Effect of season, weather and habitat on diet variation of a feeding-specialist: a case study of the long-eared owl, *Asio otus* in Central Poland

Jerzy ROMANOWSKI[1]* and Michał ŻMIHORSKI[2]

[1] *Centre for Ecological Research, Polish Academy of Sciences, Dziekanów Leśny near Warsaw, 05-092 Łomianki, Poland; e-mail: romanowski@cbe-pan.pl*

[2] *Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warsaw, Poland; e-mail: zmihorski@miiz.waw.pl*

Received 18 February 2008; Accepted 24 July 2008

A b s t r a c t . Diet variation of the long-eared owl, *Asio otus* in an agricultural landscape of Central Poland was investigated on the basis of pellets collected in the years 1983–2005. Diet composition in the spring-summer (16 April – 30 September) and autumn-winter (1 October – 15 April) seasons was compared and effect of ambient temperature, amount of precipitation and availability of foraging habitats on the long-eared owl diet variation was analysed. For diet description the multiple regression and PCA were used, and for habitat quality evaluation the GIS techniques were applied. Diet composition differed significantly between the seasons. In the autumn-winter period the contribution of Arvicolidae and of the main prey species, *Microtus arvalis*, decreased while the amount of murids, birds and amphibians increased significantly, as compared to the spring-summer season. The results did not confirm the influence of mean ambient temperature one month before pellet collection on diet composition. The amount of precipitation positively affected the share of Arvicolidae in the owl diet and was negatively correlated with the percentage of Muridae and with the food niche breadth of the owl. The higher percentage of Arvicolidae and the lower of Muridae in the diet corresponded to higher permanent grassland proportion around pellet collection sites. Mechanisms of habitat- and season-dependent diet variation are discussed.

Key words: optimal foraging theory, predation, raptors, voles, *Microtus*

Introduction

The foraging ecology of predatory birds and mammals inhabiting the temperate climate zone in Europe varies greatly and is shaped by several factors, including seasonality and the spatial structure of a habitat. Because of variable weather conditions, predatory vertebrates face temporary seasonal depletion of food resources (e.g. G o s z c z y ń s k i 1977, J ę d r z e j e w s k a & J ę d r z e j e w s k i 1998). During the cold period, a substantial proportion of prey species become inactive (e.g. invertebrates, amphibians) or migrate south (birds), which additionally impoverishes local prey communities. In some cases, deep snow cover may decrease the availability of some prey. Low ambient temperature considerably increases energy requirements and can force some predators to change their hunting techniques and foraging strategies (V i l l a g e 1983).

The second factor, habitat spatial variability, also affects the composition of prey communities and availability of individual prey species (G o s z c z y ń s k i 1977). It should also be stressed that for each type of vegetation predators apply a different optimal hunting technique (W u c z y ń s k i 2005). The aim of this study was to analyse variation in the diet of the long-eared owl, *Asio otus*, a specialist in voles (M a r t i 1976) that is

* Corresponding author

common in the temperate climate zone in Europe. As revealed in earlier works by many authors, the long-eared owl shows strong numerical response to changes in its preferred prey density (G o s z c z y ń s k i 1981, K o r p i m ä k i & N o r r d a h l 1991, K o r p i m ä k i 1992). However, less is known about the spatio-temporal variation of its diet and most studies concerning this problem were conducted in Northern Europe (N i l s s o n 1981, K o r p i m ä k i & N o r r d a h l 1991, K o r p i m ä k i 1992). This paper explores whether the composition of the diet of the long-eared owl, a vole-eating feeding specialist, is affected by season, weather conditions and foraging habitats.

Material and Methods

The study was conducted in the Vistula river valley, located in the Mazowsze Lowland, Central Poland. The study area is situated between the forest complex of the Kampinos National Park and Warsaw suburbs (52˚N; 21˚E). It is an agricultural landscape characterised by relatively high level of crop heterogeneity and dominated by arable fields and meadows, interspersed with woods, pastures and villages. These habitats form an environmental mosaic. Some roads that intersect this landscape are lined with pollarded willow *Salix* spp. trees. Willows and pine woods provided long-eared owls with nesting and roosting sites, around which pellets were collected. Long-eared owl density in the study area reached up to five territories per 10 km^2 (but 1.6 on average; D o m b r o w s k i et al. 1991).

