ABSTRACT: In the reproduction period a male Kestrel (*Falco tinnunculus*) is a central-place forager, i.e. it transports food from hunting grounds to a central location – the nest. A central-place forager is predicted to take larger or more prey when distance to a foraging site is longer. We studied kestrels breeding in a large Central European city (population 1.7 million), whose main prey are common voles (*Microtus arvalis*). Kestrel nests are located in the centre and the outskirts, although common voles are scarce in the former. The aim of our study was to analyse the body mass of common voles found in pellets under kestrel nests and relate it to the availability of common vole habitats within 1 km from the nests, controlled for vole frequency in the pellets. We assumed that the greater availability of common vole habitats, the shorter the distance to a foraging site. We found that the body mass of common voles found in pellets was significantly positively correlated with the availability of their habitats, but was not affected by their frequency in pellets. Our results may indicate that, contrary to the central-place foraging rule, and irrespectively of the amount of other prey taken, the kestrels hunted smaller voles when foraging grounds were further away. This might stem from decreased selectivity caused by competition, either in the native territory (due to the high density of kestrels in the centre) or in territories of outskirt kestrels, invaded by city centre kestrels. On the other hand, due to lack of data on the body size of common voles in our study area, the results may suggest that common voles were on average smaller in the centre than in the outskirts. Although the published data do not support the second explanation, more research is needed to verify this.

KEY WORDS: prey size selection, competition, urban environment

In the breeding season, birds make repeated excursions from and back to a central location, such as a nest, to which they carry food. This is an instance of central-place foraging (Orians and Pearson 1979). It has been shown that the choice of prey type and size by central-place foragers is affected by distance to foraging grounds, competition, demand at the delivery point (determined by e.g. brood size) and variance-sensitivity (Ydenberg 2007). For example, many studies found that when distance to foraging grounds increased, so did food load transported by a central-place forager (e.g. Kacelnik 1984, Krebs and Avery 1985, Gil and Pleguezuelos 2001). Also, in Eastern Chipmunks *Tamias stratus* load size decreased in the presence of competitors at resource collection points (Giraldeau et al. 1994).

We studied central-place foraging patterns in the urban population of European...
Kestrels *Falco tinnunculus* (L.) in Warsaw, Poland. These raptors specialise in microtine voles, especially in Central and Northern Europe (*e.g.* Korpimäki 1985, Village 1990). The Warsaw kestrels, although urban dwellers, have also been confirmed to be vole specialists, feeding predominantly on Common Voles *Microtus arvalis* (Pallas), which comprise approximately 70–80% of their prey as estimated from pellets (Romanowski 1996, Rejt 2001, Zmihorski and Rejt 2007). This prey occurs in the outskirts but is thought to be rare or absent in the city centre, where its habitat is scarce and patchy, and which is dominated by synurbic rodent species, such as the Striped Field Mouse *Apodemus agrarius* (Andrzejewski et al. 1978, Białóżej 2003, Gryz et al. 2008, Gliwicz unpubl.). Kestrels build nests both in the centre and outskirts of Warsaw, but they breed especially densely in the former, where chances for catching a vole close to the nest are very low.

The aim of our study was to examine the body mass of common voles caught by Warsaw kestrels in the breeding season (March and April), when they are central-place foragers, and relate it to the percentage of common vole habitats within 1 km from the nest. We used this percentage as an indicator of probability that a kestrel hunts further away from its central place (the nest), i.e. the more vole habitats within 1 km from a nest, the closer to it a kestrel is predicted to hunt. We expected the body mass of common voles preyed by kestrels to be negatively correlated with the amount of common vole habitats within 1 km from a kestrel’s nest.

We analysed kestrel pellets gathered as part of a larger study. The pellets were collected in 1998, 1999 and 2001, under 11 different kestrel nests situated within the administrative boundaries of Warsaw, Central Poland (52°N, 21°E, area 517 km², population 1.7 million). We narrowed our interest to the breeding period, when the male kestrel becomes a central-place forager and is virtually the only food supplier for the female and later also for the young (Village 1983, Riddle 1993). It starts feeding his partner during courtship, which in Warsaw takes place mainly in March, and continues over the incubation period (3rd decade of March – end of April) and the young rearing period, when he supplies food for the incubating female and later for the whole family (Śliwa and Rejt 2006). Because in the region of our study common voles are born between April and May (*e.g.* Adamczewska-Andrzejewska and Nabaglo 1977), we decided to limit our analysis to March and April. This was done in order to avoid the confounding effect of change in the age structure of common vole populations.

The nest surroundings varied in terms of the amount of habitat suitable for the Common Vole, such as lawns, fallow land, roadsides, weed strips, meadows and pastures (Stein 1958). We calculated the proportion of these common vole habitats within a 1-km radius from each of the nests. We assumed that this proportion negatively correlates with the distance that Warsaw kestrels need to cover to find a vole: the more common vole habitats within 1 km, the shorter the distance. The proportion of common vole habitats ranged from 0.7 to 19.6%. For the computations we used GIS software and 1:10,000 maps (as of 2004), scanned with the resolution of 1 pixel to 70 cm in the field.

