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Diet composition of Common Kestrels *Falco tinnunculus* and Long-eared Owls *Asio otus* coexisting in an urban environment

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We studied the dietary composition of urban populations of Common Kestrels (*Falco tinnunculus*) and Long-eared Owls (*Asio otus*) under fluctuating vole abundance in České Budějovice during 2002–2005. Common Voles were the dominant prey. In poor vole years, the dietary proportion of alternative prey increased in both species. Long-eared Owls fed more on mice and related rodents, whereas the Common Kestrels' diet shifted to insects. The different alternative diets may be due to species-specific daily activity, hunting techniques and/or hunting habitats. Furthermore, we examined the possible relationship between the distance from a nest to the city centre and the proportion of voles in the diet. The Kestrel diet was not markedly influenced by distance, but for Long-eared Owls an increasing distance was associated with an increasing dietary proportion of voles.

1. Introduction

The Common Kestrel (*Falco tinnunculus*) and Long-eared Owl (*Asio otus*) are two raptor species that have successfully moved into urban habitats. The Common Kestrel is the most frequent diurnal bird of prey in the cities of Central Europe (Riegert 2005). The first records of kestrels breeding in urbanized areas of the Czech Republic are from 1950s (Hudec 1986), and presently they inhabit all Czech cities in high densities (Šťastný *et al.* 2006). Similarly, in some Central-European cities, the breeding density of the nocturnal Long-eared Owl can be high (Prague: 0.29 pairs/km^2, Fuchs *et al.* 2002; Leszno: 0.16 pairs/km^2, Kuźniak 1996; České Budějovice: 0.31–0.50 pairs/km^2; Lövy 2007).

In farmland habitats both species primarily feed on small rodents, especially Microtinae voles (Village 1981, Village 1990, Korpimäki 1992). However, the urban environment differs from farmland, for example, in being free of large predators such as the Eagle Owl *Bubo bubo*, by increased threat from humans and by increased (or altered) nesting opportunities. Perhaps the most conspicuous difference between farmland and urban habitats is that vole abundance is higher in the former (Čiháková & Frynta 1996). Therefore, vole-eating predators are either forced to hunt voles outside the city and/or feed on alternative prey.

The coexistence of these vole-eating specialists has previously been studied in farmland areas (Korpimäki 1987), but data from urban areas have

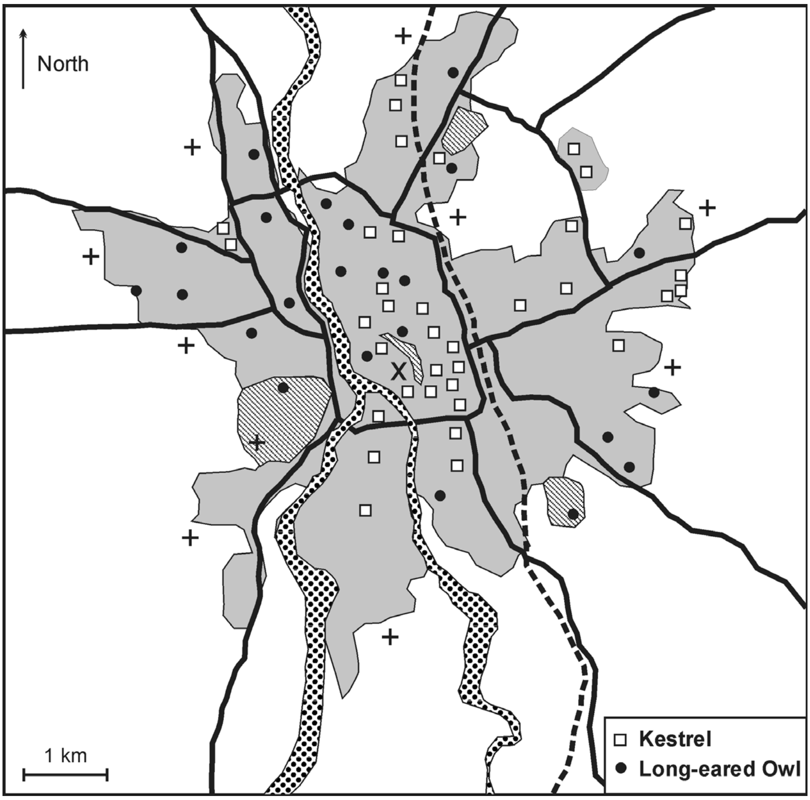

Fig. 1. Locations of Common Kestrel and Long-eared Owl nesting sites in České Budějovice. Grey area = built-up land; striped area = park or cemetery; dotted area = river; solid line = main road; dashed line = railway; x = the city centre; + = vole-trapping site.

been lacking. Neighbouring pairs of Kestrels and Long-eared Owls in Finland have shown less diet overlap than more distant nesters, and the extent of diet overlap has been shown to correlate with the availability of small mammals (Korpimäki 1987).

