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Seasonal and habitat variation in the diet of the tawny owl (*Strix aluco*) in Central Poland during unusually warm years

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Abstract: In the temperate climate zone in Europe the composition of the diet of predatory vertebrates shows evident variability between the warm and cold season. However, the recently observed climate warming can mitigate the effect of snow cover and low temperatures on the winter foraging ecology of raptors, thus affecting trophic webs in ecosystems. We analysed diet variability in the tawny owl *Strix aluco*, between the warm and cold seasons of four unusually warm years (as compared to reference years of 1950–2000) in two habitats (forest vs. farmland) in Central Poland. The most important prey group in the tawny owl's diet were mammals, constituting over 80% of prey items. There were distinct diet differences between the two seasons: insectivorous mammals, birds and amphibians were caught more often during the warm season, and Muridae and Arvicolidae during the cold season. The proportion of insectivorous mammals, voles and amphibians was significantly higher in forest than in farmland. Diet diversity, analysed with rarefaction methods and expressed as the expected cumulative mammal species number for a given number of randomly sampled preyed mammals, was independent of season and higher in forest than in the agricultural habitat. We conclude that even during unusually warm years tawny owls change significantly their feeding habits between the warm and cold season. The effect of season, habitat and weather factors on diet variability in raptors are discussed.

Key words: predation; climate change; feeding generalist; diet variability; diet diversity

Introduction

It is well established that the foraging ecology of vertebrate predators inhabiting the temperate zone changes significantly between the warm and cold part of the year. In sedentary predators it is the diet composition and food niche breadth that change (documented for primeval conditions by Jędrzejewska & Jędrzejewski 1998). These changes are driven by seasonal variability in composition of prey community (in winter many species become inactive or migrate south), prey availability (e.g. inversely related with snow depth) and shift in hunting techniques used by predators. These season-related patterns were analysed and confirmed in the case of many avian and mammalian predators (Jędrzejewska & Jędrzejewski 1998; Brzeziński et al. 2006; Żmihorski & Rejt 2007).

Recently the European climate has become warmer (e.g., Korzuchowski & Degirmendzic 2005), which can lead to shorter persistence of snow cover and increase in mean winter temperatures. One should expect that these changes will affect the foraging ecology of many predators and predator-prey interactions (Hebblewhite 2005). It is also very plausible that the differences in diet composition between the warm and cold season will become less marked with the decrease of winter severity. Influence of weather on the foraging ecology of predators has great importance for predicting the impact of global warming on food webs. In our research we analysed diet variability in the tawny owl *Strix aluco* L., 1758. It is the most important primeval forest predator in the European temperate zone in terms of prey biomass consumed per area unit (Jędrzejewska & Jędrzejewski 1998) and a common species in various woodland habitats. The composition of the tawny owl diet in Central Poland shows substantial seasonal variation during usual cold years, with the highest seasonal differences in the frequency of insectivores, rodents and amphibians (Goszczyński et al. 1993).

It has been shown that the composition of the tawny owl's diet changes significantly in severe winter conditions (Jędrzejewski et al. 1994, 1996) and mild winters may increase the number of breeding owls and their reproductive performance (Sasvári & Hegyi 2002; Solonen 2005). Moreover, the tawny owl's winter mortality is correlated with weather severity (Jędrzejewska & Jędrzejewski 1998). Therefore, we propose a hypothesis that during warm years seasonal differences in the composition of the diet of the tawny owl will be much less pronounced and will be absent in the case of some of the main prey categories. We verify this presumption by investigating seasonal and habitat variability

in the composition of the tawny owl's diet during four unusually warm years.

Material and methods

We conducted our research in the Mazovia Lowland in Central Poland, (52° N; 21° E). The mean annual ambient temperature there reaches 7–8 °C and the amount of precipitation is ca 550 mm (Stopa–Boryczka & Boryczka 2005). We collected pellets in two types of habitat: forest (NE part of the Kampinoski National Park, KNP) and farmland (north of the KNP, in the Vistula River valley). 70% of the KNP is covered by coniferous and mixed forests. Deciduous forests consist mainly of the oak-hornbeam *Tilio-Carpinetum* and ash-alder *Ribeso-Alnetum* associations. As compared to managed forests, the Kampinoski NP has more old stands, which positively affects tawny owl densities in this area (3.2 territories per 10 km^2, Kowalski et al. 1991; Żmihorski et al. 2005). The surroundings of the tawny owl's territories in the farmland area were a mosaic of meadows, arable and fallow lands, as well as built-up areas. Densities in this habitat were on average 0.6 territories per 10 km^2 (Dombrowski et al. 1991).

