR (1972) and MACARTHUR & PIANKA (1966), a predator inhabiting poor environments cannot be a food specialist, because the abundance of prey controls the time spent in search of prey. The same predator can be more specialized in a more productive environment.

The usual habitats of the Pygmy Owl are coniferous forests characterized by rather low production. In this study, the average density of the available bird prey was 173 pairs/km^2. In deciduous forests, the bird densities may be 3—4 times as high (PALMGREN 1930, MERIKALLIO 1946, HAAPANEN 1965). During years with peak populations of voles, the habitats of the Pygmy Owl become more productive, and in these years its diet can be more specialized. During such years the diversity of avian prey was, in fact, lower than during poor vole years. At nest sites where the proportion of mammals in the diet exceeded 70 %, the mean diversity of avian prey was 2.04 ± 0.47 (*S.D.*, $n=6$), but at nest sites where mammals comprised less than 30 %, the value was 2.36 ± 0.22 (*S.D.*, $n=10$), which was significantly higher ($t=2.52$, $P<0.05$). This result could admittedly be due to the correlation between the diversity of chosen and available bird prey (p. 12), but the scarcity of the data prevents further analysis.

Abundance of available prey. The Pygmy Owl exploits the most abundant of its potential prey animals. Among mammals, however, shrews formed an exception. Their proportion in the diet was only about 10 % of their proportion in the total mammal density. Further, the proportion of shrews in the diet was ± constant. Voles were exploited a little more than could be expected from their availability.

The birds exploited most abundantly were those reported by MERIKALLIO (1946) to be the commonest inhabitants of coniferous forests in southern Finland. The ratio between chosen and available bird prey was the same for the Pygmy Owl as for *Accipiter nisus* (P. SULKAVA 1972) in respect to *Erithacus rubecula, Fringilla coelebs, Anthus trivialis* and *Phylloscopus* sp.

Significance of the hunting habitat for the choice of prey. The occurrence of a certain prey animal in the diet of the Pygmy Owl is also influenced by the selection of hunting habitats. The Pygmy Owl does not hunt at random but concentrates its hunting to some types of habitats (SCHERZINGER 1970). In this study, the hunting habitats were not investigated in detail, but clear clues to them were given by the occurrence of certain animals in the food. Thus, species inhabiting open terrain or nesting in buildings (e.g. *Motacilla alba, Alauda arvensis* and *Hirundo rustica)* were used even at nests located more than 0.5 km from a suitable habitat, which indicates that the Pygmy Owl does not hunt exclusively in forests. That it can hunt rather far from its nest is seen from the occurrence of *Passer domesticus* among the prey animals at nest sites 21 and 22, which were situated more than 1.5 km from the nearest houses.

When the prey birds were divided into ecological groups according to their nest sites, the Pygmy Owl was found to choose hole-nesting birds significantly more than expected. It is possible that the Pygmy Owl inspects holes in trees even during the breeding season. In winter, this habit is well known (e.g. SCHNURRE 1942, KELLOMÄKI 1966). Of the birds nesting and feeding on the ground, *Erithacus rubecula* was exploited more than could be expected from its availability, but perhaps this was only because it is easily overlooked in censuses.

Conspicuousness. The conspicuousness of different prey animals from the point of view of the Pygmy Owl is difficult to assess. That is why I have used the so-called main belt percentages (JÄRVINEN & VÄISÄNEN 1975 and pers. comm.) of the 18 most common bird prey species. These percentages are derived from the line transect census data, and they indicate how conspicuous different birds are to a human observer. The conspicuousness of a species decreases with increasing main belt percentage. The average density of a bird species in my censuses was multiplied with the main belt percentage, and the product was correlated with the proportion of the prey species in the diet. The correlation was significant ($r=0.79$, $n=18$, $P<0.001$). This is a little higher than the correlation between the average proportions of single species in the diet and in the available prey ($r=0.77$, see p. 10), but not significantly so. The result neither proves nor disproves the influence of conspicuousness, evidently because the main belt percentages of the most important prey species (especially *Phylloscopus* sp., *Fringilla coelebs)* are quite similar (about 18 and 20 %, respectively).

