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Source: Journal of Vertebrate Biology, 73(24071)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.24071

Journal of Vertebrate Biology

Open Access

J. Vertebr. Biol. 2024, 73: 24071

DOI: 10.25225/jvb.24071

RESEARCH PAPER

Nestbox cameras reveal geographic, temporal and sex-specific variations in the composition of provisioned prey for a declining farmland raptor

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Received 1 July 2024; Accepted 14 August 2024; Published online 27 September 2024

Abstract. Understanding the foraging ecology of the rapidly declining little owl (*Athene noctua*), which faces food limitations during the breeding season, is crucial for its effective conservation and management. We assessed the composition of prey provisioned to nestlings using nestbox cameras from 2002-2022 in three countries with different landscape structures (the Czech Republic, Slovakia and the Netherlands). We particularly explored the effect of region (country), nesting stage and parental sex on prey composition. From 41,342 identified prey items, insects predominated the little owl's diet (75.6%), followed by earthworms (19%) and a smaller proportion of vertebrates (mammals and birds). The highest proportion of insects was found in the Netherlands (80.9%), whereas earthworms dominated in Slovakia (79.8%). Vertebrates (particularly small mammals) were important prey delivered during the incubation and early nesting stages, and the representation of insects increased with the progression of the breeding season. Representation of earthworms was highest in the late nesting stage. Females provisioned a higher percentage of earthworms, whereas males provisioned more vertebrates. In conclusion, the little owl's diet during the breeding season comprises a surprisingly high proportion of invertebrates. Further, differences in prey provided are most likely driven by climatic factors, habitat structure and land-use histories (causing differences between countries), different energy requirements and seasonal changes in prey availability (causing differences during individual nesting stages) and sex-specific foraging strategies and parental roles (causing differences between sexes). Conservation activities should focus on restoration and suitable management of different high-quality habitats to enhance the availability and representation of different prey taxa within little owls' territories.

Key words: avian predator, food delivery, nest monitoring, insect, food limitation, breeding season, little owl

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Introduction

Foraging is an essential aspect of a species' ecology and is directly linked to growth, reproductive success and survival (Perrig et al. 2017, Jennings et al. 2021, Wilkinson et al. 2023). Variations in foraging behaviour and prey selection at the individual and population levels may reflect differences in environmental prey availability and even changes in land-use patterns or habitat management (Grüebler et al. 2018, Garrett et al. 2022). Individuals of a species may benefit from higher survival and reproductive success if they experience environmental conditions enhancing the availability of prey, particularly those that are either nutrient-rich or require less effort in capture (Sumasgutner et al. 2014, Grüebler et al. 2018). Hence, a detailed understanding of the foraging ecology, particularly for species undergoing population declines, may provide crucial information for targeted conservation action and habitat restoration.

Farmland bird populations are rapidly declining on a continental scale (Donald et al. 2001, PECBMS 2020, Douglas et al. 2023), with a predominantly detrimental impact of agriculture intensification (Rigal et al. 2023). The little owl (*Athene noctua*) is a small-sized farmland raptor that has undergone steep population declines in most parts of Western and Central Europe, which resulted in massive range contractions and fragmentations since the half of the last century. For instance, the little owl population has declined by up to 94% in the Czech Republic and 41% in Slovakia since the 1990s. Current population estimates for these two Central European countries were approximated at 130 and 550 breeding pairs in the Czech Republic and Slovakia, respectively (Šálek & Schröpfer 2008, Chrenková et al. 2017). In the Netherlands, the little owl has declined by about 50% since the 1970s, though the current population trend appears stable and is estimated at 8,000-9,500 breeding pairs (Le Gouar et al. 2011, van Nieuwenhuyse et al. 2023). These large-scale population reductions led to the inclusion of the species in country-specific Red Lists (Haupt et al. 2009, Gerber et al. 2010) and National Action Plans (AOPK ČR 2020), aiming to reverse the steep decline of the species.

The dramatic population decline in the little owls is primarily associated with agricultural intensification, resulting in landscape homogenisation and loss of crucial foraging habitats, ultimately leading to food limitation during the breeding season (Thorup et al. 2010, van Nieuwenhuyse et al. 2023). Principal foraging habitats of little owls include grasslands (meadows and pastures) and structure-rich orchards with short vegetation that are preferentially used during the breeding season, as they offer high availability of vital prey, such as insects and small mammals (Šálek et al. 2010, Šálek & Lövy 2012, Apolloni et al. 2018). Reduction and loss of high-quality habitats can lead to higher parental investment in locating and capturing prey to feed nestlings (Jacobsen et al. 2016, Staggenborg et al. 2017). Additionally, the composition of prey provisioned to nestlings may also be altered, which may not match their dietary requirements during the breeding season. This situation is especially pertinent for altricial species like the little owl that have offspring dependent on their parents until they leave the nest, and even for several weeks after (Pedersen et al. 2013). Overall, this strain on parents during the energetically intensive breeding season can have negative consequences for adult survival and nesting success (Grüebler et al. 2018, Michel et al. 2022).