The analysis of the tawny owl's diet was based on pellets collected in seven localities. In total, we analysed 40 separate pellet collections, in which number of prey items ranged from one to 211. The pellet collections originating from the same habitat and season were pooled for the further statistical analysis. From each pellet all skeletal fragments useful for identification were separated out, according to a standard method (Raczyński & Ruprecht 1974). Mammalian prey species were identified by lower jaws, skulls and teeth (Pucek 1981), birds by parts of beaks and amphibians by femurs (using our own reference materials). Diet composition was presented as percentage of prey individuals of a given species. In total, we identified 1,218 vertebrate prey individuals.

The pellets were collected in 1982, 1983, 1994 and 1995. We compared the average ambient temperatures in these years for Poland with the average in other years of the period 1950–2000 (meteorological data: www.tyndall.ac.uk). Two independent comparisons were made: for the warm season (April–September) and cold season (October–March). The mean ambient temperature in the years of pellet collection was significantly higher than in the reference years, for both the warm (average 14.8 °C and 14.1 °C, respectively, independent samples t-test, $t = 2.3$; $P = 0.026$) and cold season (2.7 °C and 1.6 °C, respectively, $t = 3.8$; $P = 0.001$).

In order to check the effect of season and habitat on the diet composition we grouped the collected material by habitat (forest and agriculture) and season (warm and cold). This habitat division was discrete, since three territories were located in the interior of the Kampinoski NP and the remaining four in an agricultural landscape (including one territory on the forest edge). We adopted the seasonal division after Jędrzejewska & Jędrzejewski (1998) into the warm (16 April – 30 September) and cold (1 October – 15 April) season. The pellet samples were divided into cold and warm season groups according to the date of collection. We investigated the variability of each prey species proportion in the tawny owl's diet for the two habitats and seasons independently, using nonparametric tests.

In order to compare the tawny owl's diet diversity between the two seasons and habitats we used rarefaction methods. Only mammalian prey species were included in this analysis, as they are the most important prey group (> 80% prey individuals) and the less numerous birds and amphibians were often not identified to the species level. We used individual based rarefaction curves implemented in EstimateS 7.5.1 to establish the expected cumulative mammalian species number for a given number of randomly chosen individuals of mammals (Coleman Curves; see Colwell 2005 for details). Coleman Curves were applied independently for each of the four habitat/season pellet samples. Because the smallest pellet sample (forest habitat during the cold season) consisted of 87 mammals, we established the tawny owl's diet diversity as the expected cumulative mammal species number for 87 randomly chosen mammalian prey items in a given season and habitat.

Results

In general, mammals were the most important prey group in the tawny owl's diet (> 80% of prey items). Insectivora, Arvicolidae, Muridae, Aves and Amphibia were the most important prey items with regard to prey number consumed (38%, 23%, 21%, 11% and 6% of prey number, respectively). In total, 18 mammal species and 11 bird species were recorded in the diet. Common shrew (*Sorex araneus*), water shrew (*Neomys fodiens*), and bank vole (*Myodes glareolus*) were the most frequently caught prey.

Insectivorous mammals were caught more often during the warm season, in both the farmland (common shrew and pygmy shrew *Sorex minutus*) and forest (common shrew and water shrew). In both habitats seasonal differences in the proportion of the bank vole and common vole (*Microtus arvalis*) in the diet were similar: these species were caught more often in winter (Table 1). Synantropic species (house mouse *Mus musculus* and brown rat *Rattus norvegicus*) were preyed more frequently in the warm season, while the three Muridae rodents (harvest mouse *Micromys minutus,* striped field mouse*Apodemus agrarius,* wood mouse *A. sylvaticus*) were caught more often in winter, however, this pattern was significant only for the agricultural habitat. Frequency of birds in the farmland diet was higher during the warm season.

