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SMALL MAMMALS IN THE DIET OF THE TAWNY OWL (*STRIX ALUCO* L.) IN CENTRAL EUROPEAN LOWLAND

ABSTRACT: We analysed the variation of small mammal species composition in the Tawny Owl *Strix aluco* L. diet in forest habitats of Central European Lowland. We used published and unpublished materials from forest-dominated landscapes in Lithuania (n = 7 locations), Poland (n = 8) and East Germany (n = 1); marginal localities were ca. 870 km from each other. We recorded that in Central European Lowland the proportion of Arvicolidae in the Tawny Owl diet significantly increased, while that of Muridae decreased toward north-east. The proportion of less common rodent species (including Gliridae and *Sicita betulina* Pallas) in the diet also increased significantly toward NE. We did not record any trend of small mammals diversity along the analysed transect. We suggest that the change of Arvicolidae to Muridae ratio toward north-east can be caused by the replacement of mice with boreal vole species in small mammal community. Small mammal diversity in Central Europe is subject of discussion.

KEY WORDS: Voles, mice, micromammalia, diet composition, predation, owls.

1. INTRODUCTION

Central European Lowland is one of the most important regions for distribution of many forest-dwelling animals on the conti-

nent. Ranges of many species are restricted to that area, and in West Europe only small population fragments occur. For example, in Poland, Lithuania and other countries toward east, populations of two big carnivores - lynx (*Lynx lynx* L.) and wolf (*Canis lupus* L.) – still exist, while in Western Europe these species are extremely rare or do not occur any more (Mitchell-Jones *et al.* 1999). The west-east gradient can be also observed in smaller scale. In eastern Poland lynxes and wolves are more common than in western part (Jędrzejewski *et al.* 2004, Niedziałkowska *et al.* 2006). Similar pattern was described for bird community. Many forest-specialised bird species: Three-toad and White-backed woodpeckers (*Picoides tridactylus* L. and *Dendrocopos leucotos* Bechst.), Capercaillie (*Tetrao urogallus* L.), etc. are more common in eastern countries than in the western part of the continent (see also Tomiałojć 2000). Decreasing of forest fauna diversity toward west is caused mainly by Western European forest fragmentation and man-made forest structure transformation (Tomiałojć 2000). Forest management strongly influences the average tree age, stand composition and stand structure (Wesołowski 2005 and references therein),

which, in turn, affect many forest dwelling species (e.g. Wesołowski *et al.* 2005, Czeszczewik and Walankiewicz 2006).

There is lack of a clear pattern for small mammal community in Central Europe. According to Mitchell-Jones *et al.* (1999) small mammal species richness in West Europe (Spain, France, Germany) is higher than in Poland and Baltic countries. On the contrary, Baquero and Telleria (2001) stated that the highest Micromammalia species richness (bats and introduced species excluded) takes place in Central Europe. We conducted analysis of species composition and diversity of small mammals (excluding bats) in Central Europe on the basis of the Tawny Owl (*Strix aluco* L.) diet composition. This owl is a generalist, that hunts in many habitats (closed canopy forests, open areas, etc.) and uses many hunting techniques (perching, by flight, etc.). Thus in its diet, many species of different size, ecology and taxonomy can be found (see review in Galeotti 2001). Contrary to other raptors, it also hunts conspicuous and arboreal mammals (e.g. *Gliridae*), which are extremely rarely caught during standard live-trapping (Balčiauskienė 2005, Lesiński and Gryz 2008). All these features make the Tawny Owl diet a reliable estimator for species diversity in small mammal community.

2. STUDY AREA, MATERIALS AND METHODS

We analysed published and original materials concerning the Tawny Owl diet from forest dominated landscapes in Lithuania ($n = 7$), Poland ($n = 8$) and one locality from Germany (Fig. 1). Marginal localities were ca. 870 km from each other. All included localities lay along SW – NE transect in European Lowland, where forest ecosystem is a natural vegetation zone. No barriers (mountain ranges, big water bodies, etc.) occur between, thus, consecutive localities are not isolated. The climate of this region is diversified and influenced by oceanic and continental air masses from west and east, respectively. Average temperatures of the region range from +9.4°C in Berlin to +8°C in Warsaw and +6.1°C in Vilnius. Forest communities (mixed and coniferous in NE part

of the study area) are a dominating potential vegetation types.

