

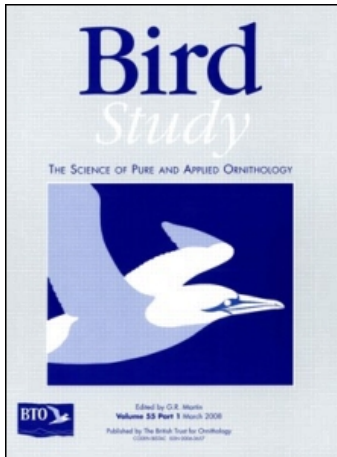
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# The impact of vegetation characteristics and prey availability on breeding habitat use and diet of Little Owls *Athene noctua* in Central European farmland

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**Capsule** Foraging habitats are determined by vegetation characteristics rather than the availability of insect prey.

**Aims** To determine the diet composition of Little Owls in relation to the availability of insects at foraging sites, and to elucidate the main factors determining the owls' habitat choice.

**Methods** The feeding ecology of Little Owls was studied during the 2002 breeding season in the agricultural landscape of western Bohemia (Czech Republic), where its population is in decline. Diet composition was determined by pellet analysis. Insect availability was studied using pitfall traps in the two most important Little Owl foraging habitats. For both habitats, we assessed the main vegetative characteristics (average and maximum vegetation height, vegetation density).

**Results** Based on number, insects were the most dominant prey, followed by small mammals; based on weight, insects comprised only a minor part of the diet. Among insect prey, Carabidae beetles were the most abundant. The proportion of insect numbers was strongly positively correlated with advancing day of the season and negatively correlated with the proportion of vertebrates. Although the highest densities of Carabidae were found in cornfields Little Owls significantly preferred grassland habitats, probably because of the lower vegetation cover.

**Conclusions** The availability of short sward vegetation in grassland habitats during the breeding season may play a key role in the conservation of Little Owls in central European farmland.

Rapid population declines of some farmland birds has concerned conservationists in many countries across Europe (Møller 1983, Fuller *et al.* 1995, Donald *et al.* 2001, Newton 2004, Batáry *et al.* 2007, Lemoine *et al.* 2007). Little Owls *Athene noctua* are a species of agricultural landscapes whose distribution and population have declined during the last 60 years (Cramp 1985, Tucker & Heath 1994) leading to extinctions in many regions (van Nieuwenhuysse *et al.* 2008). Large-scale changes and habitat loss in agricultural landscapes, especially the losses of grasslands, which are its most important feeding habitat in central Europe, are

thought to be responsible for the owls' decline (Šálek & Schröpfer 2008, Schönn *et al.* 2001, van Nieuwenhuysse *et al.* 2008). Intensive grassland management, such as increasing nitrogen availability or reseeding with competitive species (e.g. *Lolium* sp.), result in taller and denser swards and may reduce the availability of the Little Owls' principle prey species. Although the abundance of small mammals and insect prey is assumed to be relatively high, these prey may be unavailable to owls and other birds in tall and dense grassland (Southern 1954, Goodwin & Hungerford 1979, Devereux *et al.* 2004, Whittingham & Devereux 2008). On the other hand, though shorter vegetation may promote better access to food for predators such as the Little Owl, longer vegetation

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may support higher abundances of invertebrates (Devereux *et al.* 2004) or small mammals (Jacob & Brown 2000).

Little Owls are nocturnal predators that predominantly hunt ground-dwelling prey from an elevated perch (Cramp 1985, Fajardo *et al.* 1998). Dietary studies of Little Owls in agricultural landscapes usually indicate a high proportion of insect prey (Génot & Bersuder 1995, Schmid 2003). However, small passerine birds and small rodents comprise a significant part of Little Owl diets in particular study areas (Schönn *et al.* 2001, Laiu & Murariu 1997, Hounsoume *et al.* 2004). Ille (1992) reported that these owls consumed more than 82% insects (especially ground-dwelling beetles) and small mammals, while other prey items were taken only sporadically. In comparison with other owls inhabiting central Europe, the proportion of insects in the diet of Little Owls diet is very high (Cramp 1985), especially during the breeding season (Ille 1992, Schönn *et al.* 2001). Further, the proportion of insects in the diet of Little Owls increases from central Europe toward southern latitudes (Mikkola 1983) owing to the lower availability of Microtinae rodents in the Mediterranean region. The contribution of insects to the diets of Little Owls may increase when voles become rare (Schönn *et al.* 2001) or may reflect seasonal variations in insect availability (Zerunian *et al.* 1982).