There is some controversy about the significance of conspicuousness. According to NORDBERG (1935), TINBERGEN (1946) and P. SULKAVA (1972), the conspicuousness of the prey (its movement, colours, sounds, etc.) was an important factor in the choice of prey of *Accipiter nisus,* but ROYAMA (1970) observed that the variation in the food composition of *Parus major* was not determined by the crypsis of the prey animals. MUELLER (1971) reported that in *Falco sparverius* and *Buteo platypterus,* conspicuousness was not so important for the choice of prey as the searching image or the oddity of the prey compared with the other available animals.

Size of prey. Large prey animals *(Dendrocopos major, Turdus philomelos, Jynx torquilla)* did not appear in the diet of the Pygmy Owls studied by me until phase III of breeding. Apparently only the female is able to kill these larger prey animals, and she takes part in hunting only at the end of nestling period (Sonerud et al. 1972, Jussila & Mikkola 1973, Kellomäki unpubl.). *Accipiter nisus* was also observed (P. Sulkava 1972) to hunt larger prey animals at the end of the breeding season, which was due to the participation of the female in hunting at that time. In general, the average prey weight increases with increasing body weight of the predator (Schoener 1968).

Concluding remarks on the niche of the Pygmy Owl

The Pygmy Owl differs in many respects from other Finnish owls. It does not see so well as many other owl species (Dice 1945, Lindblad 1967) and, consequently, does not hunt during the darkest hours of the night (Bergman 1939, Seierstad et al. 1960, Bergmann & Ganso 1965, Mikkola 1970). However, the hunting of the Pygmy Owl is almost exclusively based on vision (Scherzinger 1970). Species such as *Strix aluco* and *Aegolius funereus,* which can hunt in almost complete darkness, locate their prey animals with the help of hearing (Norberg 1970, Sparks 1975). The Pygmy Owl hunts most actively in twilight, in both the evening and morning, but it may also catch prey during the daytime.

If the different owl species are compared, the Pygmy Owl most resembles *Aegolius funereus* in its diet. These two species catch typical forest species, e.g. *Clethrionomys glareolus,* more than other Finnish owls (P. Sulkava & S. Sulkava 1971). *Aegolius funereus* and the Pygmy Owl differ from one another as regards the largest prey animal and their alternative prey; if voles are scarce, the former switches to shrews, the latter to birds. The circadian rhythm of the Pygmy Owl is well suited to hunting birds.

The Pygmy Owl is the latest breeder of the Finnish owls, even later than our *Asio* species, which are migratory. In southern Finland *Aegolius funereus* lays eggs in late March or early April (v. Haartman et al. 1963—72), i.e. about one month earlier than the Pygmy Owl. The Pygmy Owl is the only owl species in Finland which does not start incubation before the clutch is completed (Jansson 1964, v. Haartman et al. 1963—72, Sparks 1975). Hatching usually coincides with that of most of its prey birds. This is probably an adaptation which guarantees successful fledgling even in poor vole years.

Like *Strix uralensis, S. aluco* and *Bubo bubo,* the Pygmy Owl shows nest site tenacity. In contrast, *Aegolius funereus, Strix nebulosa* and our two *Asio* species change their nest sites according to the food conditions. The site-tenacity of the Pygmy Owl has not been documented by means of ringed birds, but the same territories are inhabited year after year (Kellomäki 1970, Scherzinger 1970, Jussila & Mikkola 1973). This site-attachment may be due to the species' flexible choice of prey. The Pygmy Owl populations fluctuate, and eruptive movements may occur after good vole years and high fledgling success (Lindberg 1966, v. Haartman et al. 1963—72, Ehrenroth 1974, Hildén 1975).