Seasonal variation in proportion of the five main prey groups in the diet showed similar patterns both in the forest and farmland: Insectivora, Aves and Amphibia were hunted more often in the warm season, and Arvicolidae and Muridae in winter (Fig. 1).

In general, the forest dwelling prey, e.g. the bank vole, yellow-necked mouse (*Apodemus flavicollis*) and murids identified as *Sylvaemus* sp., were caught more often in the forest habitat (Table 1). Common dormouse (*Muscardinus avellanarius*) was preyed on by the tawny owls in the interior and edge of the forest. Rodents typical of open areas (the common vole and striped field mouse) were selected more often by the owls inhabiting the farmland habitat. Insectivorous mammals, with exception to one species, were recorded more often in the pellets collected in the forest habitat (Table 1). Also, species associated with built-up areas – the house mouse and rat – were more common in the farmland diet, however, these differences were significant only for

Table 1. Diet composition of the tawny owl (*Strix aluco*) in two habitats (farmland and forest) and two seasons (warm: 16 Apr. – 30 Sept. and cold: 1 Oct. – 15 Apr.) in Central Poland.

Species	Proportion of prey number				Statistical significance			
	Farmland		Forest		Cold vs. warm season		Farmland vs. forest	
	Warm	Cold	Warm	Cold	Farmland	Forest	Warm season	Cold season
Talpa europaea L., 1758	0.28	0.00	0.84	1.56				
Sorex araneus L., 1758	22.78	0.00	17.20	8.59	***	*	*	***
Sorex minutus L., 1758	7.78	0.00	10.96	12.50	***			***
Neomys fodiens (Pennant, 1771)	0.00	0.00	24.96	3.13		***	***	
Myodes glareolus (Schreber, 1780)	3.06	9.49	10.62	26.56	**	***	***	***
Arvicola terrestris (L., 1758)	1.39	0.00	1.69	0.00				
Pitymys subterraneus (de Sélys Longchamps, 1835)	0.28	0.00	0.51	0.00				
Microtus oeconomus (Pallas, 1776)	4.72	3.65	5.23	0.78		*		
Microtus agrestis (L., 1761)	0.00	0.00	1.35	2.34				
Microtus arvalis (Pallas, 1779)	5.28	16.06	1.35	5.47	***	**	***	**
Microtus sp.	1.39	0.00	1.35	0.78				
Mus musculus L., 1758	9.72	0.73	0.17	0.78	***		***	
Rattus norvegicus (Berkenhout, 1769)	2.50	0.00	0.34	0.78			**	
Micromys minutus (Pallas, 1778)	0.56	13.14	1.18	2.34	***			**
Apodemus agrarius (Pallas, 1778)	0.56	19.71	0.51	2.34	***			***
Apodemus sylvaticus (L., 1758)	0.28	7.30	0.51	0.00	***			**
Apodemus flavicollis (Melchior, 1834)	0.56	1.46	3.04	0.78			**	
Sylvaemus sp.	1.39	2.19	0.51	14.06		***		***
Apodemus sp.	6.67	10.22	4.38	7.03				
Muscardinus avellanarius (L., 1758)	3.06	0.00	0.67	0.00			**	
Mustela ermina L., 1758	0.00	0.73	0.00	0.00				
Aves	27.50	15.33	2.19	0.00	**		***	***
Amphibia	0.28	0.00	10.45	10.16			***	***
Total (n)	360	137	593	128	–	–	–	–

Explanations: Numbers are proportion of prey number. Significance of the observed differences was tested with the chi-square test. Significant differences are marked as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

