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Seasonal variation in the diet of the little owl, *Athene noctua* in agricultural landscape of Central Poland

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Abstract. We studied the diet of the little owl, *Athene noctua*, in an agricultural lands of Central Poland. In total, 642 pellets were collected in the years 1995-1997 and 3090 prey items were identified. In the diet, Coleoptera dominated by number (62.4 %), but vertebrates dominated in terms of biomass (98%). The most frequently found vertebrate prey was the common vole, *Microtus arvalis*, and Muridae. Birds and amphibians were found in pellets only occasionally, mostly in summer. Contribution to the main prey categories of little owl diet differed seasonally: mammals were preyed upon more frequently in winter, while invertebrates in autumn. Redundancy analysis (RDA) revealed preferences of little owl to common voles in winter and summer, house mouse (*Mus musculus*) in spring, and *Apodemus* mice in autumn-winter periods. Share of particular invertebrate groups in the diet was not random over the year. Carabid beetles were preyed upon all year round and together with cantharid larvae made up an important component of the winter diet. The high proportion of invertebrates as well as the presence of synantropic rodents in the winter diet suggests that in the winter, little owl utilise buildings as hunting sites. From the analysed pellets we noted that a high frequency of lumbricid earthworms, was present in up to 53% of the pellets in the autumn. Assuming different numbers and individual body mass of an earthworm, we estimated that the contribution of lumbricids may reach from 5 to 40 % of the total prey biomass consumed by little owl in autumn.

Keywords: predation on invertebrates, insects, raptors, voles, earthworms, Lumbricidae.

Introduction

Over the last several decades, the little owl (*Athene noctua*) has been on the decline in many European countries, especially in the western part of its range (Manez 1994, Génot & Nieuwenhuyse 2002, Żmihorski et al. 2006, Salek & Schropfer 2008, Sunde et al. 2009). However, the ecological mechanisms responsible for the decline remain poorly understood and several hypotheses have been proposed as an explanation of this trend. Large-scaled habitat transformation, food limitation and unsuitable weather conditions are taken into account but the effects of several other factors should be considered (Schaub et al. 2006, Sunde et al. 2009, Żmihorski et al. 2009, Salek et al. 2010, Le Gouar et al. 2011). Moreover, the majority of the recent studies concerning the issue was conducted in Western Europe (Denmark, Netherlands, Portugal, Spain etc.), therefore reliable implementation of the mechanisms described in these studies to populations from Central and Eastern Europe is questionable (see Tryjanowski et al. 2011 and references therein). Thus, the issue of long-term decline of the little owl in Central and Eastern Europe needs further investigations.

One of the hypothesis concerning drivers of the population changes is food limitation during the breeding period (Thorup et al. 2010). The species is sedentary, with short dispersal distances, thus the changes in the production of young or in survival are likely to cause the decline of populations. Experimental food supplementation to breeding pairs increased the number of fledged young, supporting the hypothesis on the role of food abundance during the breeding (Thorup et al. 2010). In general, changes in agrocenoses management techniques may lead to reduction of abundance of arthropods and small mammals (Morris 2000) which constitute the main prey type of the little owl (Van Nieuwenhuyse et al. 2008). Moreover, farmland habitat transformations e.g. changes in vegetation structure, can further reduce the availability of prey irrespective to their abundance (Hoste-Danyłow et al. 2010). To address the role of food limitation in the population decline of the little owl, fundamental knowledge on the foraging ecology and diet is necessary. Unfortu-

nately, the diet of the little owl has not been investigated to a sufficient extent within the breeding range of this species. Although extensive research has been carried out in Europe, the majority of studies were restricted to the southern and western part of the continent (e.g. Delibes et al. 1983, Angelici et al. 1997, Manganaro et al. 1999). In the case of most Central and Eastern European countries the number of studies is much lower (but see e.g. Kitowski & Pawlega 2010 and references within). Consequently, in many regions the diet of the little owl remains unexplored. For instance, in Poland data on the little owl's diet is scarce and mostly limited to the breeding period (Romanowski 1988, Grzywaczewski et al. 2006) and no comprehensive review has yet been published. In addition, there are high discrepancies in respect to the contribution of earthworms to the diet of little owl revealed by studies unable to detect their remains in pellets (Grzywaczewski 2006) and indicating high share among prey (e.g. Blache 2001). Therefore, it is necessary to acquire better knowledge of this species' ecology and diet. The aim of our study was to investigate the little owl's diet composition in respect to all vertebrate and invertebrate prey and describe its seasonal variation in an agricultural landscape of Central Poland. In addition we undertook evaluation of contribution of earthworms to the food consumption of little owls.

