

## Summer food of the Pygmy Owl *Glaucidium passerinum* in Białowieża National Park, Poland

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Analysis of 52 pellets of the Pygmy owl *Glaucidium passerinum* (L.) collected during the summer in the primeval forests of Białowieża National Park (BNP) in eastern Poland revealed 118 prey items and showed that the diet of owls was composed of birds (69% of prey number, 73% of prey biomass) and small rodents (31% of prey number, 27% of biomass). Of the two most numerous rodents, the bank vole *Clethrionomys glareolus* was captured more and the yellow-necked mouse *Apodemus flavicollis* less than would have been expected from their availability as measured by trapping. The most numerous avian prey of the Pygmy owl were the Great Tit *Parus major*, the Robin *Erithacus rubecula*, the Chaffinch *Fringilla coelebs*, and *Carduelis* spp. A comparison with the community of breeding birds revealed that finches *Carduelis* spp. and tits were selected by owls. A literature review on the Pygmy owl's preying preferences on passerines showed that this predator had clear seasonal, but little geographic variation in its preferences for bird prey within Europe.

### 1. Introduction

The Pygmy owl *Glaucidium passerinum* is very rare in Poland and restricted in its breeding range to the northeastern (lowland) and southern (mountainous) parts of the country (Tomiałojć 1990). In this paper, we present the diet composition of one Pygmy owl pair with young during the breeding season in Białowieża National Park (eastern Poland), and we compare it to the availability of birds and forest rodents. We relate our data to literature to find any geographic pattern to the Pygmy owl's specialisation in some bird species. The study was part of a long-term project

on predator-prey relationships in the pristine forests of Białowieża National Park (e.g. Jędrzejewski & Jędrzejewska 1993).

### 2. Study area, methods and material

Białowieża National Park (47.5 km<sup>2</sup>, 52°45'E, 23°55'N) protects the last remnants of primeval forests typical of the lowlands of central and eastern Europe. The entire Park is strictly protected and shows few signs of human activity. The tree stands are dominated by oak *Quercus robur*, hornbeam *Carpinus betulus*, spruce *Picea*

*abies*, pine *Pinus sylvestris* and other tree species (details in Faliński 1986).

Pellets (n = 52) of Pygmy owls were collected in the eastern part of the Park in mixed coniferous (spruce-pine) forests, specifically around the cavity (in a pine tree) of one Pygmy owl family frequently observed in the second half of June 1989. The pellets represented late spring and early summer food, and were analysed by a standard procedure (Raczyński & Ruprecht 1974). Prey were identified by bony remains (Pucek 1984) and by the microscopic analysis of hair (Dziurdzik 1973, Debrot 1982). Using a collection of comparative material, we identified birds by feather remains. The number of prey specimens in each pellet were counted by skeleton remains (Raczyński & Ruprecht 1974), or it was assumed to be one specimen, if the prey was detected by hair or feathers. For estimating the biomass con-

sumed by owls, the mean numbers of individuals of each prey in one pellet were multiplied by the mean body mass of that prey (after Sokołowski 1979, Pucek 1984, März 1987, and authors' own material). Then, the percentage of biomass of each prey in an average pellet was calculated.

To assess the owls' selection of particular species of rodents and birds, Ivlev's electivity index (D) was calculated, as modified by Jacobs (1974):  $D = (r-p)/(r+p-2rp)$ , where r denotes the fraction of a given species of rodent/bird in the total number of rodents/birds identified from pellets, and p - the fraction of a species in the rodent/bird community. D varies from -1 (negative selection) to 0 (catching proportional to abundance), to 1 (positive selection).

Data on rodents came from the long-term study on rodent population dynamics in BNP (Pucek et al. 1993). Removal trapping was conducted in the spring of 1989 (21 days from 15 April) and in the summer of 1989 (21 days from 1 July) in the deciduous forest on a 5 × 10 m grid of 50 funnel-traps, a line of 50 livetraps and a line of 50 snaptraps (traps placed at 10-m intervals).

Table 1. Diet composition of the Pygmy owl during the breeding season (1989) in Białowieża National Park, based on the analysis of 52 pellets. N denotes number of prey items, whereas % prey is percent of the total prey number, % Occ is percent occurrence, i.e. percent pellets containing a given prey, and %Bio is percent consumed biomass.