The composition of the long-eared owl's diet was analysed on the basis of pellets collected at nesting, roosting and wintering places. Pellets were collected irregularly in different months of the years 1983, 1985, 1994, 1995, 1998, 2002 and 2005. Pellets were divided based on the collection date into two categories: autumn-winter (1 October – 15 April) and spring-summer (16 April – 30 September) seasons according to the J ę d r z e j e w s k a & J ę d r z e j e w s k i (1998) analysis of predation in the vertebrate community of an European temperate forest. Standard methods for pellet analysis were used (R a c z y ń s k i & R u p r e c h t 1974). After soaking the pellets in water, all the skeletal elements used for prey identification were separated out. Prey were identified on the basis of lower jaws, skulls, teeth, parts of beaks and femurs, according to the identification key by P u c e k (1984), and using own collections as reference. The number of prey individuals was calculated on the basis of the most frequent skull element. Invertebrates, which occasionally occurred in pellets (0.01% of all prey items), were not included in the analysis. Prey species were grouped into four categories: Arvicolidae, Muridae, Insectivora, and Aves. Food niche breadth (FNB) index was then calculated according to L e v i n ' s (1968) formula: $1/\Sigma p_i^2$, where p_i denotes contribution of a given prey group to the diet. FNB index values ranged from one (the narrowest trophic niche) to four (the widest niche).

E f f e c t o f s e a s o n a n d w e a t h e r

To evaluate the effect of season on diet composition, contribution of individual prey categories to spring-summer and autumn-winter seasons diet was tested with Chi-square test (the continuity correction was applied when necessary, Z a r 1974).

To find whether weather factors influenced diet variation, 29 separate pellet collections containing at least 15 prey items (total 1407; mean: 49 ±41.8 SD) were analysed. Pellet collections picked at the same site on different dates were treated as independent. Due to their low contribution to the diet Aves and Insectivora proportions were pooled to avoid skew distribution. Since percentages of Arvicolidae and Muridae in the 29 pellet collections were highly negatively correlated (r = –0.96), these two variables were reduced with the Principal Component Analysis method. The component (hereafter Arv-Mur gradient), the pooled proportion of Aves and Insectivora, and the FNB index were used for further analysis of the effect of weather on the long-eared owl's feeding habits.

Since long-eared owl pellets are rather fragile and are soon settled by many scavenging invertebrates, their decomposition is relatively fast. This allowed the assumption that pellets found were no more than 1–1.5 months old, i.e. most pellets collected in a given month were produced in the preceding month.

For each pellet collection, two weather variables were recorded: mean ambient temperature (from –4.9 to 22.0°C) and amount of precipitation (from 5 to 89 mm) (source: bulletins of the Institute of Meteorology and Water Management). These two variables were used as predictors in the multiple regression analysis. The Arv-Mur gradient extracted by the PCA method, the pooled proportion of Invertebrates and Aves, and the FNB index were dependent variables (three independent regression analyses were computed). SPSS 13.0 (SPSS 2004) was used for statistical analysis.

Effect of habitat composition

Nine pellet collection sites for which at least 10 prey items were identified during the spring-summer season were used for the habitat analysis. The percentage of habitat types within a 700 m radius from each pellet collection site was computed. A digital map with 102 vegetation complexes, prepared in the working scale of 1:10,000 (Romanowski et al. 2005 and references therein) was used and analysed by means of ArcView 3.2 software (ESRI 2000). Since long-eared owls hunt mainly in open areas and prefer grassland with low vegetation (Aschwanden et al. 2005), the proportion of two main habitat types: permanent grassland (mainly meadows and pastures) and of other open areas (abandoned land and arable fields) was computed for each territory. In addition potential effect of proportion of forest habitat on the diet of long-eared owls was tested. Percentages of Insectivora, Arvicolidae, Muridae and Aves in the diet were significantly negatively correlated with one another. Therefore, the PCA method for data reduction was applied and components extracted were used for further analysis. Next, the correlation of these two components with the percentage of the three main habitat types within a 700 m radius from pellet collection sites was tested in order to establish whether habitat characteristics influence the diet composition of the long-eared owl.