The favourite habitats of the Pygmy Owl are rather old coniferous forests (Kellomäki 1970). This preference cannot be explained by the availability of nest sites or the food conditions. Usually the Pygmy Owl breeds in holes made by either *Picoides tridactylus* or *Dendrocopos major.* The latter species is much more abundant in Finland and its densities are highest in luxuriant habitats. In the old spruce forests preferred by the Pygmy Owl almost the only available nest sites are made by *Picoides tridactylus*. Thus, the abundance of nest holes cannot be a factor determining the habitat selection of the Pygmy Owl. As regards the food conditions, these are better in deciduous forests.

Acknowledgements. I am especially indebted to my wife, Mrs. Tuula Kellomäki, who has given valuable assistance at all stages of my study, to my brother, Mr. Seppo Kellomäki, who made the computer programs used in the analyses, and to all those who assisted me in collecting field data, Messrs. Matti Ahola, Matti Hannuksela, Eero Heinonen, Kari Lähteenmäki, Jouko Pihlainen, Pertti Sulkava and Jari Väliniemi. Dr. Johan Tast translated my manuscript into English. I wish to express my gratitude to my teachers, Prof. Paavo Voipio and Assistant Prof. Rauno Tenovuo, for advice and guidance. Dr. Martti Soikkeli, Dr. Olavi Hildén and Mr. Olli Järvinen read the manuscript and gave sound criticism. Mrs. Anna Damström checked the English of my manuscript.

Selostus: Varpuspöllön pesintäaikainen ravinto

Tutkimus käsittelee varpuspöllön pesintäaikaista ravintoa ja sen riippuvuutta saaliseläinkannoista Suomessa. Aineisto (*n*=2240 saaliseläintä) kerättiin vv. 1962—72 pääosaksi Pohjois-Hämeestä (62°N, 24°E) 28 pesäpaikalta, joista useimmat sijaitsivat vanhoissa kuusivaltaisissa metsissä. Saalisjätteitä löydettiin sitä enemmän, mitä useammin pesällä käytiin ($r=0.83$, $n=13$). Pesyekoko oli 5.1 ± 1.3 (*S.D.*, $n=16$). Poikaset kuoriutuivat kesäkuun alussa ja myöhäiset poikueet tulivat lentokykyisiksi vasta heinäkuun alussa. Koiras saalistaa hautomis- ja pesäpoikasaikana. Naaras aloittaa saalistamisen vasta pesäpoikasajan lopussa.

Varpuspöllön saalistettavissa olevaa ravintoa tutkittiin lintulaskennoin (koealoja yht. 1058 ha 20 pesäpaikalla) ja pikkunisäkkäiden loukkupyynnein (yht. 12 420 loukku-vrk 18 pesäpaikalla).

Varpuspöllön ravinto koostui päästäisistä (3.5 % saalisyksilöistä), myyristä (50.0 %), hiiristä (0.5 %), lepakoista (0.1 %), sisiliskoista (1.3 %), hyönteisistä (0.3 %) ja linnuista (44.5 %). Biomassan perusteella nisäkkäät muodostivat 60.0 % ja linnut 39.4 % saaliista. Lukuisimmin käytetyt saalislajit olivat metsämyyrä (28.2 %), peltomyyrä (19.7 %), peippo (8.0 %), ja pajulinnun suku (4.4 %). Saaliseläinten keskipaino oli 20.6 g. Painoluokkaan 20—29.9 g kuului 49.3 % saaliista. Painavimmat saalislajit olivat käpytikka, laulurastas ja punakylkirastas.

