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Weather-dependent variation in the cold-season diet of urban Kestrels *Falco tinnunculus*

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Abstract. The composition and variation of the diet of urban Kestrels in Warsaw (Central Poland) were studied during non-breeding periods (October–March) between 1995 and 2003. A total of 1 651 pellets were collected (at 15 sites), in which 2 390 vertebrate prey items were found. The most common prey were small rodents (80% of items, 78% of biomass), predominantly Common Voles. Birds were markedly less common (7% of items, 11% of biomass). The dietary composition was variable during the cold season. Mean ambient temperature and the consecutive day of the cold season did influence the diet composition but snow depth did not. The main prey category in the Kestrels' diet — Microtidae — remained stable and independent of weather conditions. The percentages of mice and birds were negatively affected by mean ambient temperature, and consumption of birds was higher at the beginning (October) than at the end of the winter (March). Prey number and biomass of prey per pellet decreased during the cold season but were not influenced by temperature. The index of food niche breadth was inversely proportional to temperature.

Key words: Kestrel, *Falco tinnunculus*, ambient temperature, diet variability, urban habitat

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INTRODUCTION

More and more widespread development of urban areas has become an important factor influencing animal world (e.g. Gillbert 1989, Luniak 2004). A new, artificial environment created by humans destroys habitats but can also generate new ecological niches for many species (Luniak 2004). Inhabiting urban environment is followed by changes in several aspects of their biology and ecology, including food habits and diet composition (e.g. Andrzejewski et al. 1978, Luniak 2004). For sedentary species, adjustment to new trophic conditions can be crucial during winter when food availability decreases. It can be true especially for birds of prey that unlike most synurbic species do not utilize anthropogenic food but prey upon other animals. Raptors rarely become synurbic species (e.g. Brown 1978). In western Palearctic the most common urban bird of prey is the Kestrel (e.g. Cramp & Simmons 1980, Śliwa & Rejt 2006). This species started colonising cities

about 150 years ago in Western Europe and recently is more and more common also in east European towns where they establish stable and dense populations (e.g. Salvati et al. 1999, Rejt 2001, Kübler et al. 2005).

In the case of open landscape (rural) Kestrel populations, diet composition and variation, diet preferences, as well as the relationship between diet and population productivity during whole year have been studied by several authors (e.g. Korpimäki 1985, 1986, Korpimäki & Norrdahl 1991 and others). There are significantly fewer studies concerning the foraging ecology of urban populations, especially those from Central and Eastern Europe, which have been living in cities for a relatively short period. Furthermore, most studies focused on the breeding season and/or were based on small sample sizes (e.g. Pikula et al. 1984, Romanowski 1996, Salvati et al. 1999). Consequently, there is little data on winter diet composition in urban populations (e.g. Darolova 1986).

In the autumn Kestrels do not feed young and therefore they do not need to hunt as frequently as in the breeding season. In addition, they can save energy, as autumn average temperatures are quite high. Also the most important prey of Kestrels in the rural landscape, the Common Vole *Microtus arvalis* reaches then its highest densities, and becomes much more available for raptors due to changes in vegetation structure (Aschwandten et al. 2005). On the other hand, during the second part of winter (February, March) Kestrels experience scarcity of food (Village 1990). This is because at that time, due to winter mortality, populations of rodents reach their lowest numbers in the season (e.g. Jędrzejewska & Jędrzejewski 1998) and snow cover reduces their availability for birds of prey (Canova 1989, Jędrzejewska & Jędrzejewski 1998). Additionally, low temperatures force Kestrels to cut down on energy expenditure (e.g. Village 1983).

In most cities Kestrels turned to alternative prey — small passerines, which compose bulk of their diet (e.g. Darolova 1986, Salvati et al. 1999, Kübler et al. 2005). In urban landscape this group of potential prey is abundant and available for raptors all year round. However, Kestrels inhabiting cities for a short time prey mostly upon voles (Romanowski 1996, Rejt 2004, 2007).