The little owl is a generalist predator as its diet mainly consists of various insects, earthworms, birds and small mammals (van Nieuwenhuyse et al. 2023). However, its diet may substantially vary over large spatial scales (regions) due to differences in prey availability in landscapes with contrasting habitat structure and climatic conditions. For instance, the little owl diet in warmer Mediterranean regions is dominated by insects, compared to colder areas in Northern and Central Europe, where the percentage of insects is much lower (Šálek et al. 2010, Chenchouni 2014, van Nieuwenhuyse et al. 2023). Diet composition can also vary seasonally and may reflect the seasonal changes in prey availability. Previous studies have shown that the relative contribution of insects to the little owl's diet peaks during the spring and summer, while mammals contribute more during the winter (Génot & Bersuder 1995, Romanowski et al. 2013). However, both prey groups remain important year-round (van Nieuwenhuyse et al. 2023). Prey composition may also vary within the breeding season, which may reflect different requirements of nestlings during the developmental period, which was previously demonstrated in other raptor species (e.g. van der Meer et al. 2018, St. George & Johnson 2021). A previous study found an age-dependent decline in the proportion of insects and, conversely, an increase in mammals for the nestling diet of little owls, though it did not include the first week of nestling development (Grüebler et al. 2018). Finally, the little owls show reversed sexual size dimorphism (RSD), with females being larger than males. RSD may lead to sex-specific differences in diet, which may also be reflected in the provisioning of nestlings (Panter & Amar 2021, 2022), despite this issue being poorly understood, particularly for raptors and little owls. Hence, detailed insight into differences in prey composition across larger spatial scales, individual stages across the breeding season, and between sexes is crucial for understanding the nutritional requirements of nestlings, and regarding parental roles in provisioning. Such information may also have significant implications for applied conservation measures, especially habitat management for different little owl populations.

An accurate diet assessment method should also accompany any detailed understanding of the prey composition. Most studies on the little owl diet have relied on pellet analysis (van Nieuwenhuyse et al. 2023), which, while being a useful and widespread method, may heavily underestimate the percentage of either small or soft-bodied prey, such as insects and earthworms. For example, earthworms are usually completely digested and cannot be quantified from pellets (Romanowski et al. 2013). However, advancements in camera technology in recent years specifically focused on nestbox monitoring have allowed detailed studies on breeding behaviour and ecology of cavity-nesting species, including assessment of prey composition during the breeding season (Zárybnická et al. 2016). Therefore, in this study, we considered data exclusively extracted from videos recorded with nestbox cameras to assess the composition of provisioned prey and nestling diet in declining little owls from three European countries, overcoming previous biases in assessing their spatio-temporal differences in prey composition. We studied how the composition of prey provisioned to the little owls would differ in 1) individual countries with contrasting farmland structures (i.e. the Czech Republic, the Netherlands and Slovakia), 2) nesting stages (i.e. incubation, early, middle and late nesting stage) that entail different nutritional demands for the brooding female and nestlings, and 3) between male and female parents. Moreover, we used trophic estimators (dietary overlap (DO) and food niche breadth (FNB)) to uncover finer differences at the prey class level in different countries, nesting periods and between sexes.

Material and Methods

Study area

The research was conducted in three countries with different farmland landscape structures located in Central and Western Europe: the Czech Republic (northern and central Bohemia), Slovakia (western Slovakia), and the Netherlands (eastern and southern parts). Farmland landscapes in the Czech Republic

Table 1. Mean percentages (%) of individual habitat types in home ranges (220 m radius buffers around monitored nestboxes) of the little owls in studied countries.

Country	Crop fields	Grasslands, gardens, orchards	Built-up areas
Czech Republic	24	39	32
Slovakia	25	28	37
Netherlands	56	27	10

Table 2. Sample sizes, study period, number of delivered prey and nestbox design for little owl nest monitoring in individual countries.

Country	Number of nestboxes	Number of broods	Years monitored	Number of delivered prey	Nestbox camera placement
Czech Republic	3	4	2019-2022	5,951	One camera directed to the nest entrance from the interior, and one camera in the inner chamber with nestlings
Netherlands	4	17	2002-2021	34,179	Three cameras (one directed at the nestbox entrance from outside, one directed to the entrance from inside and one in the inner chamber with nestlings)
Slovakia	1	1	2021	1,212	One camera in the nestbox interior with nestlings

and Slovakia are characterised by intensively used and homogeneous, arable-dominated agricultural landscapes with substantial loss of non-cropped habitats and large arable fields at the landscape scale (see also Šálek 2014, Šálek et al. 2016, 2021). Within the home ranges (i.e. 220 m buffer radius around studied nestboxes, see Šálek et al. 2016), study areas in both countries were represented with a similar proportion of crop fields and built-up areas. In contrast, the proportion of grasslands, gardens and orchards was greater in Slovakia (Table 1). Monitored nestboxes in the Czech Republic and Slovakia were located within human settlements, such as large collective farmsteads (one nestbox in the Czech Republic and one in Slovakia), and an electric pylon within village outskirts (one nestbox in the Czech Republic). In contrast, nestboxes monitored in the Netherlands were situated in individual small-sized former family farms and located away from larger human settlements. Moreover, landscapes surrounding the studied locations in the Netherlands are formed by more heterogeneous farmland, with grasslands and smaller arable (maise) field sizes (R. van Harxen, unpublished data). At the level of individual home ranges, the locations were composed of a higher representation of crop fields.