Myyrien ja lintujen osuus ravinnossa vaihteli huomattavasti vuosittain. Myyrien osuus oli suurempi kuin lintujen vuosina 1962, 1965, 1966 ja 1969. Tämän todetaan aiheutuneen myyrien kannanvaihtelusta, joka Etelä-Suomessa noudatteli 1960-luvulla 3—4 vuoden sykliä siten, että huippuvuosia olivat 1962, 1966 ja 1969. Loukkupyyntien perusteella myyrien osuus saadusta pikkunisäkässaaliista oli suurin 1969 ja pieneni sekä 1970 että 1971.

Lintujen osuus ravinnossa kasvoi ja vastaavasti nisäkkäiden osuus aleni pesimäkauden loppua kohden. Tämä johtui nisäkkäiden saatavuuden heikentymisestä, koska pintakasvillisuuden peittävyys kasvaa, ja lintujen saatavuuden paranemisesta, koska useimpien saalislajien poikaset kuoriutuvat kesäkuun alkupuoliskolla. Myös nuorten lintujen osuus syödyistä linnuista ja lintusaaliin diversiteetti kohosivat pesinnän loppua kohden. Varpuspöllön pesinnän ajoittuminen myöhäiseksi mahdollistaa lajin siirtymisen laajamittaiseen lintuShe ravinnon käyttöön.

Nisäkkäistä päästäisiä valittiin vähemmän kuin niiden osuus pikkunisäkkäistä edellytti. Metsämyyrällä suhde oli päinvastainen. Peltomyyrän valinta ja tarjonta eivät eronneet toisistaan. Linnuista hömötiaisen, punarinnan ja vihervarpusen valinta oli suurempi kuin niiden tarjonta. Peippoa, metsäkirvistä ja kirjosieppoa oli syöty samassa suhteessa kuin niitä oli saatavissa. Pajulinnun suvun valintaosuus oli pienempi kuin tarjontaosuus. Muiden paitsi painoluokkaan 20—29.9 g kuuluvien lintujen valinta ja tarjonta poikkesivat toisistaan. Varpuspöllö saalisti koloissa pesiviä lajeja enemmän kuin niiden tarjontaosuus olisi edellyttänyt. Valitun ja tarjotun lintusaaliin diversiteettien välillä oli merkitsevä positiivinen korrelaatio ($r=0.67$, $n=13$).

Faktorianalyysin avulla todettiin, että valitusta ja tarjotusta lintusaaliista erottuivat melko yhdenmukaiset lajikomponentit. Nisäkkäiden osalta tulos oli sen sijaan päinvastainen: lajikomponentit olivat melko erilaiset. Suoritettujen loukkupyyntien määrä oli faktorianalyysiin liian vähäinen, sillä tarjolla olleen nisäkässaaliin faktoriratkaisussa jäi vaihtelun kokonaisselitysaste alhaiseksi.

Regressioanalyysin avulla selvitettiin erikseen nisäkkäiden ja lintujen osuutta varpuspöllön ravinnossa. Selittäjinä käytettiin nisäkkäiden ja lintujen saatavuutta (tiheyttä maastossa). Tulokset osoittivat, että lintujen saatavuus oli tärkeämpi sekä nisäkkäiden että lintujen osuutta ravinnossa selittävä tekijä kuin nisäkkäiden saatavuus. Tämä tulos voi johtua siitä, että nisäkkäiden tiheyden vaikutus nisäkkäiden valintaan on monimutkaisempaa kuin lintujen tiheyden vaikutus lintujen valintaan. Aineisto oli kuitenkin liian vähäinen tarkempaan analyysiin.

Lopuksi käsitellään varpuspöllön saalistamismekanismia yleisten saalistamisteorioiden pohjalta. Varpuspöllön ravinto riippuu tulosten perusteella saaliseläimien tiheydestä siten, että niiden osuus ravinnossa kasvoi niiden saatavuuden (tiheyden maastossa) kasvaessa. Tutkimuksessa esitetään myös havaintoja etsintätottumuksen syntymiseen viittaavasta saalistuskäyttäytymisestä. Varpuspöllö ei ole ravintospesialisti ja sillä on taipumus sekaravintoon myös hyvinä myyrävuosina. Tämän katsotaan johtuvan siitä, että varpuspöllö on sopeutunut saalistamaan verraten vähätuottoisilla habitaateilla, jolloin paras saalistusstrategia on hyödyntää kaikkia saatavissa olevia saaliseläimiä.