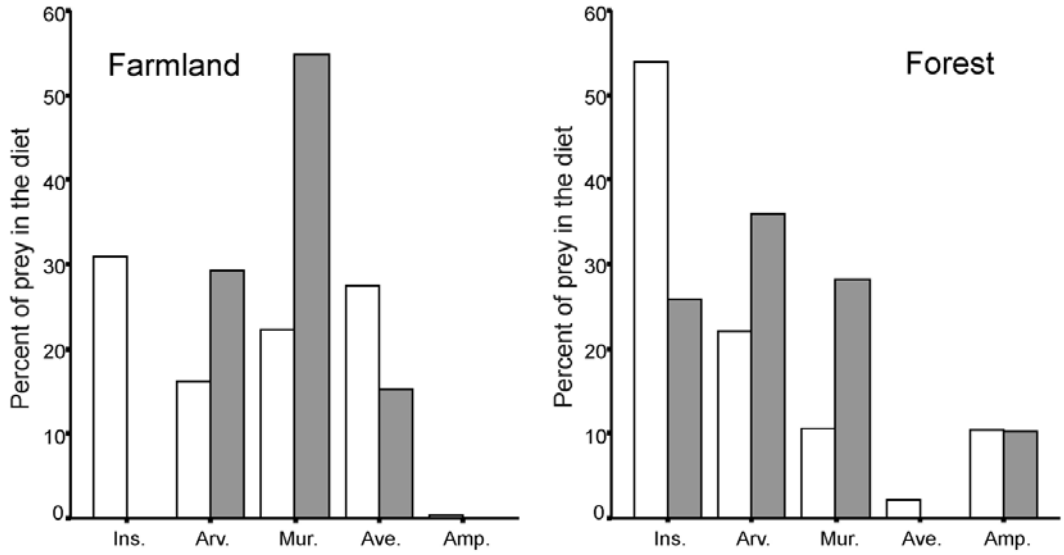

Fig. 1. Differences in the contribution (expressed as % of prey number) of the five main prey categories to the diet of the tawny owl *Strix aluco* between the warm season (16 Apr. – 30 Sept; empty bars) and cold season (1 Oct. – 15 Apr.; shaded bars), in farmland and forest habitats in Central Poland. INS – Insectivora; ARV – Arvicolidae, MUR – Muridae, AVE – Aves, AMP – Amphibians.

the warm season. In both seasons birds were caught by the owls more often in the farmland, whereas amphibians in the forest.

The pattern of diet variability between the two habitat types was similar in both seasons. In both seasons the proportion of Insectivora, Arvicolidae and Amphibia was higher in the forest habitat, and the percentage of Muridae and Aves was greater in the farmland habitat (Fig. 1).

The tawny owl's diet diversity, expressed as the expected cumulative number of mammal species for a constant number of mammalian prey individuals proved to be clearly habitat-dependent (Fig. 2). For the 87 randomly chosen mammalian prey items the expected

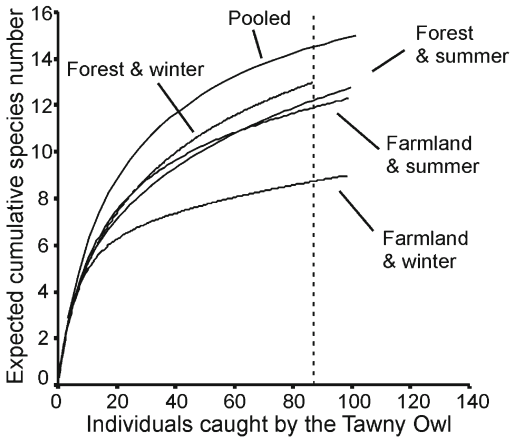

Fig. 2. The expected cumulative mammal species number for a given number of randomly sampled mammals preyed by the tawny owl *Strix aluco* in two habitats and two seasons independently, as well as for the pooled material. The dotted vertical line indicates the 87 prey individuals corresponding to the smallest sample analysed.

cumulative species number ranged from 8.7 (farmland, cold season) to 13.0 (forest, cold season). Both curves representing the forest habitat diet lie above the two farmland diet curves. In other words, the tawny owl's diet diversity was higher in the forest than in the farmland habitat.