Material and method

The research was carried out in an agricultural landscape in the Mazovia Lowland, Central Poland. The study site had an area of 10 km² and was situated within the flood terrace of the Vistula river, about 1 km north-west of the Warsaw city border (52°N, 21°E). The dominating type of landscape at the site is a mosaic of farmland, meadows and wasteland, intersected by a network of local roads that are lined with headed willows (*Salix sp.*). The study area included two old river beds of the Vistula (Lake Dziekanowskie and Lake Kiełpińskie), minor mid-field woods as well as buildings (in its southern part).

The study was conducted in 1995 – 1997. We collected data on the little owl's diet from four breeding territories in the southern part of the study area. Distances between the most remote ones and between neighbouring territories were, respectively, ca 1200 m and 350-650 m (mean 470 m). Pellets were collected every 1-2 months on each of the four territories. To analyse them we applied the standard method, which involves soaking pellets and separating out all animal pieces in order to identify prey species and determine the number of prey items (Raczyński & Ruprecht 1974). The number of vertebrate prey was assessed on the basis of the highest number of skeletal elements that enabled prey identification, such as skulls and jaws in the case of mammals; skulls, beaks and femurs in the case of birds; skulls, urostyles, forearm bones and femurs in the case of amphibians. Prey species was determined according to identification keys (Husson 1962, Yalden 1977, Pucek 1984). In the case of voles, given that out of the 157 voles identified to species level, none were short-tailed vole, when it was impossible to distinguish between *Microtus arvalis* and *M. agrestis*, the prey was classified as the common vole. Invertebrates were identified by pieces of chitin carapaces. Their number was estimated on the basis of the most frequent body parts, mainly elytra, pronotums and heads. Mean body mass of vertebrate prey was adopted from the literature (Romanowski 1988, Gunther 1996, Jędrzejewska & Jędrzejewski 1998). The mass of most arthropods was determined at the study site, by catching them with Barber traps, weighing each individual and calculating the mean body mass value, which was then used for further analysis (Table 1). The body mass of other arthropod species was estimated by comparing their size with individuals of a known mass.

Table 1. Biomass of invertebrates trapped in Barber traps in the study area in Mazovia Lowland, Central Poland.

Taxon		Mass [g]
Coleoptera		
Carabidae	*Carabus cancellatus* Ill.	0.58
	Carabus nemoralis O.F.Muller	0.59
	Nebria brevicollis (Fabr.)	0.07
	Broscus cephalotes (L.)	0.19
	Amara aulica (Panz.)	0.06
	Pterostichus caerulescens (L.)	0.05
	Pterostichus cupreus (L.)	0.07
	Pterostichus virens (O.F.Mull.)	0.05
	Pterostichus vulgaris (L.)	0.10
	Calathus erratus (C.R.Sahlb.)	0.03
	Calathus fuscipes (Goeze)	0.06
	Anisodactylus sp.	0.05
	Harpalus rufipes (De Geer)	0.11
Silphidae	*Silpha rugosa* L.	0.07
	Silpha carinata Herbst	0.26
	Silpha tristis Illig.	0.09
Staphilinidae		0.06
Scarabeaidae	*Geotrupes stercorosus* (Hartm.)	0.49
	Anomala sp.?	0.19
	Amphimallon sp.?	0.35
Elateridae	*Adelocera murina* (L.)	0.14
Curculionidae	*Otiorhynchus* sp.	0.04
Aranea		0.02
Mollusca		3.20

Presence of lumbricid earthworms in pellets was determined by searching for their chaetae. We did not assess the number of earthworms, but calculated the frequency of pellets containing their chaetae. However, we used data on the variation of the mean biomass of identified vertebrate and invertebrate (excluding Lumbricidae) prey per pellet to analyse seasonal contribution of earthworms

to the diet of little owls. Moreover, we made an attempt to assess the share of earthworms in the owl's diet in term of biomass, using available data on the mean body mass of earthworms. Finally, we compared recorded (on the basis of standard pellet analysis) and expected (resulting from daily nutrition requirements) prey biomass per pellet to evaluate potential contribution of earthworms to the little owl's diet.