Data collection

We used nestbox cameras to characterise the diet composition of the little owls, using analysis of prey delivered to offspring or incubating females during the breeding season (March to July). Monitoring of diet composition began from egg laying and ended when offspring left the nestbox, as prey delivered to nestboxes significantly decreased at this stage. We used video recordings from the cameras to record individual prey species, date and sex of the parent for each provisioning event. Ornithological rings used in different combinations allowed us to determine the parent's sex (e.g. only one parent ringed, each parent ringed on either leg), except for the brood in Slovakia, where the adults were not ringed. In total, we monitored 22 little owl broods from nine nestboxes in the Czech Republic, the Netherlands and Slovakia. Detailed information about the number of nestboxes, monitored years, number of delivered prey and nestbox camera placement in individual countries is given in Table 2.

Data analyses

To calculate the biomass of provisioned prey items, we extracted mean values of prey weight (g) from literature resources focused on individual species, genera or broader taxonomic groups (Šálek et al. 2010, Grüebler et al. 2018). For prey items that could only be identified to the species/class level, we assigned the weighted mean of prey weight, calculated from all identified species or genera within that class. Detailed information on the weight and numbers of individual prey species/taxa are given in Table S1. For further analyses, individual prey species were categorised into four main prey groups: mammal, insect, bird and earthworm. We used the chi-square test to determine statistically significant differences in proportions of the main prey groups, between countries, nesting stages and parental sexes (alpha = 0.05). We implemented the chi-square tests using the function *chisq.test* from the package *stats*, included with the base R software version 4.2.2 (R Core Team 2022). We used stacked bar charts to examine differences in prey composition graphically. For comparison of diet composition between different nesting stages, we considered four biologically relevant periods during the breeding: incubation (a total of 25 days before the chick hatching), early nesting stage (i.e. 1-10 days after hatching; when the nestlings increase body mass rapidly by around six times), middle nesting stage (i.e. 11-20 days after hatching; when most of the feather development occurs) and late nesting stage (i.e. > 20 days; when final development of feathers occurs and nestlings get ready to fledge) (van Nieuwenhuyse et al. 2023).

To compare the degree of specialisation (or generalisation) and the level of overlap in the diet composition between individual prey classes, we calculated FNB using Levin's index (Colwell & Futuyma 1971) and DO using Pianka's index (Marti et al. 1987). We used these indices to make broad comparisons between countries, nesting stages, and parental sexes, as well as finer comparisons between nesting stages in different countries, between parental sexes in different countries, and nesting periods.

Levin's index for FNB is given by:

$$B_A = 1/(n - 1) \times ((1/\sum P_i^2) - 1)$$

where n refers to the number of prey groups and P_i to the proportion of the ith prey group. FNB values range between 0 and 1, where a value closer to 0 indicates a higher specialisation (in one or a few prey groups), and a value closer to 1 implies diet generalisation or similar proportions in multiple prey groups.

Pianka's index for DO was calculated as:

$$O = \sum P_{ij}P_{ik}/(\sum P_{ij}^2 \sum P_{ik}^2)^{1/2}$$

where P_{ij} and P_{ik} refer to the proportions of the ith prey group among provisioned prey in little owls from countries i and j, nesting stages or parental sexes. DO