Our study is the first to investigate the diet of Kestrels and Long-eared Owls in urban conditions simultaneously. Our aim was to compare the dietary composition of these two species over a four-year period of fluctuating vole availability across an urban-rural gradient in České Budějovice, Southern Czech Republic. We made three predictions regarding vole availability, in concordance with the optimal diet theory (Pyke 1984). (1) With decreasing vole abundance the proportion of alternative prey should increase in the diet of both species. (2) Alternative prey should be different for Kestrels and Long-eared Owls due to different daily activities, hunting techniques and/or interspecific competition. (3) For both species, the proportion of main vole prey in the diet should be higher for pairs breeding far away from as compared to those breeding near to the city centre.

2. Material and methods

The study was conducted in the city of České Budějovice (Southern Bohemia, 49°N, 14°E; 40 km^2; 100,000 inhabitants; 250–300 m a.s.l.). Long-eared Owls breed in old Magpie (*Pica pica*) nests, often in parks (Fig. 1). Kestrels breed in old buildings, with the highest breeding density being in and adjacent to the city centre (Fig. 1). The population size of Long-eared Owl in the city area is up to 15 breeding pairs each year, while Kestrels have up to 40 breeding pairs each year. The land-cover composition (proportion of different habitat types) changed less than 3% at any Owl/Kestrel hunting area during the study period (for details, see Riegert *et al*. 2007).

The availability of the Common Vole (*Microtus arvalis*) was assessed each year. Voles have been studied from 1997 to 2005, with abundance peaks in 1998, 2002 and 2005. One hundred plastic two-litre pitfall traps, with 4% formaldehyde as killing and preserving agent, were installed at a total of ten Kestrel and Long-eared Owl hunting ar-

Table 1. Diet composition (percent of all prey items; mean ± SD) of Common Kestrels and Long-eared Owls during 2002–2005 in České Budějovice. # items = number of prey items in the data; # nesting = number of recorded nesting attempts.

Year	Microtinae	Muridae	Other mamm.	Birds	Other vertebr.	Insects	# items	# nesting
Kestrel								
2002	87.5 ± 5.2	2.1 ± 2.3	0.7 ± 0.5	2.7 ± 2.4	1.4 ± 1.9	5.6 ± 5.2	301	9
2003	74.3 ± 7.6	2.5 ± 2.0	0.9 ± 1.1	5.9 ± 3.0	1.5 ± 1.8	14.9 ± 9.9	223	7
2004	93.5 ± 6.9	0.5 ± 1.1	0.2 ± 0.4	0.3 ± 1.2	1.7 ± 5.7	3.8 ± 3.7	408	15
2005	90.6 ± 7.1	0.9 ± 1.6	0.7 ± 0.7	1.9 ± 2.2	1.4 ± 1.7	4.5 ± 4.8	692	19
Long-eared Owl								
2002	90.1 ± 5.9	7.3 ± 5.0	0.5 ± 0.8	2.1 ± 1.7	0	0	1,304	8
2003	68.9 ± 12.5	23.5 ± 9.5	2.9 ± 3.6	4.7 ± 4.2	0	0	1,351	10
2004	60.2 ± 5.2	35.3 ± 6.7	1.5 ± 2.4	3.0 ± 1.6	0	0	334	4
2005	87.7 ± 4.0	10.0 ± 0.3	0.2 ± 0.3	2.1 ± 2.1	0	0	1,060	11

eas (Fig. 1). Transects of ten traps at each of the ten areas in the second half of the July, active for 17 days, were used each year. Six transects were placed in meadows and four in urban wastegrounds (ruderal areas).

Nesting attempts and diet composition were assessed from April to July each year during 2002–2005. Nests were regularly visited to verify nesting attempts. Food composition was assessed from 33 nests of Long-eared Owl and 50 nests of Common Kestrel (Table 2). At the end of each breeding season, pellets and all remains of prey (feathers of birds, body parts of bats and lizards, etc.) were collected inside of and adjacent to the Kestrels' nesting cavities, and from the Long-eared Owl nests. Small mammals were determined by identifying skulls using Anděra and Horáček (1982), and birds by beak and humeri using a reference collection. Remains of insects were sorted into categories of similar size, morphology and colour. The numbers of voles, mice and shrews were determined by the number of jaws found, while the number of birds was estimated by detected feathers.