In total, we analysed 642 pellets and identified 3090 prey items. To investigate seasonal variation in the diet, we compared the material obtained in the four seasons: spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January, February). Results of analysis of pellets collected at the same territory in one season were pooled for further analysis. We used redundancy analysis (RDA) implemented in CANOCO 4.5 software (Braak & Šmilauer 2002) in order to assess changes in the little owl diet over the four seasons. In the input data used for the RDA procedure, the proportion of each vertebrate prey type was defined as the response (dependent) variable, while season as the explanatory variable, and territory as covariate. In the same way, RDA was conducted for invertebrate data. The biplots produced with RDA analysis (Fig. 1) facilitated the interpretation of the relationships between occurrences of different prey in the little owl diet and seasons. Monte Carlo permutation test of significance of all canonical axes was used for statistical interpretation of the RDA biplots.

Results

In terms of prey number, the diet was dominated by insects, which constituted in total 77% of all prey, however their contribution to biomass consumed by little owls was marginal (Table 2). The most frequently hunted insects were carabids (Coleoptera); the common prey were in addition forticulids (Dermaptera), cantharids, scarabaeids, including 28 individuals of hermit beetle (*Osmoderma eremita*) and curculionids (Coleoptera). Other invertebrates, including spiders (Araneae) were caught only occasionally. Molluscs were represented in the diet by a single individual of *Helix pomatia*. Earthworm chaetae occurred in approximately 30% of pellets annually.

While vertebrates constituted only 23% of the prey number, in terms of prey biomass, they represent 98% of all the consumed prey. Among vertebrates, mammals (mainly rodents) predominated contributing to 96% of vertebrate prey and 93% of all biomass consumed by little owls. The most frequent prey species was the common vole (62% of mammalian prey identified to the species level), followed by house mouse (*Mus musculus*) and mice of the genus *Apodemus*. Apart from rodents, we also found insectivores Soricomorpha, birds *Aves* and amphibians Amphibia in the diet of the little owl (Table 2). Contribution of main prey categories to the little owl diet differed seasonally. Vertebrates occurred in pellets throughout the whole year, with the maximum frequency of 33.3% in winter and minimum (7.9%) in autumn (χ^2=111.2; df=3; p<0.0001). Generally mammals were preyed predominantly in winter, while birds and amphibians in summer (χ^2=10.0; df=3; p=0.0184). Invertebrates were found in pellets throughout the whole year. The proportion of insects in the diet was the highest in autumn (91.6%) and the lowest in winter (66.2%).

Table 2. Diet of the little owl in Central Poland (all seasons and localities were pooled together). N – number of prey items, % N - percent of number, B – biomass, % B – percent of biomass, + – less than 0.01%.

Prey category	N	%N	B [g]	%B
Total	3090	100	13.639.75	100.00
Vertebrates total	707	22.88	13.367.30	98.00
Sorex araneus	4	0.13	32.00	0.23
Microtus arvalis	271	8.77	5.420.00	39.74
Microtus oeconomus	6	0.19	210.00	1.54
Microtus unid.	2	0.06	40.00	0.29
Arvicolidae unid.	49	1.59	980.00	7.18
Mus musculus	90	2.91	1.170.00	8.58
Apodemus agrarius	27	0.87	594.00	4.35
A. sylvaticus/flavicollis	19	0.61	437.00	3.20
Apodemus unid.	52	1.68	1.170.00	8.58
Micromys minutus	22	0.71	134.20	0.98
Rattus norvegicus	1	0.03	50.00	0.73
Muridae unid.	11	0.36	212.30	1.56
Rodentia unid.	26	0.84	507.00	3.72
Mammalia unid.	101	3.27	1.737.20	12.74
Aves	20	0.65	500.00	3.67
Amphibia	6	0.19	123.60	0.91
Invertebrates total	2383	77.12	272.45	2.00
Orthoptera	97	3.14	71.76	0.53
Dermaptera	269	8.71	18.83	0.14
Coleoptera	1.929	62.43	159.84	1.17
Neuroptera	1	0.03	0.04	+
Hymentoptera	33	1.07	0.58	+
Lepidoptera	2	0.06	0.30	+
Diptera	40	1.29	0.60	+
Insecta unid.	3	0.10	0.30	+
Aranea	8	0.26	0.20	+
Mollusca	1	0.03	20.00	0.15