Prey item	N	% prey	% Occ	% Bio
<i>Clethrionomys glareolus</i>	28	23.8	53.8	18.8
<i>Apodemus flavicollis</i>	5	4.3	1.9	1.2
<i>Sicista betulina</i>	2	1.7	3.8	0.6
<i>Microtus</i> spp.	1	0.8	1.9	0.9
<i>Pitymys subterraneus</i>	1	0.8	1.9	0.7
Total rodents	37	31.4	71.1	27.1
<i>Parus major</i>	11	9.3	21.1	7.8
<i>Erithacus rubecula</i>	11	9.3	21.1	7.4
<i>Fringilla coelebs</i>	10	8.5	19.2	9.9
<i>Parus caeruleus</i>	4	3.4	7.7	1.8
<i>Carduelis spinus</i>	4	3.4	7.7	2.2
<i>Carduelis</i> undet.	4	3.4	7.7	3.9
<i>Dendrocopos</i> sp.	2	1.7	3.8	6.3
<i>Pyrrhula pyrrhula</i>	2	1.7	3.8	2.4
<i>Dendrocopos</i> or <i>Pyrrhula</i>	3	2.6	5.8	6.5
<i>Certhia familiaris</i>	2	1.7	3.8	0.7
<i>Sitta europaea</i>	1	0.8	1.9	1.0
<i>Serinus serinus</i>	1	0.8	1.9	0.5
<i>Ficedula</i> spp.	1	0.8	1.9	0.5
<i>Regulus regulus</i>	1	0.8	1.9	0.2
Undetermined birds	24	20.4	46.1	21.8
Total birds	81	68.6	100.0	72.9

### 3. Results

Birds composed 69% of prey specimens and 73% of biomass consumed by owls. Small rodents made up the remaining part of the diet (Table 1). Mean biomass consumed per pellet was 48.7 g.

Table 2. Proportions of rodents available in the forest and chosen by Pygmy owls in Białowieża National Park, in 1989 (G = 13.93, df = 1, p < 0.001, G-test calculated on percentages). Index of rodent abundance: N rodents/100 trapnights. Rodents in owl pellets = number of rodent specimens recovered from pellets. D = selectivity index (after Jacobs 1974).

Available/chosen	<i>Apodemus flavicollis</i>	<i>Clethrionomys glareolus</i>
Trapped in April/May	0.22	0.95
Trapped in July	1.78	2.29
Mean availability	1.0 (38%)	1.62 (62%)
Found in owl pellets	5 (15%)	28 (85%)
Selectivity index D	-0.55	0.55

Of the two most numerous forest rodents, the bank vole *Clethrionomys glareolus* and the yellow-necked mouse *Apodemus flavicollis*, Pygmy owls captured voles more and mice less often than would have been expected from their availability (Table 2). Eighty-one birds were found in owl pellets, and 57 of them (70%) were identified as to species or genus (Table 1). Their species composition was compared to that of the bird community censused in 1989 in the spruce-pine forest plot located in the same area where the Pygmy owl pellets were collected (unpubl. data of Dr. L. Tomiałojć & Dr. T. Wesołowski, part of a long-term bird censusing in BNP; see also Tomiałojć et al. [1984], Tomiałojć & Wesołowski [1990]). Pygmy owls captured the most numerous birds: Chaffinch *Fringilla coelebs*, Robin *Erithacus rubecula*, and Great Tit *Parus major* (Table 3). The owls significantly preferred tits and finches *Carduelis* spp., whereas the Chaffinch and the Goldcrest *Regulus regulus* were taken significantly less often than would have been expected from their availability. Ground-nesting warblers *Phylloscopus* spp., which were abundant in the area, were not recorded as the owls' prey (Table 3).

#### 4. Discussion

In our study, birds accounted for 69% of prey items captured during the breeding season. In the Belarussian part of the Białowieża Forest, Golodushko & Samusenko (1961) found that birds composed 18.5% of prey specimens in spring-summer and 24.3% in autumn-winter, whereas the most numerous prey were shrews (40% of prey in summer and 60% in winter). In the predominantly deciduous forests of Białowieża, the Pygmy owl, a boreal species, is one of the few resident predators that feed mainly on birds (cf. Jędrzejewski et al. 1989, Jędrzejewski & Jędrzejewska 1993).