The main aim of this study was to investigate the composition of the diet of urban Kestrels in the cold season and to find if weather factors — snow and temperature — affect its composition and variation. The better knowledge of factors influencing feeding habits of the Warsaw population of Kestrels can help understand the dynamics of urban populations and differences between urban and rural Kestrels (Rejt et al. 2004, 2005, Rejt 2007).

MATERIALS AND METHODS

The study was conducted between 1995 and 2003 in Warsaw, Central Poland (450 km², 1.7 million dwellers, 52°N, 21°E). This region is affected by the mild and wet oceanic climate of Western Europe as well as by the harsh and dry continental climate of Eastern Europe and Asia. During the study period (October–March) snow cover lasted on average for 54 days (24–81 days in consecutive seasons) and was highest in February (average 3.6 cm). The mean ambient temperature for all the cold season months amounted 4.4°C (1.6–6.5°C in consecutive seasons) and was lowest in December

(average for all years -0.8°C) and highest in October (12.8°C). The average air temperatures were lowest in 1995/1996 season (1.6°C from October till March) and highest in 2000/2001 (6.5°C) (data of Institute of Meteorology and Water Management everyday bulletins, hereafter IMWM). The local weather conditions were influenced by the city and could change along the urban gradient, being milder in the centre.

The composition of the diet of Kestrels was estimated by pellet analysis, for the period between October in year *n* to March in year *n* + 1. The pellets were collected for 8 non-breeding periods, from 1995 to 2003, at 15 localities, which were used by Kestrels as breeding sites (Rejt 2007). All of them were situated within the central part of the city. In total, 192 pellet collections were obtained, each comprising 1 to 63 pellets, so that 1651 pellets were collected and 2390 prey items were separated.

Each pellet was put into water and all skeletal parts (jaws, skull fragments and teeth), reptilian scales, bills and feathers were separated out according to methods described by Raczyński & Ruprecht (1974). Next, they were classified after Pucek (1981) and Moreno (1985). On the basis of skeletal elements, the number of prey items in each pellet was estimated. Invertebrates were not identified to lower taxa and only their total frequency in pellets was calculated (Rejt 2004, Kübler et al. 2005). Standard values of mammalian and reptilian body masses were taken from Jędrzejewska & Jędrzejewski (1998) and Pucek (1981), and the body masses of birds — from Sokołowski (1992).

To assess diet variation, we analysed 35 independent pellet collections, each of which consisted of at least 20 prey items. Collections made at the same sites but at different times of the non-breeding period were treated as independent. For each pellet collection proportion of three main prey group (Microtidae, Muridae, Aves) as well as invertebrates frequency in the pellets were assessed. Moreover, for each collection we counted the average number of prey items per pellet (hereafter NPP), average biomass per pellet (BPP) and breadth of the trophic niche. The breadth of the trophic niche (index *B*) was calculated from the Levins's formula (1968):

$$B = (\sum p_i^2)^{-1}$$

where *p_i* is the percent of a given prey group (Microtidae, Muridae, Aves and other) in all prey

items caught. B values range from 1 (the narrowest trophic niche) to 4 (the widest niche).

We assumed that Kestrel produced one pellet per day and that the collections contained only the most recent pellets. This allowed us to estimate the time of pellet production, basing on the number of pellets in each collection ($n = 14\text{--}63$). For instance, for the collection of 20 November, which consisted of 16 pellets, it was estimated that the pellets were produced between 4 and 20 November. For each time span of pellet production, we calculated the following weather variables: 1) % of days with snow cover, 2) % of days with snow cover thicker than 10 cm, 3) mean snow cover depth, 4) mean ambient temperature, 5) % of days with temperature below 0°C, 6) % of days with temperature below -10°C. Most of these variables were strongly mutually correlated. However, variables (3) and (4) were not correlated, so they were selected for further analysis. Also consecutive day of the cold season was included in the analysis as a separate factor. These three independent variables were included in the multiple regression analysis to explain variation in the cold-season diet of Kestrels.