While these recent studies on the feeding ecology of Little Owls have focused mainly on diet composition (Cramp 1985, Manganaro *et al.* 2001, Obuch & Krištín 2004) and seasonal variations (Génot & Bersuder 1995, Schmid 2003), they have not simultaneously assessed food availability. In this study, we present these data from a region where populations of Little Owls are declining rapidly (Šálek 2004, Šálek & Schröpfer 2008). The main goals of this study were to describe seasonal changes in diet composition with respect to natural insect densities and to assess prey availability with respect to vegetation characteristics that may influence habitat choice. This information should provide an important framework for the conservation and management of this species in farmland regions.

## METHODS

### Study area

This study was carried out at six sites occupied by Little Owls in western Bohemia, southwest of the city of Plzen (Czech Republic) within a 50-km<sup>2</sup> area (350–486 m asl; 49.40° N, 13.9° E; Fig. 1). Sites were chosen based on previous research on the distribution of Little

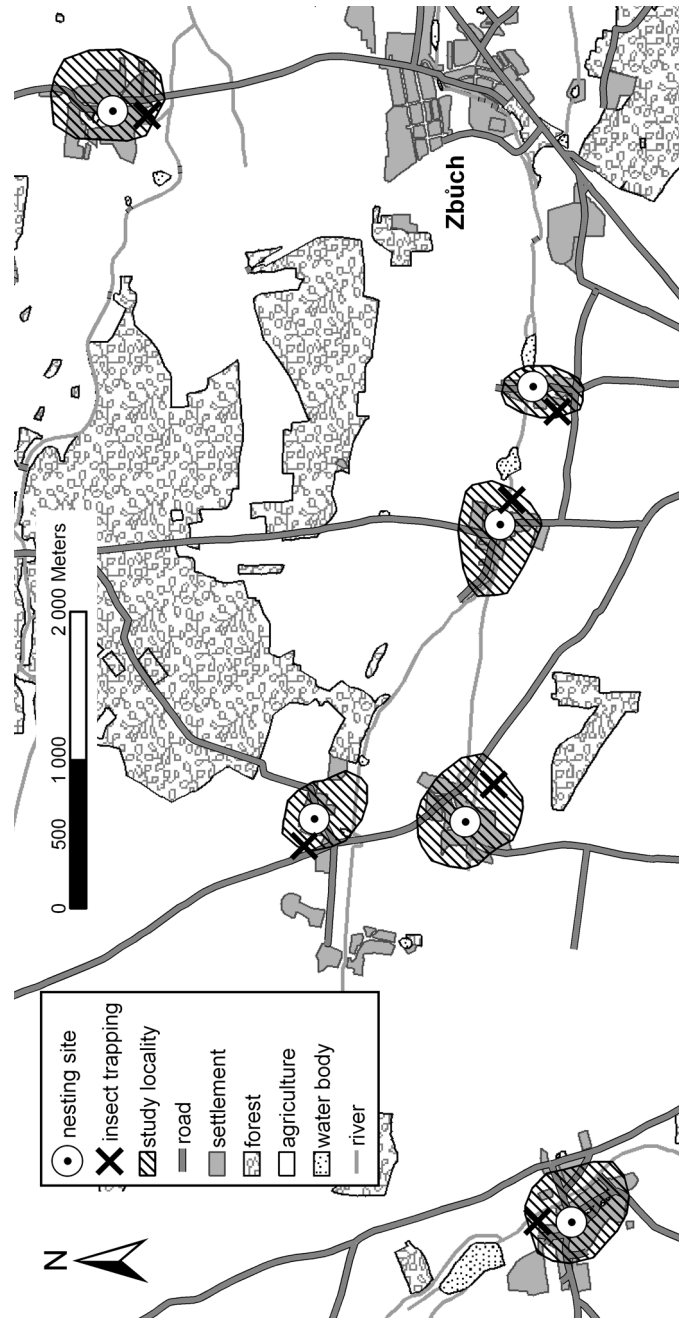
Owls with a minimum distance between adjacent sites of 2.3 km (average = 3.9 km). In this study area Little Owls utilise cavities in old buildings of small villages and they hunt in areas surrounding their nests. Population density is 2.9 pairs/10 km<sup>2</sup> (Šálek 2004). The main habitats of the surrounding areas are intensely managed fields (45%), forests (32%) and grassland patches (10%). The grasslands are dominated by *Festuca* spp., *Phleum* spp., *Trisetum* spp., *Alopecurus* spp. and *Lolium* spp., among many others.