Out of the 11 nest locations some were sampled in more than one year, whereas others only in one year. It should be noted that our replicates are in fact males (as decision-makers) and not nest locations, and so we assumed the pellet sets collected under the same nests to be independent between years. This is justified by the fact that kestrels typically change partners between years (*e.g.* Palokangas et al. 1992). Thus, it is unlikely that from 1998 to 2001 a pair breeding in a given location comprised the same male.

From the pellets we dissected all skeletal elements, according to a standard method (Raczyński and Ruprecht 1974). Bones of common voles were identified to the species level with the identification key by Pucek (1984). Next, mandibular first molars (M1s) were separated from common vole jaws and their length was measured. Most pellets contained remainings of 1 vole individual, in which case we randomly selected one of the two M1s for measurement. If there were more (2 or 3) individuals in a pellet, either left or right M1s were measured. Teeth that showed digestion traces (*i.e.* were rounded) or mechanical damage (*i.e.* were broken or cracked) were discarded. Measurements were
taken with a vernier calliper, to the nearest 0.02 mm, using a $2.3 \times$ Zeiss eyepiece. We also used data on percentage frequency of Microtus voles in the pellets relative to other prey (calculated for different purposes). From other studies on Warsaw kestrels (e.g. Rejt 2004, Żmihorski and Rejt 2007) we know that Microtus arvalis is dominant in their diet and very rarely M. oeconomus and M. agrestis are found. We therefore used percentage of Microtus voles as an indicator of common vole frequency in the pellets that we analysed. It was calculated separately for each nest and year, and was based on the average of $67.0 \pm 49$ pellets (min. 16, max. 177).

In the Common Vole, the length of M1 is significantly positively correlated with body mass ($r = 0.63$, $P < 0.001$, Balčiauskienė 2007). Because the Kestrel easily digests bones of rodents, usually only their skulls or jaws are present in pellets (e.g. Yalden 1980). Consequently, M1 appears to be one of the best indicator of body mass of common voles identified in kestrel pellets. We converted all the M1 measurements into body mass values, using the linear regression formula by Balčiauskienė (2006), and body mass was used for further analysis.

In total, we measured 562 M1s of common voles (Table 1). We excluded the nests for which the number of M1 measurements in a given year was smaller than 4. For each of the remaining nests all M1 lengths were averaged, separately for each year. The distribution of individual measurements, categorised by year, was slightly skewed to the left, but divergence from normality was significant only for 1999. The dependent variable – mean body mass per nest in a given year – did not diverge from normality. We then applied a general linear mixed model to test for the effect of year (random), % common vole habitats (covariate), % voles in pellets (covariate) and the interactions: year x % common vole habitats, year x % voles in pellets and % common vole habitats x % voles in pellets on the body mass of the common voles. The percentage variables were not transformed, but their arc-sine transformation yielded the same final model and results (not shown). The dependent variable, mean body mass of common voles per nest in a given year, was weighted by frequencies on which the means were based. The random effects hypotheses in the model were tested with the Wald Z test and the fixed effects hypotheses with the F-test. We applied backward selection and the AIC value (Akaike information criterion) to reduce the number of predictors and find the most parsimonious model explaining variation in body mass (Quinn and Keough 2002). The lowest AIC model is considered to explain the most variation in the response variable with the lowest number of independent variables. We used the corrected AIC value (AICc), which should be applied when sample sizes are small, as in our case ($N = 19$). For statistical analysis we used SAS 9.1 (with Enterprise Guide 4.1) and Statistica 8.0.

The ΔAICc value of the initial model was 21.6 and all the factors and interactions were non-significant. Backward elimination of the least significant predictors (beginning from interactions) always resulted in decreasing the AICc. After removal of all the three interactions from the model ($P > 0.150$ in all cases, not shown) the common vole frequency remained non-significant ($P = 0.550$, not shown), and consequently was dropped from the model as well. The most parsimonious model (with ΔAICc = 0) retained ‘year’ and ‘% common vole habitats’ (Table 2).

The amount of common vole habitats within 1 km from the nest of the kestrels was significantly positively correlated with the body mass of common voles caught by the kestrels ($F_{(0.05,115)} = 6.98$, $P = 0.018$). The model predicts that the kestrels with the highest percentage of common vole hunting grounds

<table>
<thead>
<tr>
<th>year</th>
<th>No of nests</th>
<th>M1s/nest</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>7</td>
<td>23.3 ± 14.2</td>
</tr>
<tr>
<td>1999</td>
<td>5</td>
<td>28.0 ± 21.3</td>
</tr>
<tr>
<td>2001</td>
<td>7</td>
<td>37.0 ± 29.6</td>
</tr>
</tbody>
</table>
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Table 2. Results from the most parsimonious general linear mixed model, testing for the effect of year and % common vole habitats within 1 km radius from the nests of kestrels *Falco tinnunculus* on the body mass of common voles *Microtus arvalis* caught by the kestrels at the beginning of the breeding season (March–April), in the years 1998–1999 and 2001 in Warsaw.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random effects</td>
<td>Z-value</td>
<td></td>
</tr>
<tr>
<td>year</td>
<td>0.93</td>
<td>0.176</td>
</tr>
<tr>
<td>residual</td>
<td>2.74</td>
<td>0.003</td>
</tr>
<tr>
<td>Fixed effect</td>
<td>F-value</td>
<td></td>
</tr>
<tr>
<td>% common voles habitats</td>
<td>6.98</td>
<td>0.018</td>
</tr>
</tbody>
</table>