The Tawny Owl diet composition was assessed on the basis of pellets and prey remains found in breeding and resting places. Published and original data used in the analysis were collected most often all year round during last ca. 40 years. Material was analysed according to standard methods (Raczyński and Ruprecht 1974), using mammal bones for species identification. We used Pucek's key (1981) and reference collection material for comparisons.

For every locality of the Tawny Owl diet studies, we assessed longitude and latitude. These two variables positively correlated, thus we reduced them with the Principal Component Analysis (PCA) method to one variable called the "transect" hereinafter. High values of the transect variable denote NE part of the study area, whereas low values SW localities. For each Tawny Owl diet sample, we divided all consumed mammals to four main prey categories (expressed as a percentage of the number of consumed specimens): Insectivora (*Sorex araneus* L., *S. minutus* L., *Neomys fodiens* Pennant, *Talpa europaea* L.), Muridae (*Apodemus flavicollis* Melchior, *A. sylvaticus* L., *A. agrarius* Pallas, *A. uralensis* Pallas, *Micromys minutus* Pallas, *Mus musculus* L., *Rattus rattus* L., *R. norvegicus* Berkenhout), Arvicolidae (*Microtus arvalis* Pallas, *M. agrestis* L., *M. oeconomus* Pallas, *M. subterraneus* de Selys-Longchamps, *Myodes glareolus* Schreber, *Arvicola terrestris* L.) and uncommon mammals (*Muscardinus avellanarius* L., *Dryomys nitedula* Pallas, *Glis glis* L., *Sicista betulina* Pallas). The percentages of the four prey categories in the Tawny Owl diet had normal distribution (Kolmogorov-Smirnov test, all cases $P > 0.38$). The first three categories (percentage of Insectivora, Muridae and Arvicolidae) inter-correlated which was expected since they sum to 100%, and high proportion of one prey category in the diet leads to low proportions of remaining two (uncommon mammals were quite independent since their contribution in the diet was marginal). Therefore we applied the PCA method for the data reduction. The fourth group (uncommon mammals) was treated independently. We applied linear regression to check if changes of the values of

the two components extracted by the PCA and the percentage of uncommon species in the diet are significant along the SW–NE transect.

We assessed the diversity of small mammal community with the help of individual based rarefaction curves implemented in EstimateS 7.5.1. (Colwell 2005), which estimates expected cumulative species number for a given number of randomly chosen individuals. The curves were created independently for each locality on the basis of specimens identified to species level only (20 species). *Apodemus sylvaticus* and *A. flavicollis* were treated jointly because of problems to distinguish them from the Tawny Owl diet remains as well as *Rattus rattus* and *R. norvegicus*. The smallest sample of the Tawny Owl diet had 67 specimens identified to species level (Biržų Giria Forest). Thus for the comparison of small mammal diversity among all sites we used the expected cumulative number of species for 67 randomly chosen specimens (i.e. values of Coleman curve – see Colwell 2005). We checked if the diversity

index showed a significant trend along the analysed transect with linear regression (the diversity index had normal distribution, Kolmogorov-Smirnov test, $P > 0.30$).

3. RESULTS

We analysed 7493 small mammal specimens of 20 species originating from 16 localities (Fig. 1, Appendix). In general, Muridae and Arvicolidae constituted main component of the Tawny Owl diet, whereas Insectivora and uncommon mammals were less important prey categories in Central European Lowland. In case of some localities both Insectivora and uncommon mammals were absent (Appendix).

For further analysis we included two independent components describing diet variation of the Tawny Owl extracted by the PCA which had eigenvalues greater than one. The first component should be interpreted as Muridae–Arvicolidae ratio in the diet, while the second one as Insectivora–Muridae ratio (Table 1). Among two analysed com-