The food composition of Pygmy owls in Białowieża, with the predominance of birds and small rodents, seems to be typical for the entire European range of Pygmy owls (review in Mikkola 1983). In our study, the bank vole was the most common small rodent in the Pygmy owl's diet, and was taken more than expected. Other studies have also shown that the bank vole was selectively chosen by owls from the available rodent community (Golodushko & Samusenko 1961, Scherzinger 1974, Kellomäki 1977).

Table 3. The Pygmy owl's choice of bird species/genera from regional bird communities: in Poland (Białowieża Natl. Park; data on bird community in 1989 from L. Tomiałojć and T. Wesołowski unpubl., plots NW and NE averaged; see Tomiałojć et al. 1984), in S Finland (from Kellomäki 1977; Tab. 11), both in breeding season, and in SW Sweden (calculated as means from Ekman 1986; Tab. 2) - in winter. Owls = percent of a given species/genus in the total number of birds killed by owls; F = percent of a given species/genus in the community. D = Ivlev's selectivity index (after Jacobs 1974). Statistical comparison of per cent available vs. captured by owls: \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001 (G-test for homogeneity of percentages; calculated only for data from Białowieża, E Poland).

Species/genus	E Poland			S Finland			SW Sweden		
	Owls	F	D	Owls	F	D	Owls	F	D
<i>Fringilla coelebs</i>	12.3*	27.5	-0.46	19.8	22.7	-0.09	-	-	-
<i>Erithacus rubecula</i>	13.6	14.7	-0.04	9.7	5.1	0.33	-	-	-
<i>Parus</i> spp.	18.5*	8.0	0.45	11.0	7.3	0.23	45.2	37.7	0.15
<i>Carduelis</i> spp.	9.9***	0	1	9.7	6.1	0.25	4.7	9.8	-0.37
<i>Pyrrhula pyrrhula</i>	3.7	1.2	0.52	3.0	1.4	0.37	1.9	4.5	-0.42
<i>Sitta europaea</i>	1.2	0.7	0.26	-	-	-	-	-	-
<i>Serinus serinus</i>	1.2	0	1	-	-	-	-	-	-
<i>Dendrocopos</i> spp.	3.7	1.2	0.52	-	-	-	-	-	-
<i>Regulus regulus</i>	1.2**	11.0	-0.82	2.6	4.1	-0.23	42.3	34.9	0.16
<i>Certhia familiaris</i>	2.5	4.5	-0.29	2.6	2.5	0	3.5	4.1	-0.08
<i>Ficedula</i> spp.	1.2	0.5	0.41	4.3	3.5	0.11	-	-	-
<i>Phylloscopus</i> spp.	0***	17.7	-1	10.8	22.0	-0.40	-	-	-
<i>Loxia curvirostra</i>	-	-	-	-	-	-	1.9	8.9	-0.67

While most resident predators in temperate Europe extensively feed on rodents year-round and particularly so in winter (Erlinge et al. 1983, Jędrzejewski & Jędrzejewska 1993), a heavy reliance on birds seems to be a specific feature of the Pygmy owl. In boreal and nemoral forests of Europe, the availability of birds exhibits seasonal variation due to a predominance of migrants in bird communities. In Białowieża National Park, the spring density of breeding birds was 603–1016 pairs/km<sup>2</sup> in deciduous forests, and 343–397 pairs/km<sup>2</sup> in coniferous forests (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990). Regular winter censuses were not conducted. However, the density of resident birds (wintering in the area, about 40% of all species) was 80–210 pairs/km<sup>2</sup>, i.e. about 20% of the spring density. Deciduous (oak-dominated) forests in southern Sweden supported 782–1445 breeding pairs/km<sup>2</sup> (Nilsson 1979, Nilsson & Liberg 1984). In the boreal virgin forests of northern Finland