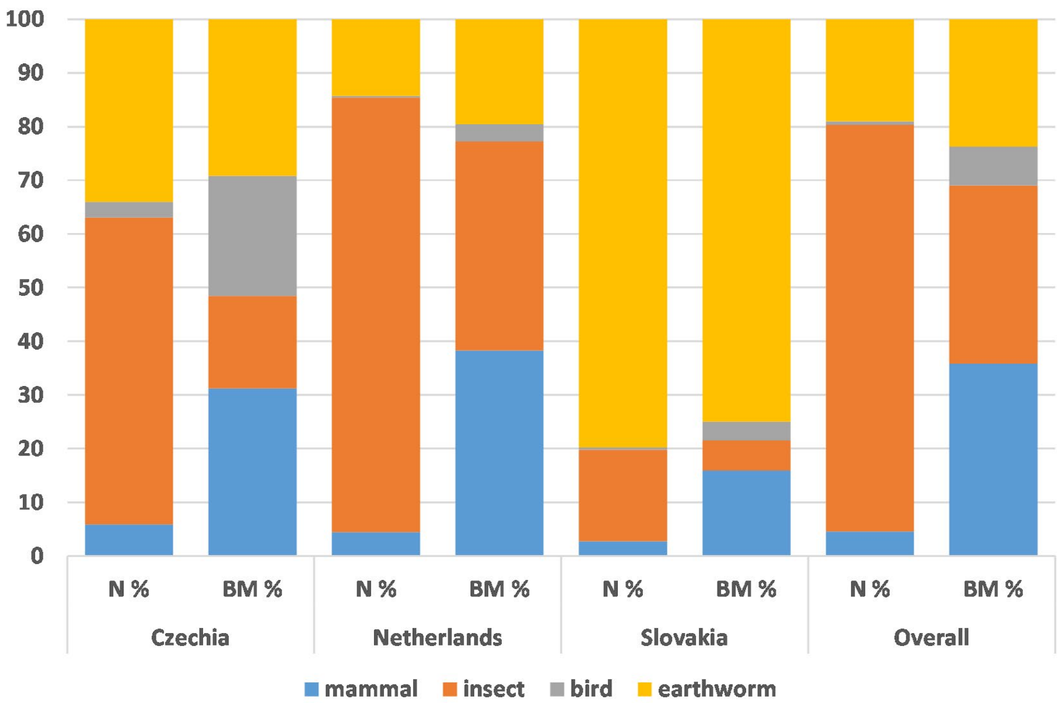

Fig. 1. Representation of individual prey groups of provisioned prey in little owls in individual countries. N – number of prey items, BM – biomass.

values also range between 0 and 1, with values closer to 0 and 1 implying a low and high degree of overlap in diet composition, respectively.

For all comparisons involving parental sex, we excluded data from the incubation stage as almost all (> 99%) prey in this period were delivered by the male. The prey composition dataset used in the study is available in Table S2.

Results

Overall diet composition

A total of 47,786 prey items were recorded, of which 41,342 belonged to the four main prey classes (see Table S1). Insects formed the highest percentage (75.6%) in the little owl diet in terms of numbers, followed by earthworms (19%), mammals (4.8%) and birds (0.6%). In contrast, mammals formed the highest proportion (37%) by biomass, followed by insects (32.7%), earthworms (23.3%) and birds (7%).

Differences between countries

The composition of provisioned prey (by numbers) varied significantly in individual countries (χ^2 = 4958.1, df = 6, $P < 0.001$). Little owls in the Netherlands brought a higher percentage of insects (80.9%) than in the Czech Republic (57.3%) and Slovakia (17.1%, Fig. 1). The percentage of mammals was similar in the Czech Republic and the Netherlands (5.9% and 4.5%, respectively) but lower in Slovakia (2.7%, Fig. 1). Provisioned prey in Slovakia was dominated by earthworms (79.8% in terms of numbers) in comparison to both the Czech Republic (34%) and the Netherlands (14.3%, Fig. 1). Birds accounted for a small percentage in all three countries, but their proportion was highest in the Czech Republic (2.9%, Fig. 1).

FNB was the highest for the Czech Republic (0.38), followed by Slovakia (0.17) and the Netherlands (0.16). DO was the highest between the Czech Republic and the Netherlands (0.93), followed by the Czech Republic and Slovakia (0.68) and the least between Slovakia and the Netherlands (0.38).

Differences between nesting stages

The composition of provisioned prey (by numbers) was significantly different in individual nesting stages (χ^2 = 2829.2, df = 9, $P < 0.001$). During the incubation and early nesting stage (1-10 days after hatching), the percentage of provisioned mammals was higher (8% and 7.2%, respectively), in comparison to the middle (11-20 days after hatching) and late nesting stages (> 20 days after hatching) with 3% and 3.9% respectively (Fig. 2). Insects comprised similar percentages in the first three nesting stages (80.1-83.2%) but their proportion declined during the late nesting stage (62.6%, Fig. 2). The percentage of earthworms increased during the breeding period,