Multivariate Regression Trees (MRT) based on Euclidean distances (De'ath 2002) were used to test the first and second predictions. The analysis was computed using R 2.8.1 software (R Development Core Team 2008). Each nesting attempt represented a sample, and the proportion of each component (voles, mice, birds, other mammals, vertebrates and insects) in the diet represented 'species' for the purpose of analysis. Raptor species (Owl/Kestrel) and study year were used as explanatory variables.

Generalized Linear Models (GLMs) were used to test the third prediction, viz. the impact of distance from a nest to the city centre on the dietary proportion of voles (the main prey for both species). As the availability of voles was expected to decrease toward the city centre (Čiháková & Frynta 1996), the proportion of voles in diet was used as the dependent variable and the distance from a nest to the city centre was used as an explanatory variable. Each nesting attempt was used as an independent replicate (sample); for pseudoreplication possibility, see below.

A Gamma error distribution was assumed and an inverse link function used (McCullagh & Nelder 1989) and forward selection of factors using Mallow's Cp-statistics were used to select the final model (Mallows 1973). The GLM factors were the distance to the city centre (an approximation of urbanization), raptor species, and an interaction between these two. Vole abundance was used as a covariate. The same analysis was also run for the Owl diet only.

Using every breeding attempt as an independent data point might introduce pseudo-replication (Hurlbert 1984). However, for both raptor species the observed nesting patterns suggest this problem to be negligible. For Long-eared Owl, no repeated breeding at the same nest was documented for consecutive years, and for Kestrels, only three pairs stayed at the same nesting site for two consecutive years. These findings were supported by wing-tag-

Fig. 2. Multivariate regression tree based on Euclidean distances for the Common Kestrel and Long-eared Owl diets (variance explained = 0.56). Diet bars, from left to right: Microtinae, Muridae, other mammals, birds, other vertebrates and insects.

ging Kestrels and using radio telemetry for both species (Riegert *et al.* 2007a, Lövy 2007).

The annual diversity of diet composition was computed using the standardized Gibson Index (Colwell & Futuyma 1971), and diet overlap was assessed according to Pianka (1974). The data unit was represented by the sum of individuals for each species or genus, depending on the accuracy of identification.

3. Results

The Common Vole was the most frequent species, making up to 79.6% of all trapped small mammals, followed by shrews (17.9%) and harvest and field mice (2.6%). The highest numbers of voles were caught in 2002 and 2005 (79 and 98 individuals, respectively). The years 2003 and 2004 were characterised by low occurrences of voles (20 and 21 individuals, respectively). The number of voles per 100 traps varied significantly between years (Chi-square test; $\chi^2 = 87.4$, df = 3, $P < 0.0001$).

The diet composition of both species changed across the study period, but Common Voles remained the dominant prey, making up over 60% of all prey items in both species (Table 1). Both species took more alternative prey in the poor vole year of 2003, and Long-eared Owls did so also in 2004 (Table 1, Fig. 2). However, the alternative prey differed between the two species (Fig. 2; 56% of variance explained in the MRT). In the diet of Long-eared Owl, the most frequent secondary prey were mice (*Apodemus, Micromys, Mus* and *Rattus*). In years with poor vole availability, mice comprised a considerable part of the owl diet (Figs. 2–3).

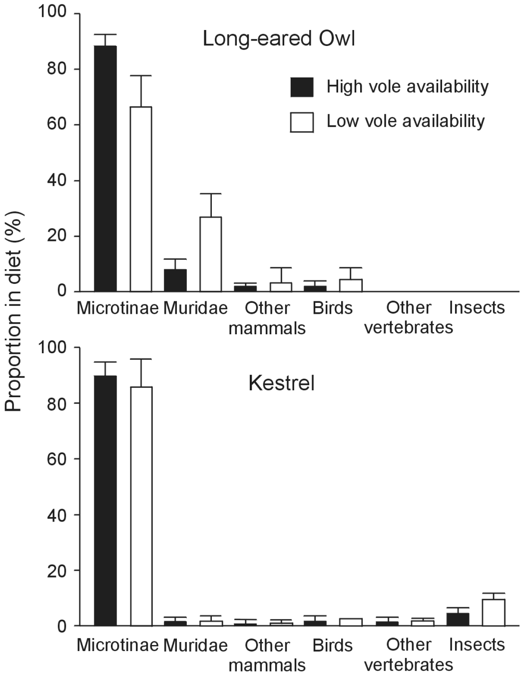

Fig. 3. Mean (± SD) proportions of diet items in the diets of Common Kestrel and Long-eared Owl during good (2002, 2005) and poor (2003, 2004) vole years.