RESULTS

The diet of Kestrels in Warsaw was composed mainly of small rodents. The dominating group were voles Microtidae, both with regard to the number of prey individuals and biomass (Table 1). Among vole specimens identified to the species level, the Common Vole constituted about 96%, while other species, the Root Vole *Microtus oeconomus* and Field Vole *M. agrestis*, were much less frequent. Mice, mainly the striped field mouse *Apodemus agrarius*, and various birds each comprised about 7% of the prey. Shrews and reptiles

Table 1. Diet composition (vertebrates) of the Kestrel in Warsaw during the cold season (October–March) of 1995–2003. All years pooled together. %N — percentage of prey individuals, %B — percentage of biomass consumed.

Prey category	%N	%B
<i>Sorex araneus</i>	0.17	0.07
<i>Sorex minutus</i>	0.12	0.02
<i>Crocidura leucodon</i>	0.04	0.02
Soricidae unidentified	0.29	0.09
Insectivora — total	0.63	0.20
<i>Microtus arvalis</i>	7.95	7.90
<i>Microtus oeconomus</i>	0.29	0.40
<i>Microtus agrestis</i>	0.04	0.05
<i>M. arvalis/agrestis</i>	22.43	22.30
Microtidae unidentified	31.13	30.95
Microtidae — total	61.84	61.59
<i>Apodemus agrarius</i>	0.59	0.52
<i>Mus musculus</i>	0.12	0.13
<i>Micromys minutus</i>	2.34	0.98
Muridae unidentified	4.43	3.94
Muridae — total	7.49	5.58
Rodentia unidentified	11.42	10.76
Mammalia unidentified	11.71	11.03
<i>Passer sp</i>	0.33	0.51
<i>Parus major</i>	0.04	0.04
<i>Columba livia</i>	0.04	0.62
Aves unidentified	6.28	9.52
Aves — total	6.69	10.69
<i>Lacerta agilis</i>	0.21	0.13
Total	2 390 (100%)	45 677 g (100%)

were hardly ever caught by Kestrels. The frequency of invertebrates (insects) in pellets was 15.7%.

The proportion of particular prey groups in diet changed significantly throughout the cold-season period. Mean ambient temperature and consecutive day of the cold season influenced Kestrel diet variability (Table 2). Snow cover depth had no effect on Kestrel feeding habits and this variable is not shown in Table 2.

Proportion of the most important group of prey, Microtidae, did not show any significant changes from October to March and was not

Table 2. Effects of consecutive day of the cold season (October 1=day1) and mean ambient temperatures on the Kestrels diet variability (percentage of prey number); results of backward multiple regression analysis. * — $p < 0.050$; ** — $p < 0.010$; *** — $p < 0.001$

Dependent variable	Independent variables — beta standardized coefficient		R_{adj}^2	p
	Consecutive day of the cold season	Mean ambient temperature		
Microtidae	ns	ns	0.023	0.263
Muridae	ns	-0.37*	0.110	0.029
Aves	-0.36*	-0.36*	0.174	0.018
Invertebrates	-0.51***	0.43**	0.474	0.000
Number of prey/pellet	-0.51**	ns	0.233	0.002
Prey biomass/pellet	-0.57***	ns	0.303	0.000
Food niche breadth (B)	ns	-0.36*	0.102	0.034

affected by temperature (Table 2, Fig. 1, 2). Proportions of two alternative prey categories, Muridae and Aves, were negatively affected by mean ambient temperatures (Table 2, Fig. 2). The opposite tendency was found for the frequency of insects which was positively related with ambient temperature and reached its lowest values at the end of the non-breeding period. The proportion of birds declined from the beginning to the end of the cold-season (Fig. 1). Consecutive day of the cold season and mean air temperatures explained nearly a half of variation in the frequency of invertebrates in kestrel pellets (Table 2). The NPP and BPP indices decreased during cold season ($Y = -0.002X + 1.61$; $R^2 = 0.255$; $n = 35$, $p = 0.002$; $Y = -0.038X + 30.97$; $R^2 = 0.323$; $n = 35$; $p < 0.001$ respectively, Fig. 3), but were not affected by mean temperatures (Table 2). The food niche of kestrels (B index) was markedly wider in low temperatures ($Y = -0.034X + 2.117$; $R^2 = 0.129$; $n = 35$; $p = 0.034$, Fig. 3).