### Pellet analysis

Pellets and prey remains from nests were collected from four nests and six roosting sites every 14 days during the 2002 breeding season (April–July). All older pellets were removed from the nests or roosting sites before sampling began to avoid mixing pellets from different periods. In total, we identified 898 prey items from 563 pellets. The pellets were dried and all feathers and other remains were identified. Small mammals were identified from skulls according to Anděra & Horáček (1982), and birds from beaks and humeri using a reference collection. All insect remains were identified according to structure, colouration, legs and size of exoskeletons. The proportion of earthworms was not assessed due to minor content of their remains in pellets. The total number of prey individuals was determined by the most numerous body parts (e.g. upper jaw). The data on weight of vertebrate prey were taken from Hudec & Černý (1977) and Anděra & Horáček (1982). Weight of Carabidae beetles was calculated from length using the formula  $\text{Weight} = 0.0307 \times \text{Length}^{2.64}$  (Jarošík 1989) and for other insect groups the formula  $\text{Weight} = 0.0305 \times (\text{Length})^{2.62}$  (Rogers *et al.* 1976) was used.

### Foraging habitat preferences of Little Owls

Data on foraging habitat preferences was acquired using telemetry carried out during the 2002 breeding season. Adult birds were caught before the monitoring period at the beginning of March. A mist-net placed near the nest sites, using a dummy combined with a territorial voice playing from a tape-recorder, was used. Birds were equipped with 'back-pack' transmitters (Biotrack TW 4, 3.5 g, battery lifespan of up to 8.5 months), which were then tracked using a three-piece Yaggi aerial and an ICOM R-10 wideband receiver. The locations of radiotracked birds were recorded at 15-minute intervals from one hour after



**Figure 1.** Distribution of study localities, Little Owl nest-sites, and insect-trapping sites in the study area, western Bohemia, Czech Republic.

dusk to (one hour after) midnight, which coincides with the period of highest foraging activity of Little Owls (Exo 1989, Fajardo *et al.* 1998).

From April to July, we recorded a total 307 locations of six adult males, which provided information on their foraging areas. To assess habitat preferences, we randomly selected the same number of control locations within Little Owl home ranges. We distinguished two main habitats, meadows and cereal fields (together 86% of all Little Owl locations). For each habitat we assessed the actual average vegetation height, maximum vegetation height and vegetation density for each 14-day period.

### Insect trapping

During spring and summer 2002, we estimated the composition of ground-dwelling insects in the Little Owls' foraging areas (Fig. 1). Ground-dwelling beetles were collected using non-baited pitfall traps (buried plastic bottles with the neck cut off, covered by a raised lid, and filled with a mixture of water and glycol) placed at the six localities from 5 May to 5 July. Traps were placed in two main feeding habitats – meadows and cereal fields (chosen based on the previous telemetry research) within the Little Owl foraging areas at each monitored locality. In both habitat types we installed a linear transect, 50 m from the habitat edge, consisting of three traps at 10-m intervals. In total, 36 traps at six localities (two habitats, six localities, three traps per locality) were installed. The sampling period was divided into six 14-day periods and the traps were controlled at 1-week intervals in the morning hours.