Discussion

In general, our results on the diet composition of the tawny owl are comparable with other material collected in Central Europe (Jędrzejewski et al. 1994; Balčiauskienė et al. 2006; Żmihorski & Osojca 2006). Rodents were the main prey component, while the three remaining prey categories – Insectivora, Aves and Amphibia – were less important and should be treated as additional prey. We recorded many prey taxons and lack of one clear dominant prey species, which is typical for the tawny owl foraging ecology and contrasts with the diet of feeding-specialists, such as the long-eared owl *Asio otus* L., 1758 (Goszczyński 1981; Romanowski 1988; Żmihorski 2005; Romanowski & Żmihorski 2008). The observed high diet diversity was driven by the feeding strategy of the raptor: being feeding-generalists, tawny owls use many hunting techniques, in many different habitat types and are able to prey upon a variety of taxa and species of diverse ecology (Goszczyński et al. 1993; Jędrzejewski et al. 1994; Galeotti 2001).

Several authors have shown that the tawny owl's diet composition is affected by severe winter conditions (Jędrzejewski et al. 1994; Solonen & Karhunen 2002), however, much less is known about the variability of this species' diet in warmer weather conditions. The average cold season ambient temperature in the four analysed years was more than 1 ℃ higher than in the reference years, and the difference was highly significant. Nevertheless, the differences between the warm and cold season diet of the tawny owl remained distinct. The proportion of some prey species in the diet clearly changed between the warm and cold season, and the differences reached up to 30% (e.g., the % of insectivorous mammals or murids in the farmland, Fig. 1). The proportion of Insectivora, Aves and Amphibia in the diet became higher and that of Arvicolidae and Muridae lower in the warm season. It should be noted that this pattern was seen in both habitat types: forest and farmland. The observed variability in diet composition was most possibly shaped by seasonal differences in prey abundance and availability. Amphibians become inactive and large number of birds migrates south in the cold season. Therefore, in winter these two prey categories are less available for the tawny owl. Consequently, it is forced to hunt other prey species, which in turn leads to the higher contribution of Arvicolidae and Muridae to the diet. The same pattern of the tawny owl's seasonal diet variability was earlier documented in the Białowieża Primaeval Forest, Eastern Poland (Jędrzejewska & Jędrzejewski 1998). This similarity is untypical, as the Białowieża Forest is characterised by more severe winter conditions than is our study area in Central Poland. Our results indicate that the observed variability is characteristic of the Central European population (Galeotti 2001).

We recorded pronounced differences in the diet composition between the two habitat types. In both seasons mice and birds were preyed more often in the farmland, while Insectivora, Arvicolidae and Amphibia were caught more frequently in the forest. This reflects differences in prey community between the two habitats. The obtained results suggest that the owls inhabiting the farmland used also woodland and/or forest edges for hunting, and that the forest dwelling owls sometimes hunted in the open habitat. These presumptions are supported by the presence of the common dormouse in the farmland diet as well as by the presence of striped field mouse, common vole and house mouse in the forest diet. These observations confirm that the tawny owl shows high level of habitat plasticity and is able to use many habitats (Redpath 1995; Sanchez-Zapata & Calvo 1999; Galeotti 2001).

The forest diet of the tawny owls was more diversified than the farmland one. Most probably, in the farmland the potential prey community was impoverished by man-made habitat transformations and agriculture management. The diet of the tawny owl is often used in faunistic studies of Micromammalia (e.g., Balčiauskienė 2005). What is important, our data indicate that in the case of limited sampling effort the most efficient way to establish the maximal number of small mammal species living in a given area is by analysis of pellets collected in a forest habitat during the cold season. However, in our study diversifying the seasonal and habitat origin of the material additionally increased the diet diversity (Curve "pooled" in Fig. 2). Therefore, it can be recommended that the tawny owl's pellets used for small mammal community evaluations should be collected in many habitats and during different seasons.

We recorded distinct differences in the composition

of the tawny owl's diet, both across seasons and habitat conditions. The pattern of diet variability was consistent across the seasons and habitats. The composition of the tawny owl's diet during unusually warm years exhibits clear and statistically significant variability between the cold and warm season. Therefore, we did not confirm the hypothesis stating that relatively high ambient temperatures during winter make seasonal differences in the tawny owl's diet insignificant. On the contrary, the reverse pattern was observed – seasonal changes in the diet variability were distinct. On the basis of these results it may be concluded that a slight decline in winter severity related to climate change should not have a considerable effect on the diet composition of the tawny owl.

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