DISCUSSION

The diet of Kestrels in Warsaw during the cold-season appeared to be similar to its diet during the breeding period (Rejt 2004). The main part of the prey consists of voles (mostly Common Voles) while proportion of other groups is only marginal. The winter diet of populations inhabiting west European cities is dominated by birds and has a significantly lower proportion of rodents (e.g. Yalden 1980). Although the Common Vole is a rare species in cities (Andrzejewski et al. 1978, Białożej 2003), Kestrels probably hunt upon it at adjacent areas with open landscape (Rejt 2007, Authors' own data).

During winter, variable weather conditions (temperature, wind, snow cover) as well as time of the season could affect the prey availability and hunting behaviour of several raptor species (e.g. Wuczyński 2005). In effect it could influence the variability of their diet. A similar behavioural response was found also in Kestrels (Village 1983, 1998) so it was probable that urban Kestrels diet would be changed in the course of winter and according to variable weather conditions.

In our study, Microtidae, the most important group of Kestrels' prey remained stable in their diet during the whole cold season. There were no significant changes connected with weather conditions. However, it was found that

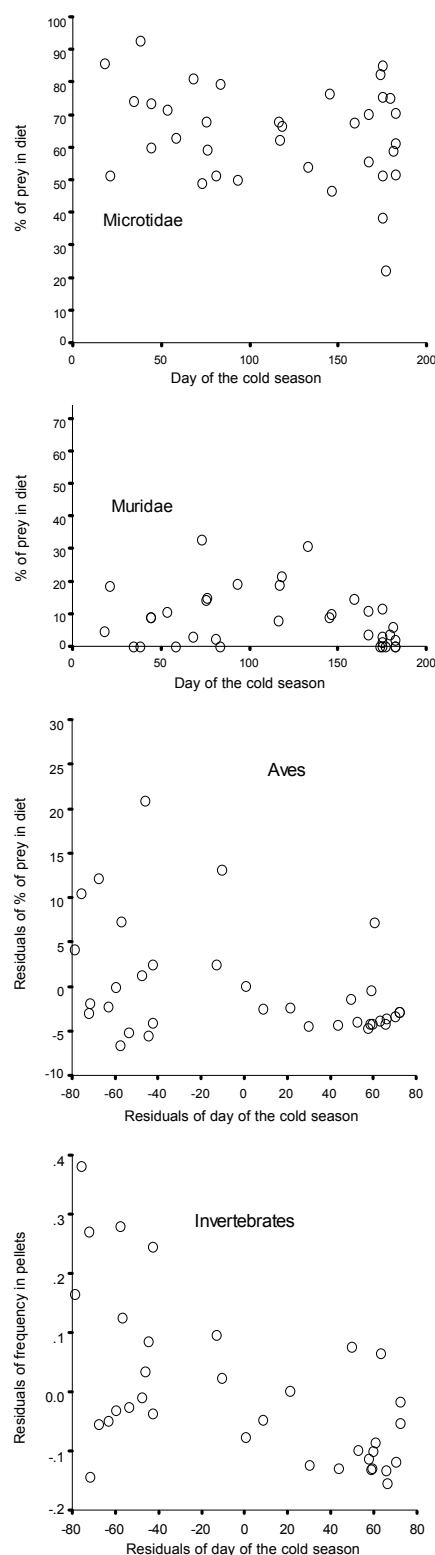


Fig. 1. Variation of the diet of the Kestrel during the cold season of 1995–2003. Data taken from the model of backward multiple regression presented in Table 2. Each point represents a collection of 14 to 63 pellets. Day 1 indicates 1st October.