### Statistical analyses

We used principal component analysis (PCA) in CANOCO for Windows (Braak & Šmilauer 1998) for analysis of the multivariate diet component data, treating proportions of prey components as 'species' data. GLMMs (lmer function, R software) were used to assess the effect of factors on diet composition and habitat preferences of Little Owls, as well as for analysis of insect trappings. We developed all combinations of independent variables. The suitability of each model was assessed according to AIC criteria and we chose the models with the lowest AIC values. We used locality as a random factor to avoid spatial pseudo-replications. STATISTICA software (Statsoft, Inc.) was used to compute  $2 \times 2$  tables and percentage differences.

## RESULTS

### Overall diet composition

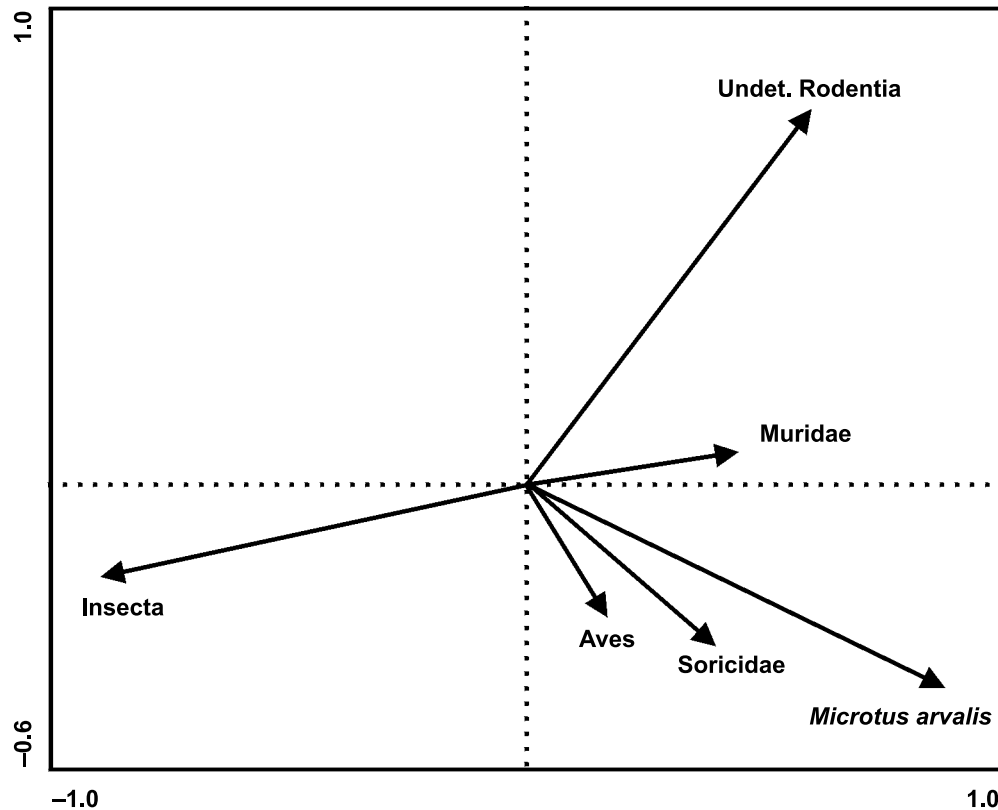
Insects were the most numerous prey based on number (64.4%), but comprised only 1.2% by weight, being far outweighed by mammalian prey (96.8% by weight). Vertebrate prey consisted predominantly of small mammals; birds were represented only occasionally (Table 1). Among mammals, Common Voles *Microtus arvalis*, were the most dominant prey species. Its total proportion was 24.4% by numbers ( $n = 219$ ) and 69.1% by weight; the genus *Apodemus*, the second most abundant mammal prey, formed 2.1% of all prey items (7.5% by weight). Insect prey consisted mostly of the order Coleoptera (see Appendix, which is available via the Supplementary content tab of the article's online page at <http://dx.doi.org/10.1080/00063657.2010.494717>).