The diet of the little owl in four seasons differed in respect to the share of vertebrate and invertebrate prey. Following the Monte Carlo permutation tests, the distribution of species and group of species was not random over the year

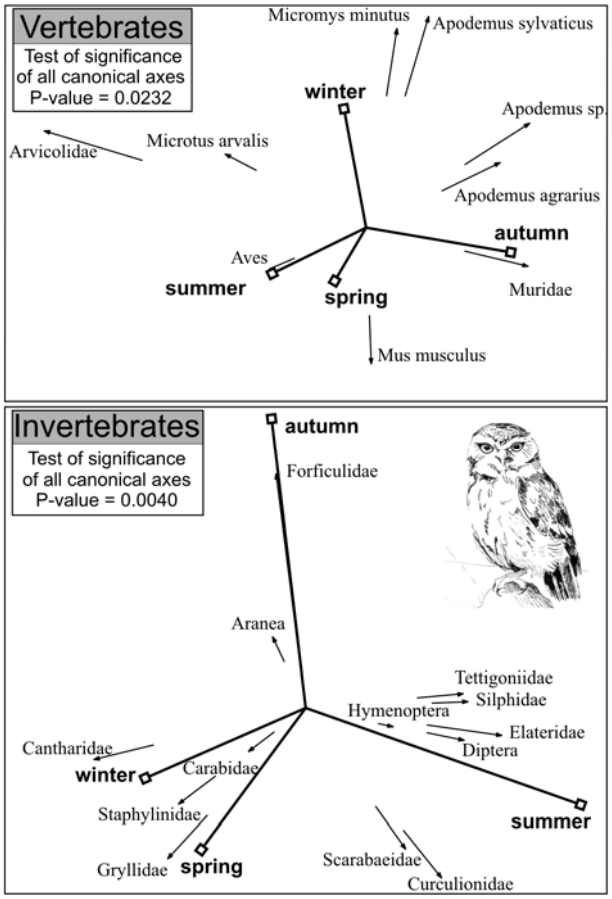

Figure 1. Redundancy analysis (RDA) biplot showing the effect of season on the share of vertebrate prey (upper panel) and invertebrate prey (lower panel) in the little owl diet in central Poland. In case of vertebrates, several categories represented by less than 5 individuals are not shown to keep the chart clear.

(Fig. 1). Spring and summer shares of vertebrates in the little owl diets were quite similar (close location of symbols on the RDA biplot, Fig.1), whereas winter and autumn diet shares were different. The common vole and unrecognised Arvicolidae were preyed upon predominantly in winter and summer, while the house mouse in spring. Remaining murids were preyed upon predominantly in autumn and winter, including two forest or bush-dwelling species (*Micromys minutus* and *Apodemus sylvaticus*) that were hunted in winter. In term of invertebrate prey the winter and spring diets of the little owl were relatively similar, whereas summer and autumn diets were different (Fig. 1). Occurrence of several groups (e.g. carabids, staphylinids and gryllids) in the diet was related with winter-spring period. Diptera, Elateridae, Hymenoptera and some others taxa were caught mainly in summer, while Forficulidae in autumn (Fig. 1). Several taxa, including cantharid larvae and some carabid beetles (i.e. *Amara ingenua, A. consularis*) were often hunted by little owls in winter.