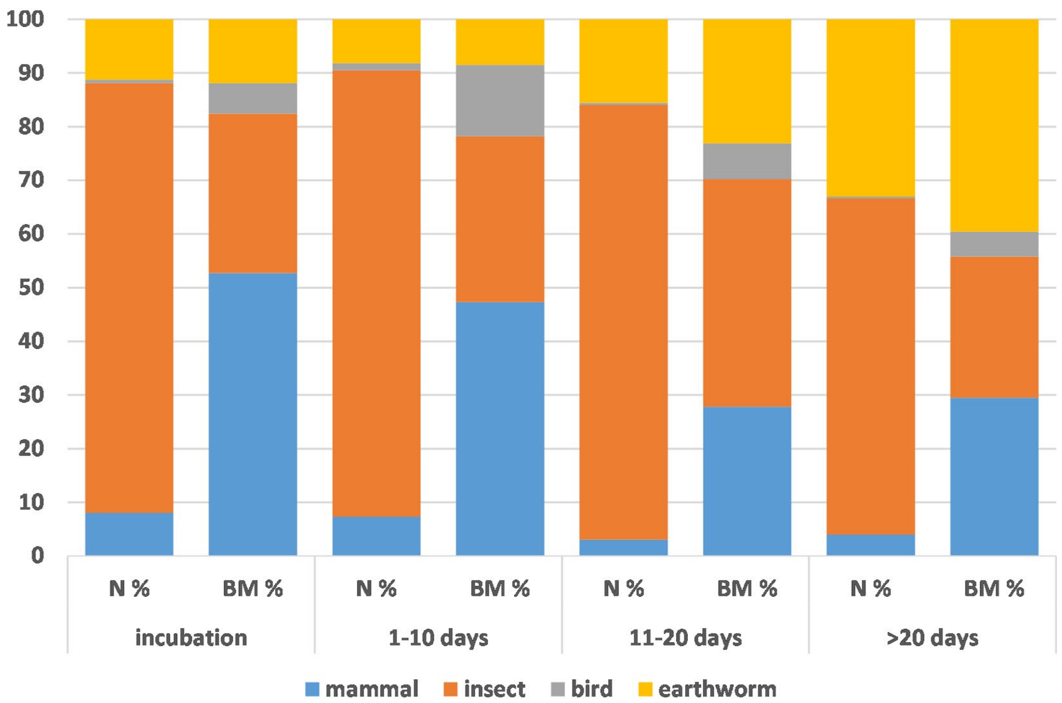

Fig. 2. Representation of individual prey groups of provisioned prey in little owls in individual nesting stages. N – number of prey items, BM – biomass.

with 11.3% and 8.1% during incubation and early nesting stage, and 15.5% and 30% during the middle and late nesting stage, respectively. The percentage of birds did not noticeably differ between individual nesting stages (Fig. 2).

FNB was similar during the first three stages (between 0.14-0.17) and increased in the late nesting stage (0.33). This pattern is likely due to the increased percentage of earthworms and decreases in insects in the late nesting stage (Fig. 2). DO increased with temporal separation between nesting stages; DO was the least between incubation and the late nesting stage (0.92) and the highest between incubation and early nesting stage (0.99).

Differences between parental sexes

The composition of provisioned prey (by numbers) differed significantly between the sexes (χ^2 = 345.5, df = 3, P < 0.001). Females provisioned a higher percentage of earthworms (22% in comparison to males at 15.1%), whereas males brought a higher proportion of vertebrates (6.4%, considering both mammals and birds) in comparison to females (3.4%, Fig. 3).

FNB was similar between females (0.22) and males (0.19) and increased across the nesting stages for both sexes, from 0.07 (for females) and 0.14 (for males) in the early nesting stage to 0.3 and 0.32 in the late nesting stage. Further, while females and males in the Netherlands had similar FNB (0.17 and 0.18, respectively), FNB differences between the sexes in the Czech Republic were greater (0.39 for females and 0.23 for males). Similarly, both sexes showed an extremely high DO (0.99) when considering the entire and individual nesting stages. Specifically, in the Netherlands, DO between sexes was similarly high (0.99), while it was lower for little owls in the Czech Republic (0.77). A closer examination of prey composition in parental provisioning showed that both sexes typically provisioned insects in the Netherlands (80%). However, in the Czech Republic, males provisioned more insects (75%), and females brought a majority of earthworms (53.6%), followed by insects (41.8%).

Discussion

Our study reveals detailed insight into the composition of provisioned prey and nestling diet of the rapidly declining farmland predator, the little owl, across three European farmlands during the breeding season, which is a critical period with peak energy expenditure and when the species faces food limitation directly contributing to its population decline. We found that the representation of invertebrates (i.e. insects and earthworms) was extremely high, based on both numbers (95%) and biomass (57%). For example, soft-bodied earthworms