The PCA analysis of insect number percentages clearly showed that insects were the most important component of the diet (Fig. 2). The proportion of insects was negatively correlated with that of vertebrates. A positive correlation was found between the abundance of *Microtus* and other rodents. Muridae, Soricidae and Aves were rather occasional supplemental food items. Further, the day of the season was strongly positively correlated with mean temperature (Spearman rank correlation,  $df = 27$ ,  $r_s = 0.91$ ,  $P < 0.05$ ) and precipitation (Spearman rank correlation,  $df = 27$ ,  $r_s = 0.75$ ,  $P < 0.05$ ) for the

**Table 1.** Weight, frequency and biomass of each component in the diet of Little Owls, based on pellet analysis.

Prey species	Weight		Number		Biomass	
	g		<i>n</i>	%	B	%
<i>Microtus arvalis</i>	20		219	24.4	4380	69.1
<i>Apodemus</i> sp.	25		19	2.1	475	7.5
<i>Mus musculus</i>	19		6	0.7	114	1.8
<i>Crocidura leucodon</i>	12		18	2.0	216	3.4
<i>Micromys minutus</i>	19		11	1.2	209	3.3
<i>Sorex minutus</i>	4		2	0.2	8	0.1
<i>Sorex araneus</i>	9		2	0.2	18	0.3
Undetermined	19		38	4.2	722	11.4
Rodentia						
Mammalia, total			315	35.1	6142	96.8
<i>Passer</i> sp.	27		2	0.2	54	0.9
<i>Carduelis chloris</i>	30		1	0.1	30	0.5
<i>Fringilla coelebs</i>	25		1	0.1	25	0.4
<i>Phoenicurus</i> sp.	16		1	0.1	16	0.3
Aves, total			5	0.6	125	2.0
Insecta	0.003– 0.870		578	64.4	75.8	1.2
Total			898	100.0	6342.8	100.0

g, average weight of prey animals in grams; *n*, number of items; B, prey biomass in grams.



**Figure 2.** Projection scores of the main components of the diet of Little Owls in western Bohemia expressed as numbers (principle component analysis, I and II axis explained 72.4 % of total variation). Horizontal axis, I; vertical axis, II.

pellet-collection period. Therefore, we included day of the season and locality into the subsequent GLMM. The proportion of insects (as the dependent variable) in the diet (by numbers) was positively correlated with increasing day of the season (GLMM gamma model, correlation 0.656; Table 2), and negative for invertebrates.

### Insects in the diet and their availability

Insect prey consisted of 578 items belonging to 3 orders, 14 families and 31 species. Coleoptera were the most abundant invertebrate prey (67.1% by numbers, 69.4% by weight,  $n = 550$ ), while Dermaptera and Hymenoptera comprised only 4.8% by number ( $n =$