Earthworm chaetae were found predominantly in the autumn pellets (53.2% of pellets). In the other seasons they were recorded with lower frequency: 11.0%, 16.7% and 28.6% of the winter, spring and summer pellet analysed respectively. To assess biomass of earthworms consumed by the little owl, we assumed different mean body mass (from 1.7 to 8.0 g, see Fig. 2 for details) and different number of individual earthworms (from one to three) per pellet containing chaetae. We then used data on frequency of pellets from one of the territories studied to find that lumbricid may constitute from about 5 % (estimate based on assumption of one earthworm of 1.7 g present per pellet with chaetae) to 40 % (3 earthworms of 8 g each per pellet with chaetae) of total prey biomass consumed by little owl in autumn (Fig. 2).

Earthworms could compose a substantial part of the biomass consumed by the owl that is indi-

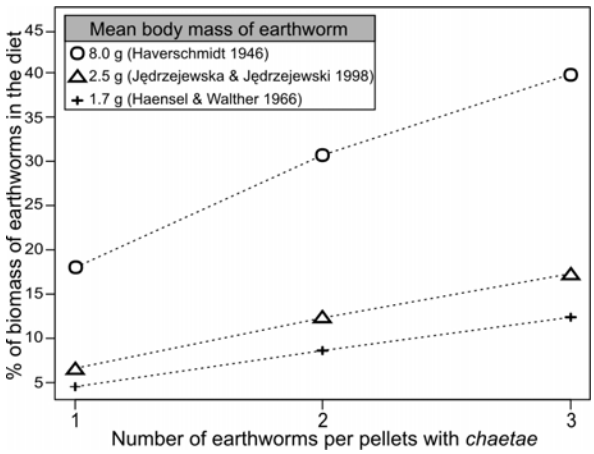

Figure 2. Proportion of earthworms in the autumn diet of the little owl at territory 3, plotted against the mean number of individuals per pellet with chaetae. Three different mean body mass values of earthworms were adopted.

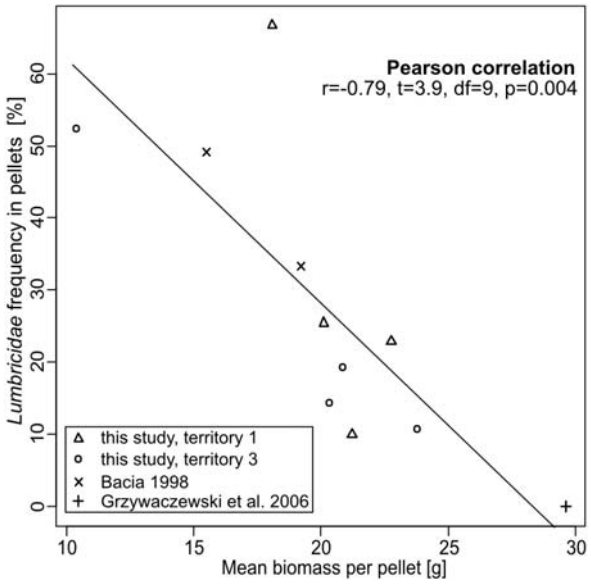

Figure 3. Correlation between the lumbricid frequency and the prey biomass (vertebrates and invertebrates excluding earthworms) recorded per little owls' pellet. Pellet samples collected during four seasons at two little owl territories were analysed (for details see methods).

rectly indicated by the high variation of the pooled of vertebrates and invertebrates (excluding lumbricidae) biomasses per pellet, which seasonally ranged from 11 g in autumn to 24 g in winter. Recorded mean biomass of vertebrates and invertebrates consumed seasonally were negatively correlated with lumbricid frequency in pellets (Fig. 3). Our findings are supported by parallel studies (that included search for chaetae) in the Netherlands and southern Poland where data on lumbricid frequency and mean prey biomass identified per pellet fit the regression (Fig 3).

In the little owl the rate of pellet production is 1-2 pellet per 24 hours (1.5 on average, Hanson 1973) while daily nutrition requirement denote 46.7g on average (Manez 1983 in Van Nieuwenhuyse et al. 2008). Therefore, the difference between the recorded (on the basis of pellet analysis) and theoretical (i.e. 46.7g) daily consumption ranges from 11 to 31 g. This may suggests that the food biomass "missing" in the daily energetic budget of little owl was in fact consumed in the form of earthworms.