Saaliseläinten alttiuteen joutua varpuspöllön saaliiksi vaikuttavat saalislajien pesimis- ja ruokailuhabitaatit. Varpuspöllö söi koloissa pesiviä lintulajeja enemmän kuin niitä oli tarjolla.

Varpuspöllö on Suomen ainoa pöllölaji, joka käyttää säännöllisesti paljon lintuja ravintonaan. Varpuspöllö on pesinnässään myöhäisin pöllölaji ja se aloittaa haudonnan vasta kun pesye on täysilukuinen. Pesintä ajoittuu siten, että pöllö voi ruokkia poikuettaan lintujen poikasilla. Tämä mahdollistaa poikueiden selviytymisen myös heikkoina myyrävuosina. Varpuspöllö on pesäpaikkauskollinen, mikä on seurausta monipuolisesta ja joustavasta tarjollaolevien saaliskantojen hyväksikäytöstä.

Taulukoissa on esitetty seuraavat tiedot: 1. pesäpaikat ja saalisnäytteiden määrät (*B* = linnusto laskettu, *M* = pikkunisäkäspyyntejä), 2. käyntikerrat, pesäpoikasten määrä, saaliseläinten lukumäärä poikasta kohden sekä saaliin koostumus (nisäkkäitä, lintuja) eräillä pesäpaikoilla, 3. vertailu höyhenten (A) ja luiden (B) perusteella määritettyjen saalislintujen määrästä, 4. saaliin koostumus koko aineiston perusteella, 5. saaliseläinten painojakauma, 6. tärkeimpien saaliseläinten %-osuudet eri vuosina, 7. lintujen, nisäkkäiden ja muiden saaliseläinten suhteellisen osuuden muuttuminen haudontavaiheesta (I) pesäpoikasvaiheen loppupuoliskoon (III), 8—10. nisäkkäiden valinnan ja tarjonnan vertailu, 11—13. lintujen valinnan ja tarjonnan vertailu (myös kuva 1), 14. eri tavoin pesivien lintujen (puussa; koloissa; maassa pesivät metsälajit; maassa pesivät avomaanlajit ja rakennuksiin pesivät) valinnan ja tarjonnan vertailu, 15—16. aineiston faktorianalyysi, 17—19. eri tutkimuksissa saatujen tulosten vertailu. Kuvassa 2 on lintujen ja nisäkkäiden suhteellista osuutta saaliissa verrattu ryhmien tiheyteen maastossa.

References

Allen, J. A. 1974: Further evidence for apostatic selection by wild passerine birds: training experiments. — Heredity 33:361—372.

Artimo, A. 1963: Variations in small mammal populations in dry and damp heath forests of Southern Häme (S. Finland). — Aquilo, Ser. Zool. 2:1—16.

Bengtsson, G. 1962: Sparvuggla och pärluggla häckande i Halland 1961. (Summary: Pygmy Owl (Glaucidium passerinum) and Tengmalm's Owl (Aegolius funereus) breeding in the province of Halland in 1961). — Vår Fågelvärld 21:210—211.

Bergman, S. 1939: Brutbiologische Beobachtungen beim Sperlingskauz Glaucidium passerinum L. — Beitr. Fortpfl. Vögel 15: 181—189.

Bergmann, H-H. & M. Ganso 1965: Zur biologie des Sperlingskauzes (Glaucidium passerinum (L.). — J. Ornithol. 106:255—284.

Cain, A. J. & P. M. Sheppard 1954: Natural selection in Cepaea. — Genetics 39:89—116.