**Table 2.** Comparison of the composition of trapped insects and Little Owl insect diet composition ( $\chi^2$ test).

Prey species	Insect trappings					Little Owl diet			$P(\text{overall})$	$P(\text{meadows})$	$P(\text{cornfields})$
	$n$	%	Meadows	%	Cornfields	%	$n$	%			
<i>Poecilus cupreus</i> (I)*	2000	81.9	519	79.4	1481	82.9	3	1.1	<0.001	<0.001	<0.001
<i>Pterostichus melanarius</i> (N)*	212	8.7	39	6.0	173	9.7	205	75.4	<0.001	<0.001	0.244
<i>Pseudoophonus rufipes</i> (N)*	122	5.0	44	6.7	78	4.4	0	0	0.001	<0.001	<0.001
<i>Carabus granulatus</i> (I)	45	1.8	7	1.1	38	2.1	35	12.9	0.052	0.001	0.803
<i>Oodes helopioides</i> (N)	19	0.8	15	2.3	4	0.2	0	0	0.598	0.002	0.103
<i>Nebria brevicollis</i> (N)	16	0.7	15	2.3	1	0.1	1	0.4	0.888	0.006	1.000
<i>Abax parallelepipedus</i> (N)	13	0.5	6	0.9	7	0.4	1	0.4	0.963	0.143	0.106
<i>Agonum muelleri</i> (D)	11	0.5	8	1.2	3	0.2	1	0.4	0.965	0.069	0.465
<i>Carabus nemoralis</i> (I)	3	0.1	1	0.2	2	0.1	26	9.6	0.575	<0.001	<0.001

The significance level after Bonferroni correction was set at 0.006; overall significant differences are marked with an asterisk; N, nocturnal activity; D, diurnal activity; I, diurnal and crepuscular activity.

28). The most dominant Coleoptera were Carabidae (67.1%), followed by Curculionidae (9.7%) and Staphylinidae (7.3%). The most dominant species were *Pterostichus melanarius* (35.5%) and *Harpalus affinis* (12.3%). *Poecilus cupreus* was not a frequent species in the diet (0.5%), but dominated the insect-trapping data (81.2%; Table 2). Most of these insect prey were likely to have been caught on the ground (69.9%,  $n = 404$ ) and only a few items taken in flight (2.4%,  $n = 14$ ). Most of the Carabidae species are ground-active, and occupy a variety of habitats.

We tested factors that affect the availability (abundance) of Carabidae prey (dependent variable). We included the 14-day trapping periods (six in total), trapped species (nine) and habitat (two) into a GLMM. All three parameters showed significant relationships

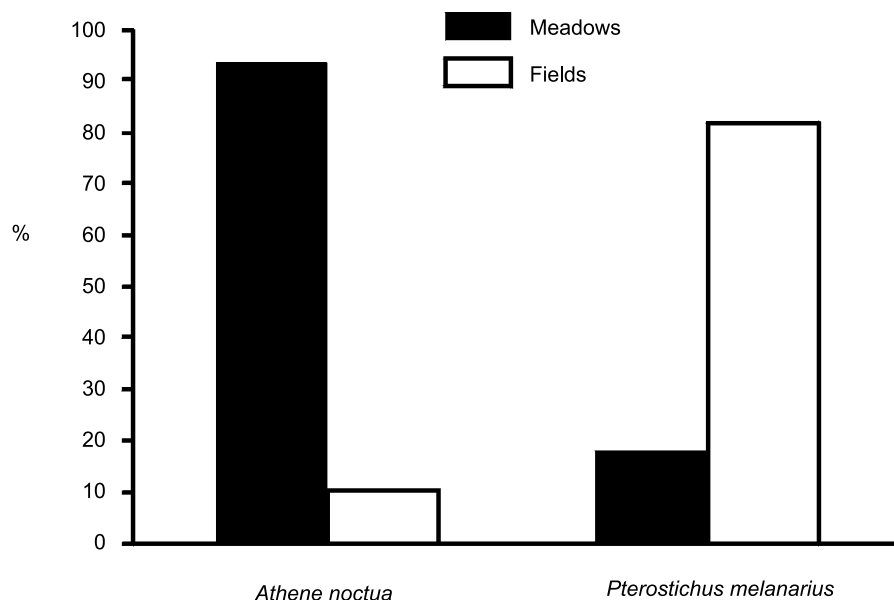
with Carabidae abundance (Table 3). Most Carabidae prey was trapped in the first 14-day period (34.5%), and *P. cupreus* dominated in the overall trapping data (81.9%). Most carabids were trapped in cornfields (73.2%).