(located approximately on the northern border of the Pygmy owl range, cf. maps in Mikkola [1983] and Virkkala [1989]), the density of breeding birds was 60–94 pairs/km<sup>2</sup>, and migratory species composed 90% of the community (Virkkala 1989). Thus, the winter abundance of birds in the mature forests of Europe may be only 10–20% of the bird abundance in spring and summer. Despite such many-fold seasonal changes in the availability of birds, their share in the Pygmy owl diet remains fairly constant year round. Mikkola (1983), who reviewed Finnish data on the Pygmy owl's food, found that birds composed, on an average, 44% of prey specimens during the breeding season, and 32% at other times. In Ekman's study in southwest Sweden (Ekman 1986), the winter share of birds in the Pygmy owl's diet was 51% of prey specimens.

The Chaffinch and the Robin are among the most numerous breeding (migratory) passerines in the nemoral and mixed forests of Europe

Table 4. Percent contribution of four bird species/genera to the total (identified and non identified) avian prey of Pygmy owls in Europe. Sources: (1) this study; (2) März (1964); (3) Scherzinger (1974); (4) Klaus et al. (1965); (5) Schönn (1978); (6) Bergmann & Ganso (1965); (7) and (10) Golodushko & Samusenko (1961); (8), (11) and (12) Likhachev (1971); (9) Kellomäki (1977); (13) Ekman (1986); (14) Solheim (1984).

Locality	<i>Parus</i> spp.	<i>Fringilla</i> <i>coelebs</i>	<i>Erithacus</i> <i>rubecula</i>	<i>Regulus</i> spp.	<i>Carduelis</i> spp.
Spring-summer (breeding season)					
1. E Poland	18.5	12.3	13.6	1.2	9.9
2. S Germany	16.2	15.4	3.1	10.1	12.3
3. S Germany	19.0	8.8	7.3	9.5	8.8
4. SE Germany	17.2	12.9	1.4	4.3	0
5. SE Germany	13.8	28.9	0.8	5.8	6.3
6. Austria	20.3	11.6	10.1	5.8	0
7. W Belarus	65.0	0	5.0	0	0
8. Russia (Moscow)	34.4	0	6.2	15.6	3.1
9. Finland	8.4	18.0	8.4	2.1	11.9
Mean	23.6	12.0	6.2	6.0	5.8
(SD)	(17.0)	(8.9)	(4.2)	(5.0)	(5.2)
Autumn-winter					
10. W Belarus	20.0	0	0	17.1	0
11. Russia (Moscow)	25.6	0	0	37.2	2.3
12. Russia (Oka r.)	50.0	0	0	15.4	0
13. SW Sweden	40.3	0	1.1	40.3	6.9
14. SE Norway	15.7	0	0	5.9	68.6
Mean	30.3	0	0.2	23.2	15.6
(SD)	(14.4)	(0)	(0.5)	(14.9)	(29.8)

(Golodushko & Danilyuk 1961, Głowaciński 1975, Kellomäki 1977, Nilsson and Liberg 1984, Tomiałoć et al. 1984). Thus, most probably, this is the reason for their high abundance among owls' prey. Tits, *Carduelis* finches, and the Goldcrest were reported as forming a small share in the breeding bird community. In winter, however, tits and goldcrests were the most numerous birds in the coniferous forests of Białowieża National Park (28% and 18% of observed species, respectively; Wołk 1985) and in southwest Sweden (38% and 35% of all observed birds, respectively; Ekman 1986).

Only two studies done during the breeding season (Kellomäki 1977, and this paper) and one study conducted in winter (Ekman 1986), provided an opportunity to quantify the Pygmy owl's selection of birds from the available community (Table 3). Tits *Parus* spp. (predominantly *P. major* and *P. ater* in Central Europe and *P. montanus* and *P. ater* in northern Europe) were preferred prey in all localities in both seasons. This suggests, that the Pygmy owl and tits form a mutual predator-prey 'duet' with specific anti-predatory behaviours of tits against the Pygmy owl (Curio et al. 1983, Curio & Regelmann 1985). The Goldcrest was rarely taken during the breeding season, but heavily preyed upon and positively selected in winter (Table 3).