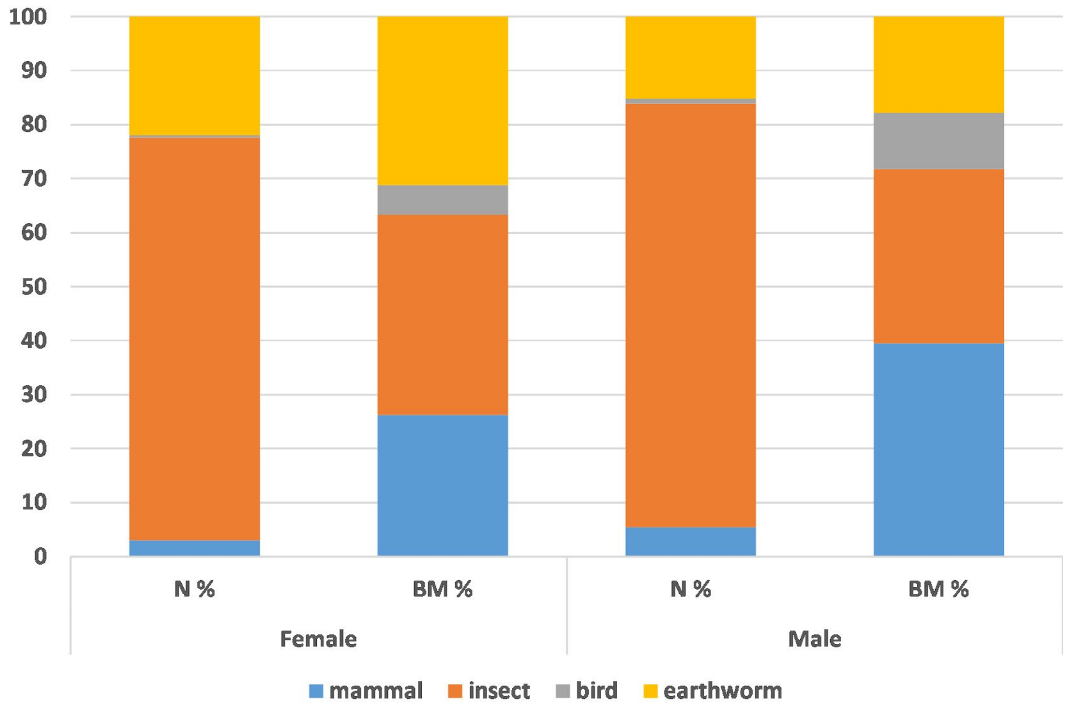

Fig. 3. Sex-specific differences in the representation of individual prey groups of provisioned prey in little owls. N – number of prey items, BM – biomass.

dominated their diet in Slovakia (79.8%), forming a third of provisioned prey in the Czech Republic. However, the analysis of the average proportion of invertebrates in 87 pellet studies across the little owl distribution range revealed that invertebrates formed 72% of their diet (van Nieuwenhuyse et al. 2023). We believe that the remarkably high invertebrate representation in our study, only comparable with other insectivorous owl species in Europe – the Eurasian scops owl *Otus scops* (where diet could be composed up to 98% by insect; Marchesi & Sergio 2005) arises from the new method used for diet analysis, i.e. nestbox cameras, which enable precise evaluation of representation of individual prey, without biasing the proportion of soft-bodied prey such as earthworms. Therefore, previous studies on the little owl diet during breeding season using pellet analysis or nestbox litter could grossly underestimate the contribution of soft-bodied prey in the diet (see also Romanowski et al. 2013, van Nieuwenhuyse et al. 2023). Hence, nestbox cameras offer significant advantages for obtaining accurate descriptions of the nestling diet (see also Zárybnická et al. 2016). Moreover, our study revealed profound differences in provisioned diet between individual countries (farmlands), nesting stages and the parental sexes. These findings may be used to set practical conservative actions and habitat restoration measures.

The geographical comparison of prey composition revealed significant differences between individual countries; however, due to uneven sample size in individual countries (especially small sample size in Slovakia), it must be treated with caution (for more details, see section Study limitations). For example, despite the similar representation of invertebrates in the little owl diet in all three countries (91-97% by numbers), insects were dominant in the Netherlands (81%), whereas earthworms in Slovakia (80%). Mammal representation was similar in the Czech Republic and the Netherlands (5.9% and 4.5%, respectively) but was slightly lower in Slovakia (2.7%). Although a previous study had demonstrated that the proportion of insects in the little owl diet generally decreases from south to north latitudes (Marks et al. 1999), we found that insect representation was highest in the Netherlands, i.e. a country located slightly northern compared to the Czech Republic and Slovakia. However, we believe that the observed differences between countries are probably more related to differences in habitat composition, vegetation structure and management around little owl breeding sites, than the latitudinal and longitudinal gradients of prey availability. In particular, study areas with monitored nestboxes in the Netherlands were situated in or close to former small-sized family farms located away from larger human settlements. Those farms usually included grasslands nearby, which are highly preferred habitats of the little owl during the breeding period (Šálek & Lövy 2012, Mayer et al. 2021), surrounded by a high proportion of crop fields (Table 2). Moreover, the studied locations are surrounded by heterogeneous farmland with smaller arable fields. The mixture of various cropped and non-cropped habitats and higher habitat heterogeneity at the landscape scale are crucial drivers of greater species diversity and abundance of various insect taxa (Jerrentrup et al. 2014, Marja et al. 2022). In contrast, nesting little owls in Slovakia used a nestbox within human settlements, specifically within an active livestock (dairy) farmstead, with a high proportion of artificial surfaces and intensively used grasslands (Table 1), such as cattle pastures with a high share of bare ground. Moreover, grassland habitats around buildings were represented mainly by intensively used short-sward grasslands, such as regularly mown lawns and gardens. At the landscape scale, the study area in Slovakia is surrounded by a homogeneous arable-dominated agricultural landscape with large arable fields and massive reductions of non-cropped habitats. Landscape homogenisation is the result of collectivisation and land consolidation programmes that have taken place in Central and Eastern European countries since the middle of the last century (Sklenička et al. 2014) and is closely linked with the massive reduction of abundance and diversity of farmland species, including insects (Konvička et al. 2016, Šálek et al. 2018). Similarly, previous studies have shown that regularly mown and intensively grazed grasslands exhibit low abundance and diversity of arthropods (Norton et al. 2019, Wintergerst et al. 2021). On the other hand, grassland habitats, such as livestock pastures with cattle dung pat or manure heaps, may offer a high abundance of earthworms (Bacher et al. 2018). Moreover, short-sward vegetation on grazed or regularly mown grasslands is suitable for hunting earthworms (van Nieuwenhuyse et al. 2023). However, since the data from Slovakia comes from a single brood and year, further research is essential to reveal links between landscape structure and prey composition (see also Study limitations).