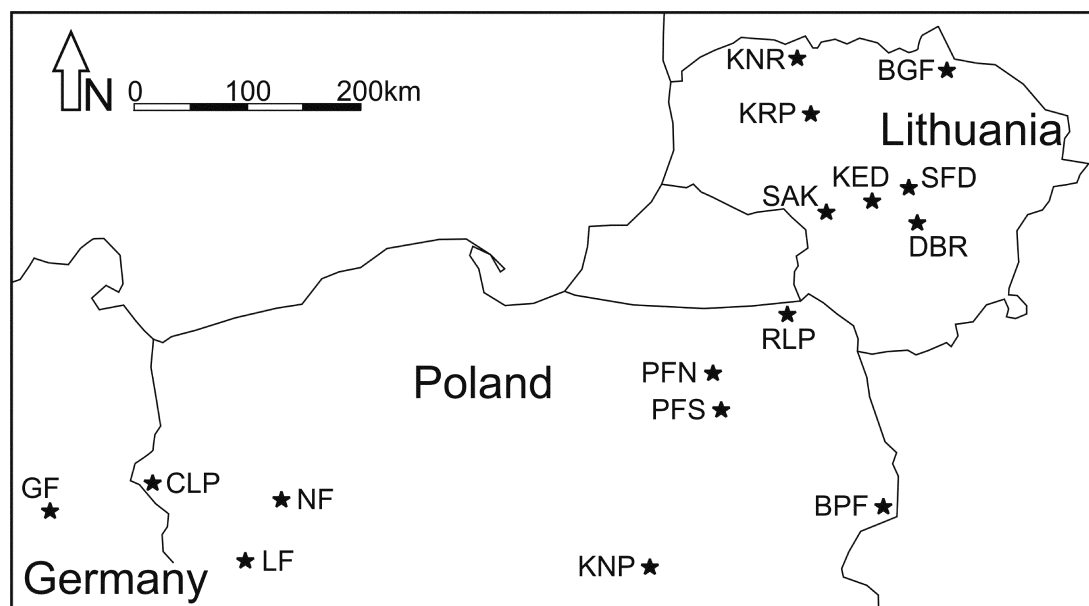


Fig. 1. Localization of the Tawny Owl diet study sites: GF – Grünewald Forest, CLP – Cedyński Landscape Park, LF – Lubrza Forest, NF – Notecka Forest, KNP – Kampinoski National Park, BPF – Białowieża Primeval Forest, PFS – Piska Forest (Southern part), PFN – Piska Forest (Northern part), RLP – Romincka Forest Landscape Park, SAK – Šakiai district, KED – Kėdainiai district, SFD – Šėta forest district, DBR – Dambraiva Botanical-Zoological Reserve, KRP – Kurtuvėnai Regional Park, KNR – Kamanos Strict Nature Reserve, BGF – Biržų Giria Forest. Source: Kowalski 1961, Wendland 1980, Ruprecht and Szwagrzak 1987, Kowalski and Lesiński 1988, Kowalski 1996, Ruprecht *et al.* 1998, Balčiauskienė *et al.* 2000, 2005, 2006, Žmihorski and Osojca 2006, Romanowski and Žmihorski 2009, J. Romanowski and M. Žmihorski, unpubl.

Table 1. Loadings of the first two components extracted by the Principal Component Analysis performed on the Tawny Owl diet from 16 localities in Lithuania, Poland and East Germany. Significant correlations ($P < 0.05$) are marked in bold.

	Component 1	Component 2
Insectivora	0.46	0.89
Muridae	0.72	-0.69
Arvicolidae	-0.99	-0.09
% of variance explained	43.0%	34.6%

ponents, the first one showed a significant negative trend along the SW–NE transect (Linear regression $R^2 = 0.47$; $n = 16$; $F = 12.20$; $P = 0.004$) (Fig. 2). It can be concluded that proportion of Arvicolidae increased while that of Muridae decreased toward NE in the diet of the Tawny Owl in Central European Lowland. The second component did not show any significant trend (Linear regression $R^2 = 0.02$; $n = 16$; $F = 0.31$; $P = 0.584$) (Fig. 2). The proportion of uncommon species increased significantly toward NE along the transect (Linear regression $R^2 = 0.28$; $n = 16$; $F = 5.52$; $P = 0.034$) (Fig. 2).

The cumulative small mammal species number for 67 randomly chosen individuals was greatly diversified among sites from 6.31 (Šėta forest district, Lithuania) to 13.73 (Kurtuvėnai Regional Park, Lithuania), however no significant trend along the SW–NE transect was recorded for the values of small mammal community diversity index (Linear regression $R^2 = 0.01$; $n = 16$; $F = 0.11$; $P = 0.745$).

4. DISCUSSION

A significant decrease of component 1 values toward NE is a result of replacement of Muridae with Arvicolidae in the Tawny Owl diet. This conclusion is supported by two facts. Firstly, the importance of Muridae in component 1 is higher than the importance of Insectivora (component 1 loadings 0.72 and 0.46, respectively). Secondly, the tendency in component 2 variability along the transect, despite its insignificance (Fig. 2), suggests that the proportion of Insectivora increased and that of Muridae decreased toward NE.