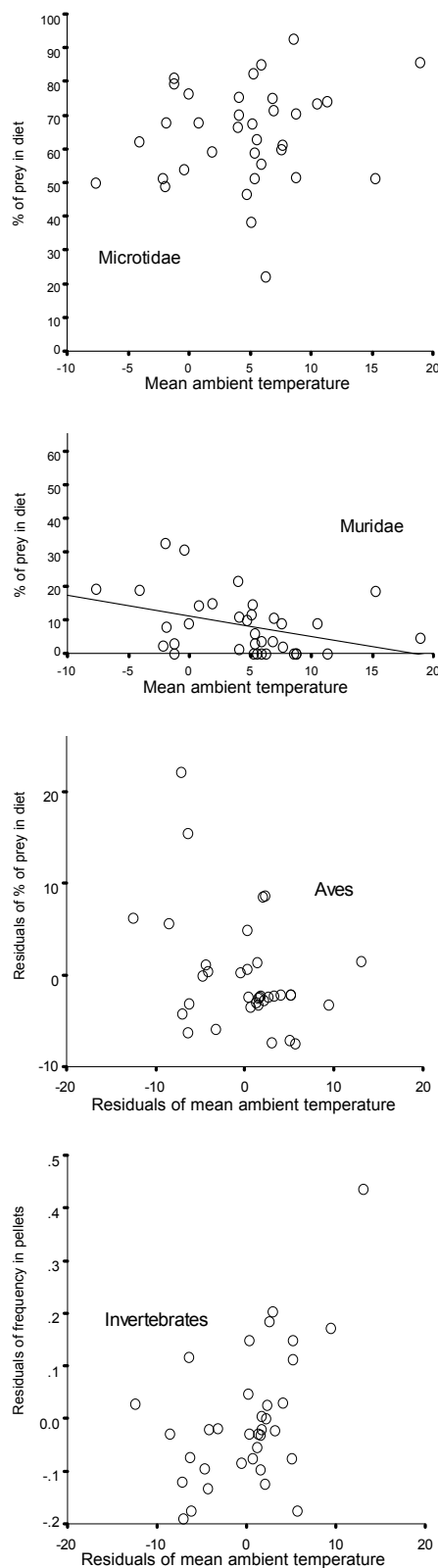


Fig. 2. Variation of the diet of Kestrels in relation to mean ambient temperatures [°C]. Other explanations as in Fig. 1.

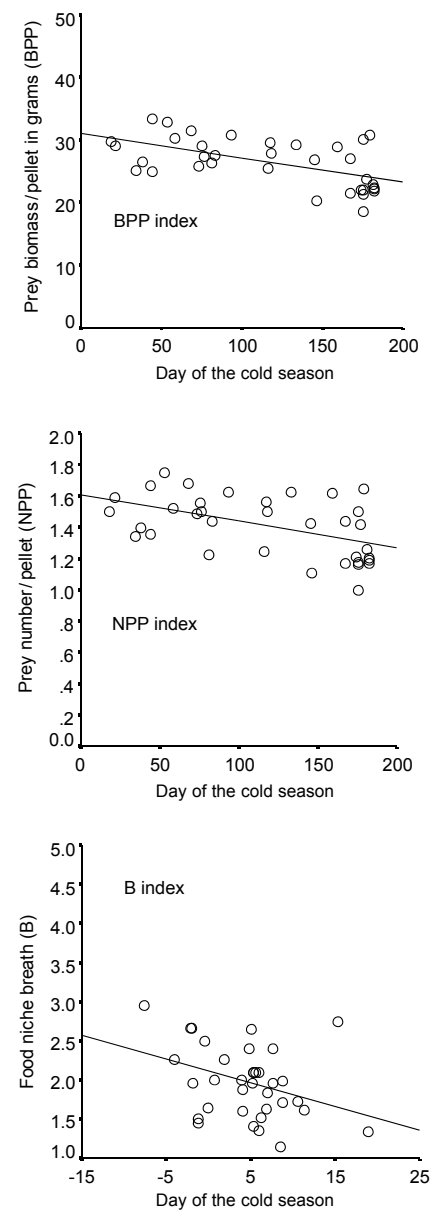


Fig. 3. Variation of the indices of Kestrel diet in relation to consecutive day of the cold season and mean ambient temperatures [°C]. Other explanations as in Fig. 1.