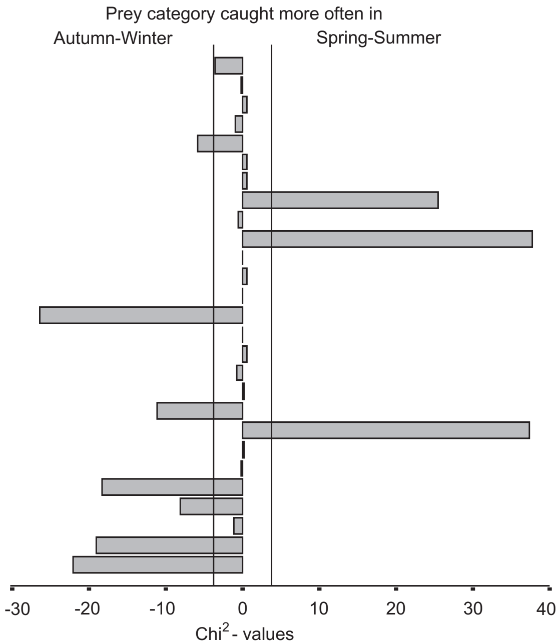
Results

Seasonal variation of the diet

In total, 1561 vertebrate prey individuals were identified: 1236 in the spring-summer and 325 in the autumn-winter season. Significant differences in the long-eared owl diet composition between the spring-summer and autumn-winter seasons were found. In the spring-summer period the percentage of voles, including the most common *Microtus arvalis* was significantly higher ($\chi^2 = 37.74$, df = 1, $p < 0.001$, Fig. 1). However, in the autumn-winter season the proportion of the alternative prey (mice, birds and amphibians), clearly increased. The percentage of Insectivora in the diet in the autumn-winter season was three times higher than in the spring-summer season, however, the difference was not significant ($\chi^2 = 0.94$, df = 1, p = 0.332). The FNB index value was higher in the autumn-winter period (1.59) as compared to spring-summer period (1.25).

Effect of weather on the diet

The component extracted (Arv-Mur gradient) was positively correlated with Arvicolidae (r = 0.99) and negatively with Muridae frequency in the diet (r = –0.99). Of the two weather factors analysed, only the amount of precipitation in the month preceding pellet collection significantly affected the Arv-Mur gradient values (Table 1). FNB index was significantly



Prey category	% of prey number in Au-Wi	% of prey number in Sp-Su	N
Talpa europaea	0.62	0.00	2
Sorex araneus	0.31	0.24	4
Sorex minutus	0.00	0.08	1
Insectivora total	0.92	0.32	7
Myodes glareolus	4.00	1.78	35
Microtus oeconomus	10.77	12.30	187
Microtus agrestis	0.00	0.08	1
Microtus arvalis	52.92	67.96	1012
Microtus unid.	8.00	6.80	110
Arvicolidae total	75.69	88.92	1345
Mus musculus	1.23	1.29	20
Rattus norvegicus	0.00	0.08	1
Micromys minutus	0.92	0.65	11
Apodemus agrarius	8.92	2.67	62
Apodemus sylvaticus	1.23	1.29	20
Apodemus flavicollis	0.00	0.08	1
Sylvaemus	1.23	0.57	11
Apodemus sp.	2.15	2.67	40
Muridae total	15.69	9.30	166
Mammalia total	92.31	98.54	1518
Passer domesticus	0.00	0.32	4
Passer montanus	0.62	0.24	5
Turdus sp.	1.85	0.00	6
Aves other	1.54	0.16	7
Aves unid.	1.54	0.73	14
Aves total	5.54	1.46	36
Amphibia	2.15	0.00	7

Fig. 1. Diet composition of the long-eared owl in Central Poland, in spring-summer (16 April – 30 September) and autumn-winter (1 October – 15 April), during 1983–2005. The values represent percentage of a given prey item. Bars represent χ^2 values computed for each prey category (2x2; df = 1) which indicate if a given species is more common in autumn-winter diet ($\chi^2 < 0$) or spring-summer diet ($\chi^2 > 0$). Vertical lines denote significance level ($\alpha = 0.05$).