The observed changes in Muridae-Arvicolidae ratio along the transect may be driven by two different processes: changes of

the Tawny Owl feeding habits, and changes of small mammal community in the field. There are no clear proofs for the geographical trends in prey selection by the Tawny Owl. Moreover, Arvicolidae (mainly the Bank vole *Myodes glareolus*) spend more time under the snow and therefore are less frequently hunted by the Tawny Owl during snow occurrence as compared to mice, which move more often on the snow surface (Jędrzejewski *et al.* 1994). Since the snow cover is thicker and occurs longer in the NE than in SW part of the transect, the reverse pattern of the Tawny Owl diet variability may be expected (i.e. increase of mice proportion in the diet towards NE). Therefore it seems more plausibly that the observed pattern is caused by variability in small mammals community inhabiting forest ecosystems of the temperate Europe. However, more research is needed to confirm the hypothesis.

The long-term data on small mammal trapping in Lithuania confirm this conclusion on the increasing contribution of Arvicolidae in the small mammal community towards NE. In 10-year-long trapping series (1981–1990) from NE Lithuania, *M. glareolus* formed 68% of the total catch; *M. arvalis*, – 5%; while *A. flavicollis*, – merely 7%; and *A. agrarius*, – 3% (Balčiauskas 2005). In Central Lithuania 8-year-long trapping series (1997–2004) give the following small mammal share averages: *M. glareolus* – 48%, all *Microtus* vole species – 16%, *A. agrarius* – 19% and *A. flavicollis* – 10% (Balčiauskienė and Naruševičius 2006). In the Białowieża Primeval Forest, a share of *A. flavicollis* in two long-term trapping series (1985–1992 and 1986–1991) was much higher: – 24% and 35%, respectively (Jędrzejewski *et al.* 1994).

What could be possible reasons for the hypothesized changes in the Muridae/Arvi-

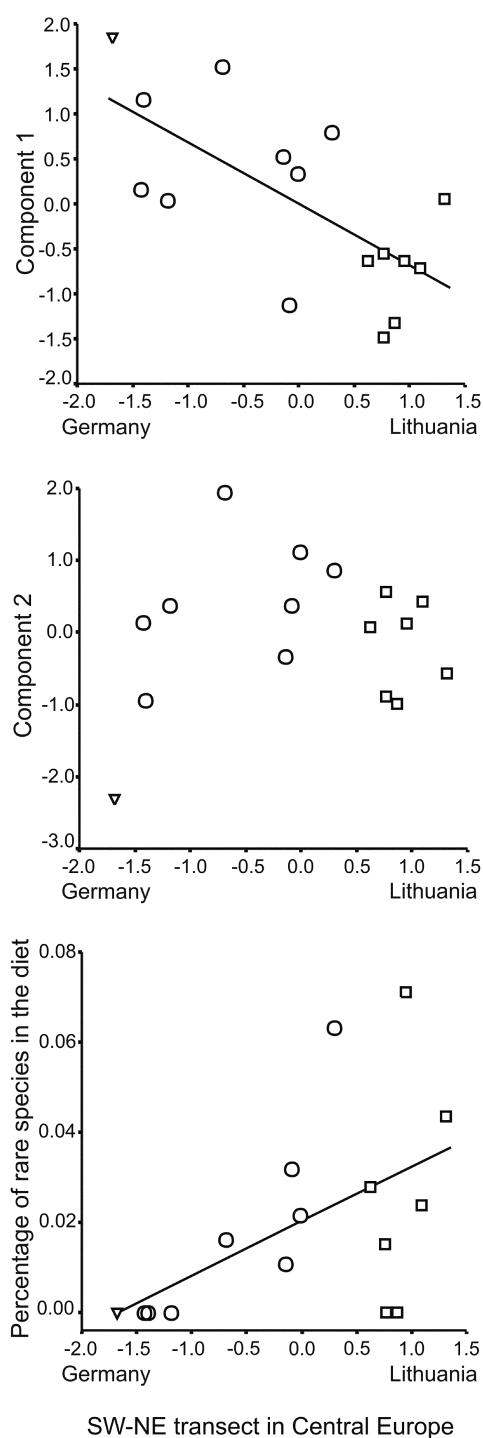


Fig. 2. Variability of small mammals in the Tawny Owl (*Strix aluco*) diet expressed as two components extracted by the PCA and percentage of uncommon mammals (see Table 1 and methods for details) along the SW-NE transect in Central European Lowland. Triangle denotes locality from Germany, circles from Poland and squares from Lithuania.