Connell, J. H. 1971: On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. — Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970): 298—312.

Croze, H. 1970: Searching image in carrion crows. — Z. Tierpsychol. 5:1—85.

Curry-Lindahl, K. 1958: Photographic studies of some less familiar birds: Pygmy Owl. — Brit. Birds 54:72—74.

Curry-Lindahl, K. (ed.). 1960: Våra fåglar i Norden. — Stockholm.

Dice, L. R. 1945: Minimum intensities of illumination under which owls can find dead prey by sight. — Amer. Naturalist 79:385—416.

Ehrenroth, B. 1974: Höstrapport från Hammarö fågelstation. — Cirkulär till nordiska fågelstationer.

Elton, C. S. 1927: Animal ecology. — London.

Enemar, A. 1959: On the determination of the size and composition of a passerine bird population during the breeding season. A methodological study. — Vår Fågelvärld Suppl. 2: 1—114.

Ezekiel, M. & K. A. Fox 1959: Methods of correlation and regression analysis. — New York & London.

Haapanen, A. 1965: Bird fauna of the Finnish forests in relation to forest succession. I. — Ann. Zool. Fennici 2:153—196.

Haartman, L. v., O. Hildén, P. Linkola, P. Suomalainen & R. Tenovuo 1963—72: Pohjolan linnut värikuvin. — Helsinki.

Hagen, Y. 1952: Rovfuglene og viltpleien. — Oslo.

Hagen, Y. 1965: The food, population fluctuations and ecology of the Long-eared Owl (Asio otus (L.) in Norway. — Meddelelser fra Statens Viltundersökelser 2:3—38.

Hagen, Y. 1969: Norske undersökelser over avkomproduksjonen hos rovfugler og ugler sett i relasjon til smågnagerbestandens vekslinger. — Fauna 22:73—126.

Harman, H. H. 1960: Modern factor analysis. — Chicago.

Hildén, O. & P. Linkola 1962: Suuri lintukirja. — Helsinki.

Hildén, O. 1975: Vaelluslintujen esiintyminen lintuasemilla. (Summary: Occurrence of irregular migrants at Finnish bird stations in 1974). — Lintumies 10:61—69.

Holling, C. S. 1965: The functional response of predators to prey density and its role in mimicry and population regulation. — Mem. Entomol. Soc. Can. 45:1—60.

Jansson, E. 1964: Anteckningar rörande häckande sparvuggla (Glaucidium passerinum). (Summary: Notes on a breeding pair of Pygmy Owls (Glaucidium passerinum) in Central Sweden (approx. 60°10'N., 16°10'E.). — Vår Fågelvärld 23:209—222.

Jussila, E. & H. Mikkola 1973: Varpuspöllön pesinnästä, pesintäaikaisesta käyttäytymisestä ja ravinnosta Lahden ympäristössä 1966—73. — Päijät-Hämeen Linnut 4:73—80.

Järvinen, O. 1974: Valitsevatko lintumme runsaimpia saalistyyppejä? (Summary: Do our birds choose the most abundant food?). — Lintumies 9:19—24.

Järvinen, O. & R. A. Väisänen 1975: Estimating relative densities of breeding birds by the line transect method. — Oikos 26:316—322.

Kellomäki, E. 1966: Havaintoja varpuspöllöstä Suomenselän alueella. — Lintumies 2:39—43.

Kellomäki, E. 1969: Varpuspöllön (Glaucidium passerinum) ravintobiologiasta Etelä- ja Keski-Suomessa 1960-luvulla. — Manuscript, Dept. Zoology, Univ. Turku.

Kellomäki, E. 1970: Havaintoja varpuspöllöstä I, II. — Suomenselän Linnut 5:64—70, 99—102.

Klaus, S., F. Vogel & J. Wiesner 1965: Ein Beitrag zur Biologie des Sperlingskauzes. — Zool. Abhandl. 28:165—204.