Table 1. Effects of mean ambient temperatures in the preceding month (one month before pellet collection date) and amount of precipitation in the preceding month on the diet composition and the food niche breadth of the long-eared owl. Results of a multiple regression analysis based on 29 independent pellet collections. Significant effects are marked in bold.

Dependent variables	Independent variables – Beta standardised coefficients: Mean ambient temp. in the preceding month	Independent variables – Beta standardised coefficients: Amount of precipitation in the preceding month	R_{adj}^2	p
Arv-Mur gradient	–0.18	**0.75**	0.400	0.001
% of Insectivora and Aves	–0.15	–0.04	0.044	0.672
Food niche breadth	0.19	**–0.71**	0.345	0.002
Collinearity statistic – Tolerance	0.71	0.71		

negatively correlated with the amount of precipitation. The percentage of Insectivora and birds pooled together was not affected by any of the two weather factors.

Habitat variability and diet composition

The PCA method extracted two components with eigenvalues grater than one (Table 2).

The percentage of grasslands around pellet collection site was related with diet composition: component 1 increased significantly with the rise in the proportion of permanent grasslands in the vicinity of pellet collection sites and this relationship was best explained by a logarithmic model ($r = 0.54$, $n = 9$, $p = 0.024$, Fig. 2). Since component 1 shows differences between Arvicolidae and Muridae (see Table 2 for details), this relationship should be interpreted as an increase in Arvicolidae and a decrease in Muridae proportions in the diet, corresponding to the grassland availability increase. The proportion of other open areas and forest areas had no significant contribution to diet variation. Component 2 did not show significant relationship with any of the three habitat variables.

Table 2. Loadings of the first two components extracted by the Principal Component Analysis performed on the long-eared owl diet composition values. Significant ($p < 0.05$) correlations of prey categories (expressed as percentage of prey items) and two components are marked in bold.

Prey category	Component 1	Component 2
Insectivora	–0.324	0.469
Arvicolidae	**0.979**	0.196
Muridae	**–0.913**	0.257
Aves	–0.212	**–0.915**
Variance explained	48.5%	29.1%

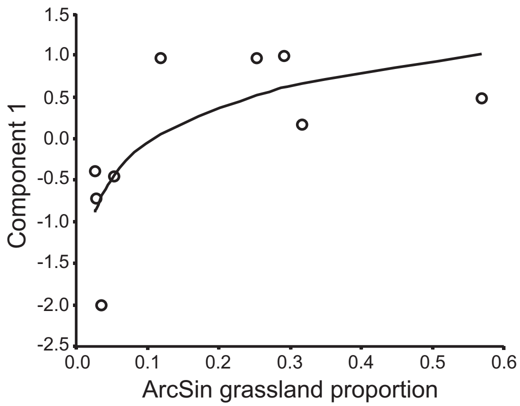


Fig. 2. Relationship between the long-eared owl diet composition, referred to as component 1 (see Table 2 for description), and the proportion of permanent grassland in the vicinity of pellet collection sites in the spring-summer season (16 April – 30 September), throughout 1983–2005.

Discussion

Arvicolidae rodents, especially the common vole *Microtus arvalis*, were found to be the most important prey in both the autumn-winter and spring-summer seasons, as observed in previous studies on feeding habits of the long-eared owl in agrocenoses of temperate Europe (G o s z c z y ń s k i 1977, 1981, R o m a n o w s k i 1988, Ż m i h o r s k i 2005, B e n c o v á et al. 2006, S h a r i k o v 2006). Murids remain the second important prey category, whereas Insectivora, birds and amphibians have much less significance in the owls' diet. It should be noted that the observed increase of the FNB index during the cold part of the year confirms the pattern recorded earlier in southern Europe (T o m e 1994). However, seasonal variation of the long-eared owl's diet in higher latitudes shows the opposite tendency, i.e. the FNB index is wider in summer (N i l s s o n 1981, W i j n a n d t s 1984). Reasons for the geographical variation in the FNB index seasonality remain unknown. It is possible that the observed divergence results from differences in vegetation structure (see below) or winter severity.