*Pterostichus melanarius* were the main insect prey in contrast with its low numbers in hunting areas, especially from meadows (Table 2). Moreover, Little Owls mainly preferred meadows, and *P. melanarius* was most abundant in fields (Fig. 3); these differences were significant ( $2 \times 2$  tables,  $\chi^2 = 47.5$ ,  $df = 1$ ,  $P < 0.0001$ ).

Because of the fact that Little Owls mainly preferred grasslands – particularly meadows and pastures – when foraging (Fig. 3), we tried to explain which factors could affect the choice of hunting habitat. We included three factors in the GLM: mean vegetation height,

**Table 3.** Factors affecting the availability of insect prey on Little Owl hunting areas and the proportion of insect prey in the diet (Generalized linear mixed model with Poisson and Gamma distribution, respectively). BIC, Bayesian information criterion.

Explained variability	Model	df	>AIC	BIC	LogLik	$\chi^2$	$\chi^2$ df	P
Insect abundance	Null (abundance: +1, locality: random effect)	2	4909.9	4916.3	-2453			
	Abundance: species	10	2141.7	2173.4	-1060.9	2784.2	8	<0.001
	Abundance: species + 14-day period	15	1553.5	1601.1	-761.8	598.2	5	<0.001
	Abundance: species + 14-day period + habitat	16	1147.8	1198.5	-557.9	407.8	1	<0.001
Proportion of insects in the diet	Null (proportion of insects: +1, locality: random factor)	2	377.0	379.6	-186.5			
	Proportion of insects: day in the season	3	252.9	256.8	-123.4	126.1	1	<0.001



**Figure 3.** Hunting habitat preferences of Little Owls in meadows and fields based on telemetry ( $n = 307$  locations), and the proportional abundance of *Pterostichus melanarius* ( $n = 212$  individuals) from traps in meadows and fields within Little Owl territories ( $2 \times 2$  tables,  $\chi^2 = 47.5$ ,  $df = 1$ ,  $P < 0.0001$ ).

maximal vegetation height and density of vegetation cover. The density of vegetation was positively correlated with mean vegetation height ( $r_s = 0.64$ ) and was excluded from the analysis. The control locations had significantly higher mean vegetation cover than did Little Owl locations (binomial GLM, 35% of explained variability,  $F = 18.7$ ,  $P < 0.0001$ ).

## DISCUSSION

Little Owls are generalist predators feeding on a variety of prey species (Cramp 1985, Ille 1992, Schönn *et al.* 1991). In central Europe, vertebrate species (mainly mammals and birds) are the most important prey during winter, and insect prey dominates during the breeding season (Ille 1992, Schönn *et al.* 2001). In contrast, insects play a major role throughout the year in the Mediterranean area (Mánez 1983). Our results, consistent with earlier results obtained in central Europe, show the diet markedly changed during the breeding season. Small mammals were mostly captured at the beginning of breeding, with *Microtus arvalis* being the most frequent species. The proportion of this species in Little Owl diets can reach up to 80% (Laiu & Murariu 1997), but in central Europe generally ranges from 25 to 50% (Ille 1992, Schmid 2003). Higher proportions of vertebrate prey are probably linked with continental climatic conditions, especially during cold winters (Mlíkovský 1996, Obuch & Krištín 2004) when insects are not available.

Birds do not usually play an important role in the diet of Little Owls (Cramp 1985), though there can be exceptions (Hounscome *et al.* 2004). Hell (1964) found a higher proportion of birds (especially passerines) during the harsh winter 1962/63 in Czechoslovakia. Our results show a low frequency of birds in the diet during the breeding season.