Discussion

Diet composition

Our data regarding the high share (in terms of biomass) of the common vole in the little owl's

diet is in consistence with other studies conducted in Poland (Romanowski 1988, Grzywaczewski et al 2006, Romanowski & Żmihorski 2006) and in Central Europe (Ille 1992, Genot & Bersuder 1995, Obuch & Kurthy 1995, Mlikovsky 1996). This rodent is also an important prey in the diet of other owls Strigiformes that inhabit farmland ecosystems of Central Europe (Goszczyński 1981, Obuch & Kürthy 1995, Romanowski & Żmihorski 2008, 2009, Kitowski 2013, Petrovivi et al 2013) and is preyed even by the eagle owl (*Bubo bubo*) nesting in the vicinity of agriculture fields (Sándor & Ionescu 2009). As for Arthropods, their contribution to the little owl diet was marginal – they constituted only a few percent of biomass consumed by the owls, although they prevailed by number, the result being similar to two recent studies in south eastern Poland (Grzywaczewski et al 2006, Kitowski & Pawlega 2010). Romanowski (1988) found even lower biomass percentage of invertebrates in the little owl's diet at the same study area, which presumably was a result of less frequent pellet collection. Pellets that contain insects are less durable than those with vertebrate remains. If pellets are collected at too long intervals, considerable part of "insect" pellets is already disintegrated and therefore omitted in the analysis. The invertebrate prey occurrence in the little owl's diet that we recorded (77 %, exclusive of lumbricid) is lower than in Western and Southern Europe, where it reaches up to 95 % (e.g. Jaksic & Marti 1981, Delibes et al. 1983, Bacia 1998, Fattorini et al. 2001, Goutner & Alivizatos 2003, Obuch & Kristin 2004). In Central and South Eastern Europe this prey's contribution is smaller, and local little owl catches almost exclusively vertebrates (Barbu & Sorescu 1970, Mikkola 1983, Simeonov 1983, Obuch & Kürthy 1995).

Coleopteran beetles dominated the insect fraction in the little owl diet, as has been observed in other studies in Europe (Genot & Bersuder 1995, Fattorini et al. 2001, Grzywaczewski 2006 and references therein). This is probably due to the fact that they are of relatively large size and compose a substantial portion of the epigeic invertebrate community of grassland areas in Central Poland (Hoste-Danyłow et al. 2010). Domination of coleopterans in the little owl's diet has been noted in many European countries (Fattorini et al. 1999, Manganaro et al. 1999, Goutner & Alivizatos 2003), although locally other invertebrate taxa were also prevalent, e.g. Dermaptera (Laursen 1981) and Orthoptera (Goutner & Alivizatos 2003, Obuch & Kurthy 2004). Little owl pellets may provide information on rare and vulnerable insects species: identification of hermit beetles in this study area (Altenburg-Bacia et al. 2006) led to a follow-up field surveys and the recognition of important local population of the species in the Vistula valley (Romanowski et al. 2011).

Seasonal variation

The seasonal variation of bird and mammal predators' diet in Central and Northern Europe is affected by substantial weather changes throughout the year, which directly influence the number and availability of prey (e.g. Jędrzejewski et al. 1996, Romanowski & Żmihorski 2009). The diet of the little owl in Central Europe is marked by a relatively high percentage of invertebrates in the warm period of the year and of vertebrates in the winter (e.g. Laursen 1981, this study). This is caused by limited availability of invertebrates that is linked to the decrease in mean temperatures. However, there is no clear pattern of variation of main prey's proportion (Jaksić & Marti 1981, Génot & Van Nieuwenhuyse 2002). The high proportion (by numbers) of invertebrates in the winter diet of little owls in Central Poland is puzzling. In Southern Europe this prey category is frequently recorded in the owl's winter diet and can comprise over 90 % of all prey caught over the winter (Delibes et al. 1983, Fattorini et al. 1999). However, the percentage of invertebrates in the winter diet in Central and Eastern Europe appears to be low: winter material collected in the Czech Republic did not reveal any invertebrates (Gusev 1956, Hell 1964, Mlikovsky 1996), and in Belgium invertebrates found in the winter, at three different sites, constituted respectively 24 % (total number of prey n=75), 28 % (n=137) and 46 % (n=633) of all prey (after Libois 1981, modified data). Similarly, in Moldova, in the autumn-winter period, invertebrates made up as little as 24.9 % of all prey (Mikkola 1983). Since in Poland the climate is more severe than in the Czech Republic, Belgium and Moldova (lower mean temperatures in the winter and longer snow cover duration), the winter abundance of invertebrates is lower than in other seasons. Hence, in Poland invertebrate contribution to winter diet should be the lowest relative to the three other countries. Among the invertebrates found in the winter diet of the owls, those living on snow surface (e.g. cantharids) constituted only a small part. The mean winter temperature (December, January, February) in the years 1995-1997