The indices of the owls' selection of 9 passerine species/genera during the breeding season in Poland and Finland (Table 3) were positively correlated (Kendall's tau = 0.78,  $p < 0.01$ ,  $n = 9$ ). The indices of summer selection of birds, in both Poland and Finland, showed a tendency to negatively correlate with those in winter (E Poland-SW Sweden: tau = -0.60,  $n = 5$ ,  $p = 0.14$ ; S Finland-SW Sweden: tau = -0.80,  $n = 5$ ,  $p = 0.05$ ).

This indicates that the owls' selection of bird prey changes seasonally, but has little geographic variation. In fact, the review of 9 studies conducted in summer and 5 studies from winter (Table 4) corroborated this view: tits were an important and stable component of the owl's diet year round, the migratory Chaffinch and the Robin played a role in summer only, whereas the share of the Goldcrest increased from an average of 6% of all birds in summer to 23% in winter. It is also consistent with the findings of Suhonen et

al. (1993) who reported that Goldcrests were selectively taken by owls from winter flocks of Paridae.

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### Selostus: Varpuspöllön kesäravinto

Kirjoittajat analysoivat 52 Itä-Puolasta, Białowieżan kansallispuistosta kerättyä varpuspöllön oksennuspalloa. Linnut muodostivat 69% saaliista. Loput olivat pikkunisäkkäitä. Varpuspöllöt pyydystivät metsämyyriä useammin kuin niiden runsauden perusteella oli odotettavissa. Metsähiiret näyttivät välttävän varpuspöllön saalistuksen. Varpuspöllöt näyttivät pyydystävän erityisen mielellään *Carduelis*-suvun lajeja. Vertailu kirjallisuuteen osoitti, ettei varpuspöllön saalisvalikoimassa ole suurta maantieteellistä vaihtelua.

### References

- Bergmann, H.-H. & Ganso, M. 1965: Zur biologie des Sperlingskauzes (*Glaucidium passerinum* (L.)). — *J. Ornithol.* 106:255–284.
- Curio, E., Klump, G. & Regelmann, K. 1983: An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? — *Oecologia* 60:83–88.
- Curio, E. & Regelmann, K. 1985. The behavioural dynamics of Great Tits (*Parus major*) approaching a predator. — *Z. Tierpsych.* 69:3–18.
- Debrot, S. 1982: Atlas des poils de mammifères d'Europe. — Université de Neuchâtel.
- Dziurdzik, B. 1973: Key to the identification of hairs of mammals from Poland (In Polish with English summary). — *Acta zool. crac.* 18:73–91.
- Ekman, J. 1986: Tree use and predator vulnerability of wintering passerines. — *Ornis Scand.* 17:261–267.
- Erlinge, S., Goransson, G., Hansson, L., Hogstedt, G., Liberg, O., Nilsson, I. N., Nilsson T., von Schantz, T. & Sylven, M. 1983: Predation as a regulating factor on small rodent populations in southern Sweden. — *Oikos* 40:36–52.