Differences in prey composition across the breeding period may reflect changes in energy requirements, prey availability, composition and vegetation structure of foraging habitats. We found that insects were the dominant prey across the entire breeding season, and their proportion declined in the late nesting stage when they were partially substituted by earthworms. Mammals were more represented during the incubation and early nesting stage. Similarly, FNB was similar during the first three stages and increased in the late nesting stage. The twofold higher proportion of small mammals provisioned during the incubation and early nesting stage compared with middle and late nesting stages might be associated with generally lower insect abundance and diversity in the early spring and higher availability of small mammals that may be effectively hunted on short-sward vegetation. Subsequent vegetation growth progress during the breeding season may limit their accessibility to foraging raptors, and little owls in particular (Šálek & Lövy 2012, van Nieuwenhuyse et al. 2023). In addition, small mammals, prey rich in calcium, may be crucial for 1) females, as egg-laying period (i.e. incubation) is a highly physiologically and energetically demanding process, drawing from the adult female's calcium reserves (Reynolds & Perrins 2010) and 2) nestlings due to their rapid growth and development soon after hatching, including mineralisation of their skeletons (Reynolds & Perrins 2010, van Nieuwenhuyse et al. 2023). With the progression of the breeding (growing) season (i.e. under higher temperatures), insect biomass and activity rapidly increase (Hallmann et al. 2017) and become more available for foraging little owls, resulting in their higher representation in the prey delivered to nestlings. During this period, little owls may prey on a high diversity of insects, with beetles, moths, larvae and caterpillars forming the most important part (see Table S1, but also see van Nieuwenhuyse et al. 2023), and reflecting daily availability and activity of individual species (e.g. cockchafers *Melolontha melolontha* swarming). Additionally, with the progression of the breeding season, parents are forced to also hunt during the day hours (van Nieuwenhuyse et al. 2023) to satisfy the energetic demands of growing chicks (van Nieuwenhuyse et al. 2023), and therefore, may prey on insects with daytime activity. Earthworm representation in prey delivered to chicks increased with the breeding season and peaked in the late nesting stage. This finding also corresponds with an increase in FNB, which may imply that parents become more opportunistic in prey capture as the nestlings grow, leading to higher deliveries of earthworms due to their lower capture effort. However, this increase is surprising since the surface activity of below-ground invertebrates, and earthworms in particular is negatively correlated with less soil moisture and higher ambient temperatures (Edwards & Bohlen 1996, Onrust et al. 2019), and thus, they may move deeper into the soil as the breeding (growing) season progresses. Similarly, despite the high digestibility of earthworms for nestlings, they contain a large proportion of water and soil and, thus, may represent nutrition-poor prey, especially for small chicks. Feeding with a larger number of earthworms has been observed to leave nestlings in a wet, dirty and poor condition (van Nieuwenhuyse et al. 2023). It also results in strong gaseous ammonia in the nestbox, which likely affects the nest microclimate and could negatively affect the nestlings (van Nieuwenhuyse et al. 2023).

Finally, differences between males and females in the prey composition suggested sex-specific differences in parental effort and foraging strategies. In particular, larger females provisioned a 1.5 times higher proportion of earthworms, whereas smaller males provided nearly a two times higher proportion of vertebrates (i.e. birds and small mammals). Sex differences in parental roles might have caused these differences since females incubate and protect the young (van Nieuwenhuyse et al. 2023). Therefore, females generally forage in proximity to the nest (Mayer et al. 2021), which might be connected to the selection of prey in the vicinity of nests that require less effort to capture, such as earthworms. In contrast, males have generally larger home ranges and foraging areas during the breeding stage and, therefore, may forage in more distant areas/habitats with higher availability of vertebrates, such as rodent-rich ruderal vegetation, fallow land, road verges, and field edges (see also Mayer et al. 2021). Similarly, they may invest more time and effort into catching vertebrates, which generally need longer search times (Mayer et al. 2021). Moreover, a higher representation of vertebrates in males' provisioning may be related to a higher representation of mammals in the early nesting stage, when males are the primary food providers (see above).