Significant differences between autumn-winter and spring-summer composition of the long-eared owl's diet were recorded in this study. In autumn-winter the percentage of the common vole in the diet was 15% lower, as compared to the spring-summer season, and the importance of the alternative prey including mice strongly increased (Fig. 1). Several explanations for these differences in diet composition can be proposed. First of all, when snow cover is deep Arvicolidae are much less available for avian predators than Muridae. This is because voles more frequently move under snow whereas mice prefer moving on snow surface (J ę d r z e j e w s k i & J ę d r z e j e w s k a 1993, J ę d r z e j e w s k a & J ę d r z e j e w s k i 1998). Similar interpretation was earlier proposed by C z a r n e c k i (1956) to explain the long-eared owl's diet variation in western Poland. In addition, severe winter conditions may force the owls to change hunting habitats. For example, due to deep snow cover they may shift their hunting activity into woods, partially afforested areas and forest-field edges, where snow is usually shallower (C a n o v a 1989, J a c o b s e n & S o n e r u d 1993). This is evidenced in the present study by the two-fold wintertime increase in the percentage of bank voles *Myodes glareolus*, which is a rodent typical of forest habitats (Fig. 1). In the habitat edges (including forest edges) the rodent community is usually more diverse (L i d i c k e r 1999) and vole domination less pronounced, which explains the observed diet changes and wider food niche breadth in the autumn-winter period. J a c o b s e n & S o n e r u d (1993) observed that the Tengmalm's owls *Aegolius funereus* used forest habitats more frequently than open areas, but only when snow was deep. They also found that the activity of rodents on snow surface was more intense in forest than in open areas.

The observed significant shift in the long-eared owl diet between the two periods is an unexpected result for a feeding-specialist predator (G o s z c z y ń s k i 1981). According to the literature (C r a m p 1985, T o m i a ł o j ć & S t a w a r c z y k 2003), this owl species is not a sedentary bird and outside the breeding season it is nomadic. Because of this, wintering of the long-eared owls in central Poland seems to be contrary to the expectations, since in winter – as shown in this study – the owls are forced to change their diet to alternative prey. Saving energy needed for migration as well as the possibility of earlier reproduction may be potential advantages of remaining in the breeding areas during the winter.

Strong effect of the amount of rainfall on the long-eared owl's diet variation was observed in the present study. Interestingly, however, diet composition was not affected by mean ambient temperature. It has been found that temperatures can influence hunting techniques and diet variation of the kestrels *Falco tinnunculus* which hunt mainly voles (V i l l a g e 1983, R o m a n o w s k i 1996, Ż m i h o r s k i & R e j t 2007). Since the range of mean ambient temperatures during the analysed months was relatively large (ca. 27°C), it was expected that this weather variable would strongly affect the feeding habits of the studied species. However, the results did not confirm these expectations, which might suggest that the foraging ecology of the long-eared owl is insensitive to ambient temperature and that in times of variable temperatures this raptor can maintain stable diet composition (see also R u b o l i n i et al. 2003).

The increase of rainfall corresponded to the increase in the proportion of voles and to the decrease in the proportion of murids in the diet. Two explanations may be proposed for this pattern. First, it has been shown that at bright moonlight nights, rodents lower their activity or move from open areas to forested habitats, where predation is usually lower (T r a v e r s et al. 1988, L i m a & D i l l 1990). Because rain is associated with clouds, precipitation considerably reduces the amount of moonlight, which in turn can positively affect the activity of rodents in open areas. Thus, in the time of rainy weather the availability of the preferred prey (the common vole) can remain high, which allows long-eared owls to prey on voles. Higher availability of preferred voles leads to decrease in mice proportion in the diet, parallel to the increase in the amount of precipitation. Second, rain itself can positively affect rodent activity, as it was demonstrated by V i c k e r y & B i d e r (1981). Water may be an important factor affecting the occurrence of small mammals, especially in large, open areas (fields, meadows). Long-lasting drought can reduce their activity, leading to a decrease of vole percentage in the long-eared owl diet.

In the spring-summer season the availability of grasslands, optimal foraging habitats (A s c h w a n d e n et al. 2005) affected positively the percentage of voles and negatively the percentage of murids in the diet. The owl's functional response to habitat availability increase was very rapid (and best explained by the logarithmic function, Fig. 2) and even a small proportion of grasslands in the vicinity of pellet collection sites resulted in the change in diet composition. This reaction was analogous to changes in the long-eared owl's diet according to variation in vole density (T o m e 2003). In the light of the observed habitat-diet relationship, the occurrence of the long-eared owl in some habitats with limited availability of grasslands is surprising. It is possible that weak competitors and/or young individuals that search for nests are pushed to marginal feeding habitats, but more research is needed to confirm this hypothesis.