Knobloch, H. 1966: Sperlingskauzes (Glaucidium passerinum) erbeutet Eidechse. — Vogelwelt 87:118—119.

Krebs, C. J. 1972: Ecology. The experimental analysis of distribution and abundance. — New York.

Lack, D. 1954: The natural regulation of animal numbers. — Oxford.

Lack, D. 1968: Ecological adaptations for breeding in birds. — London.

Lindberg, P. 1966: Invasionen av sparvuggla (Glaucidium passerinum) i södra Skandinavien 1963—64. (Summary: Irruption of the Pygmy Owl (Glaucidium passerinum) into Southern Scandinavia 1963—64). — Vår Fågelvärld 25:106—142.

Lindblad, J. 1967: I ugglemarker. — Stockholm.

Linkola, P. & A. Myllymäki 1969: Der Einfluss der Kleinsäugerfluktuationen auf das Brüten einiger kleinsäugerfressenden Vögel in südlichen Mittelfinnland 1952—66. — Ornis Fennica 46:45—78.

Lund, H. M.-K. 1951: A contribution to the knowledge of the biology of Glaucidium passerinum in the breeding season. — Nytt Mag. for Naturvidenskapene 88:247—262.

MacArthur, R. H. 1972: Geographical ecology. Patterns in the distribution of species. — New York.

MacArthur, R. H. & E. R. Pianka 1966: On optimal use of a patchy environment. — Amer. Naturalist 100:603—609.

Markkanen, T. 1964: Sosiaaliset ja psykologiset faktorit väkijuomien käytön selittäjinä. — Alkoholipoliittisen tutkimuslaitoksen tutkimuslaitoksen tutkimusseloste 12. Helsinki.

Merikallio, E. 1946: Über regionale Verbreitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. I. — Ann. Zool. Soc. 'Vanamo' 12: 1—140.

Mikkola, H. 1970: On the activity and food of the Pygmy Owl Glaucidium passerinum during breeding. — Ornis Fennica 47:10—14.

Mikkola, H. & E. Jussila 1974: Varpuspöllön pesintäaikaisesta ravinnosta Lahden ympäristössä 1971—73. — Päijät-Hämeen Linnut 5: 19—21.

Murdoch, W. W. 1969: Switching in general predators: Experiments on predator specificity and stability of prey populations. — Ecol. Monogr. 39:335—354.

Mueller, H. C. 1971: Oddity and specific searching image more important than conspicuousness in prey selection. — Nature 233:345—346.

Mäkelä, J. 1968: Puunkorjuun tuottavuuteen vaikuttavat tekijät. (Summary: Factors affecting logging productivity in farm forests.) — Acta Forestalia Fennica 85:1—116.

März, R. 1964: Zur Ernährung des Sperlingskauzes. — Vogelwelt 85:33—38.

Nordberg, S. 1935: Zur Ernährungsbiologie des Sperbers (Accipiter nisus nisus L.) während der Zugzeit. — Ornis Fennica 12:65—68.

Norberg, R. Å. 1970: Hunting technique of Tengmalm's Owl Aegolius funereus (L.). — Ornis Scandinavica 1:51—64.

Palmgren, P. 1930: Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands mit besonderer Berücksichtigung Ålands. — Acta Zool. Fennica 7:1—218.

PASANEN, S. & S. SULKAVA 1971: On the nutritional biology of the Roughlegged Buzzard, Buteo lagopus lagopus Brünn., in Finnish Lapland. — Aquilo Ser. Zool. 12:53—63.

RAPPORT, D. J. 1971: An optimizing model of food selection. — Amer. Naturalist 105: 575—587.

RETTMEYER, N. 1925: Vom Brutgeschäft des Sperlingskauzes. — Mitt. Vogelwelt 2:136.

ROOS, J.-P. 1971: Monimuuttujamenetelmien perusteet. — Sosiaalipolitiikan laitoksen tutkimuksia 1/1971. Helsinki.