Invertebrates were the most dominant prey, comprising almost 65% of all prey remains by numbers. However, there was a great difference between invertebrate and vertebrate prey biomass (1.2% versus 98.8%) as has been demonstrated previously (Bon *et al.* 2001, Schmid 2003). This proportion of invertebrates in the diet is comparable with other studies from central and western Europe; Germany (Haensel & Walther 1966), Switzerland (Schmid 2003), France (Génot & Bersuder 1995), but is far below values from the Mediterranean region (Zerunian *et al.* 1982, Mánez 1983, Fattorini *et al.* 2001) and the Middle East (Obuch & Krištín 2004). The difference might stem from a greater abundance and availability of invertebrates in southern

regions. Carabidae beetles have been found to be the most frequent prey species (Ille 1996, Schmid 2003), while Carabidae and Lumbricidae represent the main invertebrate prey in the Little Owl diet throughout Europe (Cramp 1985, Schönn *et al.* 1991). In our material, the proportion of Carabidae was 67.1% of the total insect prey numbers. We neglected Lumbricidae because of its sporadic occurrence in pellets; however, our analysis is likely to be biased toward prey items whose remains can be found after digestion. Camera monitoring of prey species brought to Little Owl nestlings have shown that Lumbricidae proportions are variable, but could be up to 65% of the diet (van Nieuwenhuysse *et al.* 2008). Similarly, the high proportion of Carabidae in pellets may also be because of the fact that those species have highly chitinised elements like elytra and are thus difficult to digest.

Little Owls have been described as ground hunters, which generally hunt from a perch and only occasionally take prey in the air (Cramp 1985, Mlíkovský 1998, Fajardo *et al.* 1998). These findings are in agreement with the Little Owls' hunting habits in our study area, where most strikes are carried out from perches to the ground (Cramp 1985, Šálek 2004). Based on the known ecology of insect prey, we were able to infer some ecological characteristics of insect prey groups. At the family level, most Carabidae beetles taken by Little Owls were ground-dwellers with nocturnal or intermediary activity.

*Pterostichus cupreus*, the main insect species found in traps, was not a frequent prey species, probably because it is most active during the day. *Pterostichus melanarius*, the most numerous insect prey, was most affiliated with cornfield habitats in our study. In contrast, Thiele (1977) and Hůrka (1996) describe this species as a typical inhabitant of flat open agricultural landscapes (fields and grasslands), with a slight preference towards moist habitats. Our analyses of the Little Owls' hunting preferences demonstrate that one of the major factors determining habitat choice were vegetation height and the density of vegetation cover. Little Owls preferred grassland patches (especially grassy pastures, short sward lawns and mowed hayfields), which enabled efficient hunting on surface-active soil insects. Hunting beetles in tall and dense swards is likely to be more difficult and energetically more costly, and may result in lower breeding success (Gassman & Bäumer 1993) or higher adult mortality (Exo 1988). During summer, especially during breeding, parents are likely to pay high costs to nourish themselves and their offspring. Although this period is characterised by increasing



insect abundance, tall and dense vegetation will decrease its availability to the owls.

This importance of grasslands and pastures for Little Owls in the breeding season has been demonstrated by many studies (Loske 1986, Schön *et al.* 1991, Dalbeck *et al.* 1999, Šálek & Berec 2001, Šálek & Schröpfer 2008), and has also been shown for many other grassland birds (Vickery *et al.* 2001, Atkinson *et al.* 2004, Devereux *et al.* 2006). The availability of short-sward grassland patches in Little Owl territories (close to nesting sites) appears to be a limiting factor for the persistence of Little Owls in central European farmland areas. Although the amount of grasslands in the region has increased during the last two decades (Miko & Hošek 2009), current management practices (in most cases mowing twice per year) are not favourable for many animal taxa, including butterflies (Konvička *et al.* 2008), mammals (Šálek *et al.* 2009, Šálek *et al.* unpubl. data) and birds (Atkinson *et al.* 2004, Whittingham & Devereux 2008). Although the species richness of some of the ground-dwelling beetles and other insects found in the Little Owl diet may be positively correlated with fertilisation levels or longer swards (Morris 2000, Söderström *et al.* 2001), tall and structural vegetation may result in changes to hunting practices and a dietary shift to alternative prey (Southern 1954, Bertolino *et al.* 2001), resulting in critically higher energy costs during the Little Owl's breeding season.

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