- Faliński, J. B. 1986: Vegetation dynamics in temperate lowland primeval forest. — Dr. W. Junk Publishers, Dordrecht.
- Głowaciński, Z. 1975: Succession of bird communities in the Niepołomice Forest (southern Poland). — *Ekol. pol.* 23:231–263.
- Golodushko, B. Z. & Danilyuk, I. I. 1961: Chislennost' i stacialnoe raspredelenie vorob'inykh ptic Belovezhskoi Pushchi [Numbers and spatial distribution of passerine birds in Belovezha Primeval Forest]. — In: Fauna i ekologiya nazemnykh pozvonochnykh Belorussi [Fauna and ecology of terrestrial vertebrates of Belarus] (in Russian). 133–142. Izd. Min. vyssh., sred. i prof. obraz. BSSR, Minsk.
- Golodushko, B. Z. & Samusenko, E. G. 1961: Pitanie vorob'inogo sychika v Belovezhskoi Pushche [Food of the pygmy owl in Belovezha Primeval Forest] (in Russian). — Trudy IV Pribaltiiskoi ornitologicheskoi konferencii, Riga. 135–140.
- Jacobs, J. 1974: Quantitative measurements of food selection; a modification of the forage ratio and Ivlev's Electivity index. — *Oecologia* 14:413–417.
- Jędrzejewski, W. & Jędrzejewska, B. 1993: Predation on rodents in the Białowieża primeval forest, Poland. — *Ecography* 16:47–64.
- Jędrzejewski, W., Jędrzejewska, B. & Szymura, A. 1989: Food niche overlaps in a winter community of predators in the Białowieża Primeval Forest, Poland. — *Acta Theriol.* 34: 487–496.
- Kellomäki, E. 1977: Food of the Pygmy owl *Glaucidium passerinum* in the breeding season. — *Ornis Fennica* 54:1–29.
- Klaus, S., Vogel, F. & Wiesner, J. 1965: Ein Beitrag zur Biologie des Sperlingskauzes. — *Zool. Abhandl.* 28:165–204.
- Likhachev, G. N. 1971: Materialy po pitaniyu vorob'inogo sychika [Data on food of the Pygmy owl] (in Russian). — Trudy prioksko-terrasnego gos. zapovednika 5:135–145.
- März, R. 1964: Zur Ernährung des Sperlingskauzes. — *Vogelwelt* 85:33–38.
- 1987: *Gewoll- und Ruffungskunde*. — Akademie-Verlag, Berlin.
- Mikkola, H. 1983: Owls of Europe. — T. & A. D. Poyser, Calton.
- Nilsson, S. G. 1979: Density and species richness of some forest bird communities in South Sweden. — *Oikos* 33:392–401.
- Nilsson, I. N. & Liberg, O. 1984: Bird communities in a three oak-dominated woodlands in southern Sweden. — *Ann. Zool. Fennici* 21:379–381.
- Pucek, Z. (ed.) 1984: *Klucz do oznaczania ssaków Polski*. [Key to identification of Polish mammals] (in Polish). — PWN-Polish Scientific Publishers, Warszawa.
- Pucek, Z., Jędrzejewski, W. Jędrzejewska, B. & Pucek, M. 1993: Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. — *Acta Theriol.* 38:199–232.
- Raczyński, J. & Ruprecht, A. L. 1974: The effect of digestion on the osteological composition of owl pellets. — *Acta orn.* 14:25–38.
- Scherzinger, W. 1974: Zur Ökologie des Sperlingskauzes *Glaucidium passerinum* im Nationalpark Bayerischer Wald. — *Anzeiger der Ornithologischen Gesellschaft in Bayern* 13: 121–156.
- Schönn, S. 1978: Der Sperlingskauz *Glaucidium passerinum passerinum*. — A. Ziemsen Verlag, Wittenberg Lutherstadt.
- Sokołowski, J. 1979: *Ptaki Polski* [Birds of Poland] (in Polish). — Wydawnictwa Szkolne i Pedagogiczne, Warszawa.
- Solheim, R. 1984: Caching behaviour, prey choice and surplus killing by Pygmy Owls *Glaucidium passerinum* during winter, a functional response of a generalist predator. — *Ann. Zool. Fennici* 21:301–308.
- Suhonen, J., Halonen, M. & Mappes, T. 1993: Predation risk and the organization of the *Parus* guild. — *Oikos* 66:94–100.
- Tomiałojć, L. 1990: The birds of Poland, their distribution and abundance (in Polish with English summary). — PWN-Polish Scientific Publishers, Warszawa.
- Tomiałojć, L. & Wesołowski, T. 1990: Bird communities of the primaevial temperate forest of Białowieża, Poland. — In: Keast, A. (ed.), *Biogeography and ecology of forest bird communities*: 141–165. SPB Academic Publishing bv, The Hague, The Netherlands.
- Tomiałojć, L., Wesołowski, T. & Wałankiewicz, W. 1984: Breeding bird community of a primaevial temperate forest (Białowieża National Park, Poland). — *Acta orn.* 20:241–310.
- Virkkala, R. 1989: Short-term fluctuations of bird communities and populations in virgin and managed forests in Northern Finland. — *Ann. Zool. Fennici* 26:277–285.
- Wołk, K. 1985: Occurrence of birds in the annual cycle versus the structure of forest in the Białowieża National Park (in Polish with English summary). — *Parki Narodowe i Rezerwaty Przyrody* 6:57–75.