ROUGHGARDEN, J. & M. FELDMAN 1975: Species packing and predation pressure. — Ecology 56:489—492.

ROYAMA, T. 1970: Factors governing the hunting behaviour and selection of food by the Great Tit (Parus major L.). — J. Anim. Ecol. 39: 619—668.

SCHERZINGER, W. 1970: Zum Aktionssystem des Sperlingskauzes (Glaucidium passerinum, L.). — Zoologica 41:1—130.

SCHNURRE, O. 1942: Ein Beitrag zur Biologie des Sperlingskauzes. — Beitr. Fortpfl. Vögel 18: 45—51.

SCHOENER, T. W. 1968: Sizes of feeding territories among birds. — Ecology 49:123—41.

SCHOENER, T. W. 1971: Theory of feeding strategies. — Ann. Rev. Ecol. Syst. 2:369—404.

SEIERSTAD, A., S. SEIERSTAD & I. MYSTERUD 1960: Et lite bidrag til kjennskapet til spurveugla, Glaucidium passerinum (L.). (Summary: A contribution to the knowledge of the Pygmy Owl, Glaucidium passerinum (L.). — Sterna 4:153—168.

SIIVONEN, L. 1967: Pohjolan nisäkkäät. — Helsinki.

SLOBODKIN, L. B. 1961: Growth and regulation of animal populations. — New York.

SONERUD, G. A., A. MJELDE & K. PRESTRUD 1972: Spurveuglehekking i fugleholk. (Summary: Breeding of Pygmy Owl in nest box). — Sterna 11:1—12.

SOUTHERN, H. N. 1954: Tawny Owls and their prey. — Ibis 96:384—410.

SPARKS, J. 1975: Pöllöt. In: Eläinten maailma, Pp. 1507—1513. — Helsinki.

SPARROWE, R. D. 1972: Prey-catching behaviour in the Sparrow Hawk. — J. Wildl. Mgmt. 36: 297—308.

SULKAVA, P. 1964: Varpushaukan pesimisaikaisesta käyttäytymisestä ja ravinnosta. — Suomen Riista 17:93—105.

SULKAVA, P. 1972: Varpushaukan, Accipiter nisus (L.), pesimisbiologiasta ja pesimisaikaisesta ravinnosta. — Manuscript, Dept. Zoology, Univ. Helsinki.

SULKAVA, P. & S. SULKAVA 1971: Die nistzeitliche Nahrung Rauhfusskauzes, Aegolius funereus, in Finnland 1958—67. — Ornis Fennica 48:117—124.

SULKAVA, S. 1964: Zur Nahrungsbiologie des habichts, Accipiter a. gentilis (L.). — Aquilo Ser. Zool. 3:1—103.

SULKAVA, S. 1966: Huuhkajan pesimisaikaisesta ravinnosta Suomessa. — Suomen Riista 18: 145—156.

SULKAVA, S. & P. SULKAVA 1967: On the small-mammal fauna of Southern Ostrobothia. — Aquilo Ser. Zool. 5:18—29.

SUOMUS, H. 1952: On the food of the Buzzard. — Suomen Riista 8:36—41.

THURSTONE, L. 1961: Multiple factor analysis. — Chicago.

TINBERGEN, L. 1946: Sperver als Roofvijand van Zangvogels. (Summary: The Sparrow-Hawk (Accipiter nisus L.) as a predator of passerine birds). — Ardea 34:1—123.

TINBERGEN, L. 1960: The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. — Arch. Neerl. Zool. 13:265—343.

UTTENDÖRFER, O. 1939: Die Ernährung der deutschen Raubvögel und Eulen. — Neudamm.

UTTENDÖRFER, O. 1952: Neue Ergebnisse über die Ernährung der Greifvögel und Eulen. — Stuttgart.

Received October 1976, revised December 1976