The long-eared owl is a typical feeding-specialist and shows a strong numerical and weak functional response to variation in accessibility of the preferred prey species (G o s z c z y ń s k i 1981, K o r p i m ä k i & N o r r d a h l 1991, T o m e 1991, 2003, K o r p i m ä k i 1992). The present study shows that the owls' diet composition varies significantly between the two analysed periods of the year and is affected by some weather factors as well as by habitat configuration. The observed diet variation is unusual for the feeding-specialist predator. The results also show that long-eared owls occur commonly in areas (with little grassland proportion), or periods (winters with thick snow cover) where availability of the preferred prey, i.e. the common vole is highly limited. Hence, there arises an important question concerning why does a feeding specialist occur in these times and places if it has to considerably change its feeding habits? It can be suggested that the change in feeding habits is the cost of some important benefits for the predator. Perhaps these benefits are associated with reducing energy requirements for migration or the year-round nest defence. Importantly, the present results suggest that large scale man-made habitat transformations (e.g. agriculture intensification in the study area – R o m a n o w s k i et al. 2005) and changes in weather conditions (e.g. those related to the global climate warming) may affect not only generalist predators (P o s t et al. 1999, H e b b l e w h i t e 2005), but also the foraging ecology and predator-prey interactions of typical feeding-specialists (this study).

A c k n o w l e d g e m e n t s

We are grateful to M. P o s ł u s z n y and two anonymous reviewers for comments on the manuscript. J. K u b a c k a kindly improved the English.

LITERATURE

Aschwanden J., Birrer S. & Jenni L. 2005: Are ecological compensation areas attractive hunting sites for common kestrel (*Falco tinnunculus*) and long-eared owls (*Asio otus*)? *J. Ornithol. 146: 279–286*.

Bencová V., Kašpar T. & Bryja J. 2006: (Seasonal and interannual changes in diet composition of the long-eared owl (*Asio otus*) in Southern Moravia). *Tichodroma 18: 65–71 (in Czech with English summary)*.

Canova L. 1989: Influence of snow cover on prey selection by long-eared owls *Asio otus*. *Ethol. Ecol. Evol. 1: 367–372*.

Cramp S. (ed.) 1985: The birds of the Western palearctic. Vol. 4. *Oxford University Press, Oxford*.

Czarnecki Z. 1956: Obserwacje nad biologią sowy uszatej (*Asio otus* L.) [Observations on the biology of the long-eared owl (*Asio otus* L.)]. *Pr. Kom. Biol. PTPN 18 (4): 1–38. (in Polish)*.

Dombrowski A., Fronczak J., Kowalski M. & Lippoman T. 1991: (Population density and habitat preferences of owls Strigiforems on agriculture areas of Mazowsze Lowland (Central Poland)). *Acta Ornithol. 26: 39–53 (in Polish with English summary)*.

ESRI 2000: ArcView 3.2. *Environmental Systems Research Institute, Redlands, California*.

Goszczyński J. 1977: Connection between predatory birds and mammals and their prey. *Acta Theriol. 22: 399–430*.

Goszczyński J. 1981: Comparative analysis of food of owls in agrocenoses. *Ekol. Pol. 23: 431–439*.

Hebblewhite M. 2005: Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. *J. Anim. Ecol. 74: 226–233*.

Jacobsen B.V. & Sonerud G.A. 1993: Synchronous switch in diet and hunting habitat as a response to disappearance of snow cover in Tengmalm's owl *Aegolius funereus*. *Ornis Fenn. 70: 78–88*.

Jędrzejewska B. & Jędrzejewski W. 1998: Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. *Springer Verlag, Berlin, 450 pp*.

Jędrzejewski W. & Jędrzejewska B. 1993: Predation on rodents in Białowieża primeval forest, Poland. *Ecography 16: 47–64*.

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

Korpimäki E. & Norrdahl K. 1991: Numerical and functional response of kestrels, short-eared owls and long-eared owls to vole densities. *Ecology 72: 814–826*.