Table 2. Diet composition (Gibson's index) of Long-eared Owls and Common Kestrels, and their diet overlap during 2002–2005 in České Budějovice. The right-hand column refers to the number of voles caught per 100 traps.

Year	Long-eared Owl	Kestrel	Overlap	Voles /100 traps
2002	1.27	1.27	0.78	79
2003	2.09	1.60	0.51	20
2004	2.43	1.46	0.43	21
2005	1.33	1.17	0.80	98
Mean	1.78	1.38	0.63	218

Kestrels had a more diverse diet than Long-eared Owls (Table 2). For example, Kestrels used a higher proportion of insects than did Short-eared Owls, particularly in 2003 (Fig. 2, Table 1). The insect prey mainly comprised ground beetles (Carabidae) and grasshoppers (Tettigonidae). The diet overlap between the two species was lower in the poor vole years of 2003 and 2004 (0.43–0.51) than in good vole years (0.78–0.80).

The dietary proportion of voles significantly differed between the two species (GLM, 12.2% of variation explained df = 81, F = 12.77, P = 0.0006). The distance between nest and city centre alone had no impact on the proportion of voles, when tested using pooled Kestrel and Long-eared Owl data (GLM; $P > 0.2$). However, the interaction between distance and raptor species was marginally significant, suggesting a species-specific distance response (GLM; 8.1% of variation explained, df = 79, F = 5.69, P = 0.0916). Kestrel diet was not influenced by the distance between nest and city centre, but Long-eared Owl individuals breeding further from the city centre had a higher proportion of voles in their diet than those breeding closer (Fig. 4). A separate analysis of Long-eared Owl diet along the urbanization gradient confirmed this distance response (GLM; 7.1% of variation explained, df = 31, F = 5.93, P = 0.0212).

4. Discussion

The diet of raptors may change when they inhabit urban areas. For example, Kestrels in large cities often enrich their diet with birds (Witkowski 1962, Beichle 1980, Darolová 1986, Romanowski 1996). However, we did not observe such a switch in České Budějovice. The proportion of birds was consistently low. The proportion of *Microtus* voles was very high, however, resembling the diet composition of rural Kestrels. The proportions of Muridae, other mammals, birds and other vertebrates were generally low.

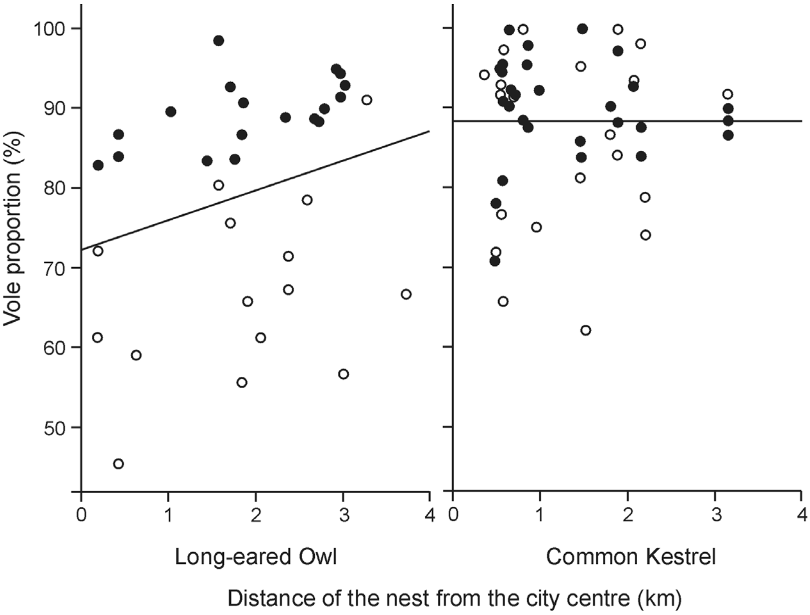

Fig. 4. The effect of distance between nest and city centre on the proportion of voles in the diets of Long-eared Owls and Common Kestrels. Filled circles = years of high vole abundance (2002, 2005); open circles = years of low vole abundance (2003, 2004).

The breeding-season foraging ecology of the Long-eared Owl in urban environments is poorly understood. In our study, *Microtus* voles were the most frequent prey. The observed food composition, with abundant voles, an increased proportion of Muridae and low proportion of other mammals and birds, is comparable with data collected from natural sites in Europe (Wijnandts 1984, Korpimäki 1992, Tome 2003). Moreover, we did not detect remains of insects in the diet of Long-eared Owl, which is in line with the above-mentioned studies.