Study limitations

We are aware of several limitations of our results. First, the little owl is an opportunistic avian predator which adapts to different environmental conditions and its prey composition is based on weather conditions, vegetation structure, habitat management, or habitat composition (Šálek et al. 2010, Šálek & Lövy 2012, van Nieuwenhuyse et al. 2023), i.e. factors that determine spatio-temporal variability in the abundance and availability of food resources at individual localities and different spatial scales (Tscharntke et al. 2005, Gabriel et al. 2010). Therefore, our interpretation of differences between individual countries and nesting stages is limited without such detailed data. Second, the low number of monitored nestboxes in Slovakia and the Czech Republic limits the comparison of differences in diet composition between individual countries, and the general pattern of diet may be biased towards the country with the largest sample size and numbers of nesting attempts/prey deliveries (i.e. the Netherlands). Third, the diet composition of the little owl may significantly differ between years (Grüebler et al. 2018, van Nieuwenhuyse et al. 2023) and depends on the abundance of preferred high-nutrition prey, such as small mammals that have regular population cycles and its population dynamics that may vary considerably in different regions. Therefore, even at the level of the individual locations, there may be large interannual variability in prey composition and density of small mammals, which may be a critical factor affecting prey composition. Despite its limitations, we believe our study brings details and comprehensive new insight into the foraging ecology of the species in different environmental conditions and during the most critical phase of little owls' lifecycle – the provisioning of the young.

Conservation implications

The extremely high representation of insects in provisioned prey and nestling diet in declining little owls suggest that widespread population declines of insects may represent a crucial problem for the species and other farmland birds specialising on larger insects (e.g. European roller *Coracias garrulus*, Eurasian scops owl) and may result in their population declines in intensively used agricultural landscapes (Grüebler et al. 2018, Hebda et al. 2019, Theux et al. 2022). In particular, the shortage and inaccessibility of preferred prey during the energetically demanding breeding period, ultimately causing food limitation, was previously identified as the main reason for the little owl population reduction in various European countries (e.g. Thorup et al. 2010, Grüebler et al. 2018). Therefore, conservation priority should focus on restoration and suitable management of different high-quality habitats, resulting in the increased availability and representation of various prey species within little owls' territories. For example, enhancing the habitat heterogeneity through the increasing representation of short-sward habitats in the combination of biodiversity-rich habitat boundaries (e.g. field margins, hedges, ditches) and high-quality habitats (e.g. orchards, grasslands, ruderal patches, perennial fallows, set-asides) may increase prey availability and abundance of different prey taxa (i.e. insects, earthworms and small mammals) in time and space and offer crucial foraging structures for effective prey capture across the whole year (see also Šálek & Lövy 2012, Mayer et al. 2021, van Nieuwenhuyse et al. 2023). Alternatively, food supplementation during the breeding period may buffer the shortage of natural food by reducing parental costs and increasing breeding performance and nestling survival (Jacobsen et al. 2016, Grüebler et al. 2018). Finally, we recommend that future research should focus on concurrently investigating diet composition (using nestbox cameras), foraging behaviour (using high-resolution GPS telemetry) and spatio-temporal changes in prey availability of different taxa (to reveal variation in food availability in individual habitats across the breeding season) across its distribution range (to explore latitudinal and longitudinal gradients of prey composition) to expose the crucial links between habitat composition and management with breeding success and survival within contrasting farmlands.

Acknowledgements

We are grateful to Miroslav Bažant and Vlasta Osoba for their help with the installation and data curation of nestbox cameras in the Czech Republic. We would also like to thank the volunteers who did much of the counting at the Dutch camera boxes and Vogelbescherming Nederland for installing the cameras. We appreciate valuable comments from Jitka Uhlíková and two anonymous reviewers on an earlier draft of the manuscript. This work was partly supported by the Nature Conservation Agency of the Czech Republic, Czech Academy of Sciences in the frame of the program Strategy AV 21 and the research aim of the Czech Academy of Sciences (RVO 68081766). S.S. Sailas was also supported by the University of South Bohemia (GAJU n. 014/2022/P).

Author Contributions

M. Šálek and S.S. Sailas conceived the ideas and methodology. R. van Harxen, P. Stroeken, M. Šálek and F. Reipricht collected the data. S.S. Sailas curated the data. S.S. Sailas and I. Stýblová analysed the data. S.S. Sailas and M. Šálek wrote the manuscript. All the authors contributed critically to the drafts and gave final approval for the publication. The authors declare that they have no conflict of interest.

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Supplementary online material

Table S1. Detailed composition of individual prey items of the little owl during the breeding season assessed from nestbox cameras. Weight is in grams, N refers to number of prey items and BM is biomass (N × weight) (https://www.ivb.cz/wp-content/uploads/JVB-vol.-73-2024-SailasS.S.-et-al.-Table-S1.pdf).

Table S2. Prey composition dataset used in the analysis (https://www.ivb.cz/wp-content/uploads/JVB-vol.-73-2024-SailasS.S.-et-al.-Table-S2.xlsx).