mean temperature affected the proportion of alternative prey: mice, birds and invertebrates, as well as the breadth of trophic niche. Surprisingly, there were no effects of snow cover on Kestrels diet variability. Several studies focused the importance of snow cover for diet composition among rodent eating raptors. High snow cover could negatively affect the availability of some rodents, for both birds of prey and mammalian predators (Jędrzejewski &

Jędrzejewska 1993). Voles which move under snow are safer from an attack in spite to mice, which move on the snow surface (Jędrzejewski et al. 1994). In effect it changes the proportion of various groups of prey in raptor diets (e.g. Canova 1989, Jędrzejewska & Jędrzejewski 1998). A lack of such relationships in the case of Warsaw Kestrels can be partly explained by specific of the urban environment. Milder climate and manual snow cleaning at several plots as well as hunting over the railways could lower the snow cover effect.

The increasing occurrence of alternative prey in Kestrel diet in Warsaw was affected by temperatures. While the proportion of their main prey (voles) remained stable throughout the cold season (at about 60% of food biomass consumed), Kestrels shifted from one type of alternative prey (invertebrates) to another (mice and birds) as ambient temperatures decreased. A relatively high frequency of the latter in the Kestrel diet resulted in a wider food niche (calculated for vertebrate prey, only) in periods with low temperatures.

A decrease in NPP and BPP during the course of the cold season probably reflected changes in day length and worsening weather conditions. Furthermore, towards early spring rodent and bird populations decline due to winter mortality (Pucek et al. 1993).

The Polish population of urban Kestrels is partly migratory (Village 1998, Tomiałojć & Stawarczyk 2003). It is known that a part of the Warsaw population migrates, but several individuals stay in the city for the whole winter (Ł. Rejt, unpubl. data.). The availability of the alternative prey, such as mice and birds, can be important for urban Kestrels especially in the winter. During cold-season kestrels wintering in Warsaw experience unfavourable weather conditions, and, as it was shown, have to considerably change their diet. It should be underlined that Kestrels which are adapted to hunting voles (e.g. Viitala et al. 1995) are less efficient in catching mice and birds, as suggested by Korpimäki (1986 and references therein). On the other hand, the birds which spend winter in their breeding areas can choose better nest sites in early spring. Rejt (2001) observed high competition for breeding sites among Kestrels in Warsaw. Therefore, our results suggest that Kestrels can benefit from wintering in the city, although they have to adjust their diet to seasonally varying availability of prey.

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STRESZCZENIE

[Zmienność składu pokarmu miejskich pustulek w Warszawie w zależności od warunków pogodowych w sezonie pozalęgowym].

Badano skład pokarmu i zmienności diety warszawskich pustulek w okresie od października do marca w latach 1995–2003. W 15 różnych lokalizacjach na terenie miasta zebrano 1651 wypluwek, z których wypreparowano 2390 ofiar kręgowych. W diecie dominowały drobne gryzonie stanowiąc 80% ofiar i 78% biomasy. Najliczniejszą ofiarą był nornik zwyczajny. Udział ptaków był znacznie niższy (7% ofiar i 11% biomasy). Skład diety zmieniał się istotnie w czasie sezonu objętego badaniami. Stwierdzono, że na skład pokarmu pustulek miały wpływ średnia temperatura powietrza i czas trwania sezonu niełęgowego, natomiast grubość pokrywy śnieżnej nie miała wpływu. Udział norników, które były główną kategorią ofiar zimujących pustulek, był stabilny i niezależny od warunków pogodowych. Średnia temperatura powietrza wpływała negatywnie na udział myszy i ptaków w diecie pustulek a pozytywnie na frekwencję bezkręgowców w wyplawkach. Znaczenie ptaków w diecie pustulek i frekwencja bezkręgowców w wyplawkach zmniejszały się istotnie w ciągu badanego okresu. Zarówno średnia liczba ofiar w jednej wypluwce jak i średnia biomasa w jednej wypluwce istotnie zmniejszały się w trakcie badanego sezonu i osiągały najniższe wartości wczesną wiosną i były niezależne od temperatury powietrza. Z kolei szerokość niszy pokarmowej była odwrotnie proporcjonalna do temperatury powietrza i osiągała najwyższe wartości w środku sezonu.