colidae ratio in Central Europe? Both Muridae and Arvicolidae contain forest dwelling (e.g. *A. flavicollis*, *M. glareolus*) and field dwelling species (*A. agrarius*, *M. arvalis*), so the possible decrease in forest coverage along the transect should not be responsible for the pattern observed. The effect of temporal changes in the populations of small mammals during last 40 years cannot be excluded. However, the exact time of pellet collections seem to be randomly distributed along the transect (e.g. most recent data come from both NE part of the region – Balčiauskienė *et al.* 2006 – as well as from its SW part – Ruprecht *et al.* 1998, Żmihorski unpublished). The European ranges of Arvicolidae species, commonly recorded in the Tawny Owl diet (*M. glareolus*, *M. arvalis*, *M. oeconomus* and *M. agrestis*), with the exception of *M. arvalis*, are more northern than the ranges of Muridae species (*M. minutus*, *A. agrarius*, *A. flavicollis* and *A. sylvaticus*) (Mitchell-Jones *et al.* 1999). In the case of two rodent species dominating in the Tawny Owl diet, i.e. *M. glareolus* and *A. flavicollis* (Jędrzejewski *et al.* 1994), the difference in the European ranges is also true (Mitchell-Jones *et al.* 1999). It is known that competition in small mammal community is important (e.g. Rychlik and Zwolak 2005), and this process can shape the densities of Arvicolidae and Muridae species (Fasola and Canova 2000). Therefore, it can be expected that closer to the northern limit of its range, average densities of *A. flavicollis* as well as its competitive ability should be smaller as compared to *M. glareolus*. Gradual replacement of Muridae with Arvicolidae in small mammals community toward NE seems to be a reliable explanation for the observed changes in the Tawny Owl diet composition. Moreover, it should be noted that in general, forests become more fragmented toward SW in central Europe, which can influence competition between small mammal community species (Orrock and Fletcher 2005). Additionally, dispersal ability through man made barriers, as roads, is higher in the case of *A. flavicollis* as compared to *M. glareolus* (Rico *et al.* 2007). However, all those presumptions need to be verified and changes of the Tawny Owl foraging ecology cannot be excluded.

The proportion of uncommon species in the Tawny Owl diet is significantly higher in the NE part of the investigated transect. *Muscardinus avellanarius*, *Glis glis* and *Sicista betulina* occur also in Western Europe; so the observed pattern is not the result of the naturally restricted range of those species. It is most possible that the observed pattern was influenced by anthropogenic transformations of forest structure on landscape level (fragmentation) and stand level (e.g. introducing the coniferous trees) (Wesołowski 2005). High level of habitat fragmentation in Western Europe and lack of spatial continuity of forest ecosystems can significantly restrict ranges of forest-specialised species with low dispersal abilities (e.g. *Glis glis*), which was clearly proved in the case of large ungulates and carnivores (e.g. Groot Bruinderink *et al.* 2003, Niedziałkowska *et al.* 2006). On the other hand, the variability of diversity index of small mammal community does not show any significant pattern along the investigated transect. This suggests that the diversity of small mammal community in Central European Lowland depends on habitat structure in a given locality rather than on large-scale factors (see also Bertolino *et al.* 2001).

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APPENDIX

Diet composition of the Tawny Owl (*Strix aluco*) expressed as percentage of prey items in 16 localities included in the analysis. Only mammalian prey data are presented. See Fig. 1 for the full localities names and data source.

Locality	Latitude	Longitude	Insectivora %	Muridae %	Arvicolidae %	Uncommon mammals %	Total number
GF	52.509	13.065	3	71	26	0	1417
CLP	52.802	14.297	15	49	36	0	353
LF	52.315	15.437	21	28	51	0	113
NF	52.728	16.042	23	24	53	0	420
KNP	52.345	20.774	49	23	26	2	923
PFS	53.593	21.683	16	10	71	3	282
PFN	53.812	21.648	33	19	46	2	699
BPF	52.708	23.741	18	36	45	1	276
RLP	54.337	22.427	32	25	37	6	245
SAK	54.986	23.057	15	18	64	3	358
KED	55.111	23.731	22	15	62	1	1535
KRP	55.845	23.071	15	17	61	7	169
KNR	56.280	22.882	19	14	65	2	169
BGF	56.094	25.034	12	32	52	4	71
SFD	55.163	24.329	0	23	77	0	99
DBR	54.930	24.264	0	20	80	0	364