Vole availability appeared to be the single most important factor determining diet composition for both Kestrel and Long-eared Owl, as voles formed the major portion of the diet for both species. Furthermore, the dietary proportion of voles generally decreases when this prey is scarce. However, Kestrel diet did not follow this trend, a result that is difficult to interpret. Nevertheless, the superior significance of voles (our first prediction) is in accordance with other studies dealing with this topic: for the Long-eared Owl, see Tome (1994, 2003) Korpimäki (1992) and Wijnandts (1984), and for the Kestrel, see Village (1982), Korpimäki (1985) and Korpimäki and Norrdahl (1991).

Insect abundance in Kestrel diet increased during vole scarcity, while Muridae represented an alternative prey for Long-eared Owls. Such dietary diversification was further supported by a smaller diet overlap during years of low as opposed to years of high vole abundance. Our results from a medium-sized city are consistent with those of Korpimäki (1987), who found a less pronounced diet composition overlap in sympatric Kestrels and Long-eared Owls during poor vole years in farmland. The different alternative prey between the two species may be partly explained by differences in daily activities (Korpimäki 1987) and different hunting techniques. Kestrels, as diurnal predators, hunt almost exclusively by sight, which is suitable also for catching ground beetles during daylight. Moreover, insect prey may often be taken after non-successful strikes, whose frequency increases during periods of vole scarcity (Riegert & Fuchs 2004). In contrast, the nocturnal Long-eared Owl hunts mainly by hearing (e.g., Henrioux 2000, Wijnandts 1984). Relatively quiet beetles do not represent a suitable alternative prey, and hence the mainly nocturnal Muridae species become the predominant alternative prey, supporting our second hypothesis.

Our third prediction was not fully supported by observations. Distance between nest and city centre had a marginally significant effect on the diet of Long-eared Owls, coinciding with the decreasing vole abundance (and consequently proportion in the owl diet) toward city centre. The difference between the two species is similar to our earlier results on hunting activities revealed by telemetry and wing-tagging. While kestrels almost exclusively hunt in rural areas (Riegert *et al.* 2007a), Long-eared Owls often hunt in edge habitats within the city area, such as waste-grounds along streams, power-line openings and railway-track verges (Fig.1; see also Lövy 2007). Such habitats host a high diversity of small mammals, especially Muridae mice (Briner *et al.* 2005, Suchomel & Heroldová 2006). Kestrels hunt mostly by hovering (Village 1990), which allows them to control a large area (Village 1983). This technique is thus well-suited for hunting on large waste-ground areas at the city periphery. Long-eared Owls, on the other hand, hunt using harrier-like flight near the ground, and hovering is rare (Cramp 1985). Galeotti *et al.* (1997) and Henrioux (2000) also mention a perch-and-wait hunting technique, which is common in raptors. These strategies do not allow large areas to be controlled, but represent suitable techniques to hunt along corridor-like habitats (Galeotti *et al.* 1997).

We suggest that the observed differences between Common Kestrel and Long-eared Owl diet in the urban environment of České Budějovice are caused by several factors. Apart from the obvious difference in diurnal activity, habitat types used for hunting and particularly hunting techniques also have significant impacts on diet composition.

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Tuulihaukan ja sarvipöllön ravinnon koostumus kaupunkiympäristössä

Tutkimme tuulihaukan (*Falco tinnunculus*) ja sarvipöllön (*Asio otus*) ravinnon koostumusta vaihtelevien myyräkantojen aikana České Budějovice'n kaupungissa 2002–2005. Peltomyyrä oli tavallisin saalis. Huonoina myyrävuosina muun ravinnon osuus kasvoi molemmilla lajeilla. Tällöin sarvipöllöt saalistivat enemmän hiiriä ja niiden lähisukulaisia, tuulihaukkojen alkaessa saalistaa enemmän hyönteisiä. Erilaiset vaihtoehtoiset saaliskohteet voivat selittyä petojen erilaisella vuorokausirytmillä, saalistustekniikalla tai saalistusympäristöillä. Tutkimme myös, vaikuttaako pesän ja kaupungin keskustan välinen etäisyys saaliin koostumukseen. Tuulihaukalla vaikutusta ei havaittavasti ollut, mutta sarvipöllöllä kasvava etäisyys kaupungin keskustaan näkyi myyrien kasvavana osuutena ravinnossa.

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