Fig. 1. Relationship between percent common vole (*Microtus arvalis*) habitats within 1-km radius from the nests of urban kestrels (*Falco tinnunculus*) and the body mass of common voles found in pellets collected under the nests in 1998–1999 and 2001, in Warsaw, Poland. Each data point corresponds to one nest in a given year. Symbol size denotes number of measurements per each nest in a given year.

(19.6%) on average catch voles that are 1.8 g heavier than in the case of the birds with the lowest ranking hunting grounds (0.7%) (Fig. 1). The body mass of common vole prey captured by the kestrels did not differ significantly between the years \((P = 0.176)\). The mean frequency of *Microtus* voles in the pellets was 85 ± SD 14%, and the range was 58 to 100%.

Contrary to the expectations, our results showed that the body mass of common voles caught by urban kestrels increased with the amount of common vole habitats within 1 km from the nest (Table 2, Fig.1). Importantly, both the percent frequency of voles in the pellets (of which the Common Vole was dominant) and its interaction with the percent common vole habitats were non-significant. These results may suggest that kestrels, when central-place foragers, are less selective when opportunities to find a vole close to their central location are worse, irrespectively of the relative number of alternative prey they consume. One of the causes of decreased selectivity in central foragers may be intraspecific competition, as observed in the Eastern Chipmunk (Giraldeau et al. 1994). In Warsaw, kestrels reach high densities (approx. 1.2 pairs per 10 km²), and nest especially densely in the city centre (approx. 25.7 pairs per 10 km²) (Luniak et al. 2001), which offers extremely limited common vole resources. It follows that kestrels occupying territories
with small amount of common vole habitats must suffer increased intraspecific competition for their main prey and consequently may be less selective towards the size of this prey. It is also possible that the kestrels which nest in territories poorer in common vole habitats visit more distant common vole patches. This is consistent with observations of Riegert et al. (2007) in the Czech Republic, who found that territories of city-centre krestel males, with scarcer vole habitats, were larger than and overlapped with territories of outskirts krestels. This suggests that city-centre krestels may forage in more distant hunting grounds, which are occupied by other krestels. In our study krestels with fewer common vole habitats in their territories may have invaded richer territories of other krestels, which eventually may have lead to enhanced competition between ‘intruders’ and ‘owners’ of a territory. It should be emphasized that since in the breeding season the male krestel is a central-place forager, it should carry larger prey when it covers longer distance to hunting grounds (e.g. Ydenberg 2007). Our results suggest an opposite pattern, pointing out that other factors, such as competition, may interact with this optimal foraging rule. This result, to our knowledge, has only been documented in the case of mammalian foragers, Eastern Chipmunks.

On the other hand, our results might be confounded by variation in body mass in the common vole populations in our study area, for which we did not control. First, it is probable that in the different krestel hunting territories the population dynamics of the Common Vole was asynchronous (e.g. in some locations voles started breeding earlier than in others, and the mean body mass in their populations was lower). It has been shown, however, that common vole populations inhabiting areas that are relatively close to each other may be expected to breed at the same time in a given year (e.g. Adamczewska-Andrzejewska and Nabaglo 1977, Mackin-Rogalska and Nabaglo 1990). Second, since the potential vole habitats located in the centre are smaller and patchier, which implies that they are poorer and more vulnerable to disturbance, common voles may be expected to be smaller in the centre and larger in the outskirts. However, Jacob (2003) reported that in more disturbed agricultural land (crop field, pasture) body weight of common voles was higher than in less disturbed areas. This suggests that common voles may not necessarily be smaller in the city centre. Third, it is also possible that common vole densities vary between the centre and the outskirts, and that there are density-dependent effects on body mass in these populations (Chitty 1952). Finally, due to the low amount of suitable habitats the city centre common voles may be subordinate, and hence smaller individuals forced to the sub-optimal area of the city. In general, we cannot conclusively say that the pattern that we found stems from selectivity of the krestels and not differences in common vole populations between the hunting sites.

In sum, we observed that the amount of vole habitats within 1 km from the nests of krestels is positively correlated with the size of their main prey – the Common Vole. We propose that our result may suggest a relationship between availability of hunting sites and selectivity in the krestels, which may be decreased by competition either in a bird’s territory (given the very high krestel density in Warsaw) and/or in territories of other individuals, visited by the krestels whose territories are scarcer in voles. In the latter case, it is plausible that competition may alter the effect of distance to foraging grounds on prey size selection by krestels. It should be stressed that we did not control for the abundance or body mass structure of common vole populations at the nest locations which we studied, and hence it is also possible that our results stem from these factors and not selectiveness of the krestels. Although literature data does not lend support for this explanation, more research is needed to clarify this.

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