Levins R. 1968: Evolution in changing environments. *Princeton University Press, Princeton, 120 pp*.

Lidicker W. Z., Jr. 1999: Responses of mammals to habitat edges: an overview. *Landscape Ecol. 14: 333–343*.

Lima S.L. & Dill M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool. 68: 619–640*.

Marti C. D. 1976: A review of prey selection by the long-eared owl. *Condor 78: 331–336*.

Nilsson I. 1981: Seasonal changes in food of the long-eared owl in southern Sweden. *Ornis Scand. 12: 216–223*.

Post E., Peterson R.O., Stenseth N.C. & McLaren B.E. 1999: Ecosystem consequences of wolf behavioural response to climate. *Nature 401: 905–907*.

Pucek Z. 1984: Keys to Vertebrates of Poland. Mammals. *PWN, Warszawa, 366 pp*.

Raczyński J. & Ruprecht A. L. 1974: The effect of digestion on the osteological composition of owl pellets. *Acta Ornithol. 14: 25–38*.

Romanowski J. 1988: Trophic ecology of *Asio otus* (L.) and *Athene noctua* (Scop.) in the Suburbs of Warsaw. *Pol. Ecol. Stud. 14: 223–234*.

Romanowski J. 1996: On the diet of urban kestrels (*Falco tinnunculus*) in Warsaw. *Buteo 8: 123–130*.

Romanowski J., Matuszkiewicz J., Bouwma I.M., Kowalczyk K., Kowalska A., Kozłowska A., Solon J., Middendorp H., Reijnen R. & Rozemeijer R. 2005: Evaluation of ecological consequences of development scenarios for the Vistula River Valley. *Warsaw, Wegeningen, Utrecht, 127 pp*.

Rubolini D., Pirovano A. & Borghi S. 2003: Influence of seasonality, temperature and rainfall on the winter diet of the long-eared owl, *Asio otus*. *Folia Zool. 52: 67–76*.

Sharikov A.V. 2006: (Peculiarities of winter feeding in the long eared owl (*Asio otus*) in settlements of Stavropol krai). *Zool. Zh. 85: 871–877 (in Russian with English summary).*

SPSS 2004: SPSS 13.0 for Windows. *SPSS, Chicago, Illinois, USA.*

Tome D. 1991: Diet of the long-eared owl (*Asio otus*) in Yugoslavia. *Ornis Fenn. 68: 114–118.*

Tome D. 1994: Diet composition of the long-eared owl in central Slovenia: seasonal variation in prey use. *J. Raptor Res. 28: 253–258.*

Tome D. 2003: Functional response of the long-eared owl (*Asio otus*) to changing prey numbers: a 20-year study. *Ornis Fenn. 80: 63–70.*

Tomiałojć L. & Stawarczyk T. 2003: (The Avifauna of Poland. Distribution, Numbers and Trends). *PTTP "proNatura", Wrocław, 870 pp (in Polish with English summary).*

Travers S.E., Kaufman D.W. & Kaufman G.A. 1988: Differential use of experimental habitat patches by foraging *Peromyscus maniculatus* on dark and bright nights. *J. Mamm. 69: 869–872.*

Vickery W.L. & Bider J.R. 1981: The influence of weather on rodent activity. *J. Mamm. 62: 140–145.*

Village A. 1983: Seasonal changes in the hunting behavior of kestrel. *Ardea 71: 117–124.*

Wijnandts H. 1984: Ecological energetics of the long-eared owl (*Asio otus*). *Ardea 72: 1–92.*

Wuczyński A. 2005: Habitat use and hunting behaviour of common buzzards *Buteo buteo* wintering in south-western Poland. *Acta Ornithol. 40: 147–154.*

Zar J. H. 1974: Biostatistical Analysis. *Prentice Hall, Upper Saddle River, 662 pp.*

Żmihorski M. 2005: (The long-eared owl *Asio otus* diet in agriculture and forest landscape). *Not. Ornitol. 46: 121–126 (in Polish with English summary).*

Żmihorski M. & Rejt Ł. 2007: Weather-dependent variation in the cold-season diet of urban kestrels *Falco tinnunculus*. *Acta Ornithol. 42: 107–113.*