was 1.3°C lower than the previous 23 years (1980-2003) (source: Institute of Meteorology and Water Management, Poland), which precludes a massive occurrence of invertebrates during our study period. The only explanation of the observed high proportion of invertebrates in the winter diet seems to be that little owl could hunt for its prey in buildings, such as stables, barns, pigsties or warehouses, etc. In buildings invertebrates can be active and available also in the winter. This hypothesis is supported by the fact that the winter diet included species closely associated with buildings, such as the house mouse or the brown rat. Temporary use of buildings for hunting has been seen in the little owl also in other regions of Poland (Kitowski & Pawlega 2008 and references therein) and in Denmark (Laursen 1981). Contribution of *Micromys minutus* and *Apodemus sylvaticus* in winter diet may also indicate that in that period little owls hunt in proximity to human settlements, as both species of rodents are known to migrate to buildings during the cold season. It is interesting to note that the majority of Muridae was hunted in autumn whereas *Microtus arvalis* was less often preyed in this period. The reasons of this discrimination are not clear and should be addressed in future research.

Earthworm contribution to the diet

Determining the contribution of earthworms to the little owl's diet is usually impossible by means of the standard analysis (Raczyński & Ruprecht 1974), because to establish the number of individuals per pellet on the basis of chaetae number is difficult. For this reason, many studies regarded the significance of lumbricid as marginal (Laursen 1981, Romanowski 1988), even when authors put efforts to detect their remains in pellets (Grzywaczewski 2006). However, observations of little owl that were foraging and feeding their offspring revealed that earthworms constituted a considerable part of their diet, ranging from 20 to 60% of prey biomass (e.g. Blache 2001, Génot & Van Nieuwenhuyse 2002 and references therein). Additionally, a high proportion of earthworms in the little owl's diet has been reported through pellet analysis by Bacia (1998) and Hounsome et al. (2004).

Our material also indicates a high share of lumbricid in the diet of little owls. Earthworms were found in a high portion of pellets: in the autumn they were found from over 50% of the pellets. Although we do not know how many individuals were consumed by the owls, it can be suspected that with respect to biomass, earthworms can seasonally compose a significant portion of the little owl's diet. The discrepancy between recorded and theoretical daily consumption may to some extent result from the fact that some bones are lost when prey is torn apart before being eaten and owls partly digest skeletal elements. (Raczyński & Ruprecht 1974). However, in the case of rodents eaten by adult long-eared owls (*Asio otus*), barn owls (*Tyto alba*) and tawny owls (*Strix aluco*), loss of skeletal parts due to digestion was as low as 10 % (Raczyński & Ruprecht 1974). Consequently, such loss cannot account for considerable differences between the biomass of prey identified in pellets and daily energy requirements of little owls. More plausibly, it is the earthworms that are missing in the prey biomass, being the only taxa recorded in pellets but not included in evaluation of prey biomass.

Determining the contribution of invertebrates to total biomass of prey consumed by the little owl depends to a large extent on the mean insect body mass values used for calculation. In the literature on the little owl's diet authors have applied different body mass values for the same prey species. In addition, many papers do not provide information about the values used in calculation. For instance, mean body mass values of some invertebrates adopted by Haensel & Walther (1996) are often one order of magnitude higher than those measured at our study area and applied in our analyses (see Appendix 1). As a result, the studies on the contribution of invertebrates in little owl diet published in recent years can be best compared in respect to percentage of occurrence only.

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