




Apodemus mice as the main prey that determines reproductive output of tawny owl (*Strix aluco*) in Central Europe

Václav Luka¹ · Jan Riegert¹ 

Received: 31 May 2017 / Accepted: 3 April 2018 / Published online: 20 April 2018
© The Society of Population Ecology and Springer Japan KK, part of Springer Nature 2018

Abstract

During the years 2008–2014, we studied diet composition, the number of breeding pairs, and reproductive output of tawny owls in Central Europe (Czech Republic) in relation to availability of main prey in the field. We also performed a meta-analysis on diet composition of tawny owl in Europe that confirmed the important role of *Apodemus* mice in tawny owl diet in Central Europe. In concordance, *Apodemus* mice were the main prey of tawny owl in our study area (38.7%), and *Microtus/Myodes* voles (15.4%), birds (12.1%) and others (33.8%) were alternative prey. We found a positive relationship between the proportion of *Apodemus* mice in the diet and their abundance in the field ($\beta = 0.23$, $P = 0.001$). Availability of main prey (*Apodemus* mice, *Microtus/Myodes* voles or *Sorex* shrews) in the field was not correlated with the number of breeding pairs. Proportion of birds in diet (expressed by scores from multivariate analysis), which was inversely related to proportion of *Apodemus* mice, was positively correlated with laying date ($\beta = 0.66$, $P = 0.012$) and negatively correlated with clutch size ($\beta = -0.45$, $P = 0.004$) and brood size ($\beta = -0.16$, $P = 0.076$). We also found negative relationships between laying date and clutch size ($\beta = -0.13$, $P = 0.014$) and brood size ($\beta = -0.07$, $P = 0.057$). Our results support the idea that diet and breeding ecology of owls in Central Europe is mainly driven by the availability of *Apodemus* mice that are suitable prey due to their similar habitat requirements and nocturnal activity.

Keywords Diet composition · Hunting · Laying date · Nocturnal predator · Prey choice · Reproduction

Introduction

The consumption of main prey by raptors is often positively correlated with prey density in the field (i.e., functional response). These relationships have been documented for various raptor species (e.g., snowy owl *Nyctea scandiaca*—Gilg et al. 2006; tawny owl *Strix aluco*; —Roulin et al. 2009; Rough-legged Hawk *Buteo lagopus*; —Therrien et al. 2014). However, variation in the proportion of main diet components can also be found within 1 year. For example, Boreal Owl (*Aegolius funereus*) males in Norway hunted mainly *Myodes* voles during snow cover and when the snow

disappeared they switched to *Microtus* voles (Jacobsen and Sønnerud 1993). Thus, availability of main prey can considerably change both between- and within-years which may cause changes in raptors' feeding tactics.

Changes in prey density may further trigger different responses that depend on the importance of main prey in the diet and availability of alternative prey. Predators that depend on a main prey whose abundance fluctuates widely on a cyclical basis and where alternative prey does not compensate for these changes often show a positive relationship between density of main prey and number of breeding pairs (i.e., numerical response). These responses have been found in some avian predators, especially at northern latitudes (e.g., six raptor species —Korpimäki 1994; Ural Owl *Strix uralensis*; —Brommer et al. 2002; Snowy Owl *Nyctea scandiaca*; —Gilg et al. 2006; tawny owl *Strix aluco*; —Karell et al. 2009; Northern Saw-whet Owl *Aegolius acadicus*; —Bowman et al. 2010), but also at temperate latitudes of the Northern Hemisphere (e.g., Montagu's Harrier *Circus pygargus* - Salamolard et al. 2000; Millon and Bretagnolle 2008). The mechanisms beyond these relationships are

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10144-018-0611-z>) contains supplementary material, which is available to authorized users.

✉ Jan Riegert
honza@riegert.cz

¹ Department of Zoology, Faculty of Science,
University of South Bohemia, Branišovská 1760,
370 05 Ceske Budejovice, Czech Republic

nomadism and changing proportion of breeding/non-breeding individuals according to food supply at a locality, however the factors that influence population size and growth may be more complex (Hone and Sibly 2002). Some studies from temperate latitudes show a lack of numerical response (e.g., boreal owl—Zárybnická et al. 2013, 2015a) that may be caused by exploiting more than one main prey type or no pronounced between year changes in prey abundances (i.e., small mammals), both leading to more stable numbers of breeding pairs between years. Similarly, owl populations in urban areas may not exhibit a numerical response to main prey because of the use of more than one alternative prey types or modified hunting behaviour (e.g., Long-eared Owl *Asio otus*—Lövy 2007).

Prey abundance may also affect demographic components. Most evidence in birds of prey abundance comes from variations in breeding performance. During good trophic years pairs produce more young compared to poor trophic years (e.g., Long-eared Owl—Korpimäki 1992; Sergio et al. 2008; Montagu's Harrier; —Millon and Bretagnolle 2008; Barn Owl *Tyto alba*; —Pavlůvčík et al. 2015). Beyond these relationships various behavioural adaptations such as hatching asynchrony (e.g., Valkama et al. 2002) and siblicide or fratricide (e.g. Margalida et al. 2004) have been brought to light. However, within-year variability in reproductive performance has also been described (e.g., Verhulst and Nilsson 2008). Both observational and experimental studies have shown that under good trophic conditions raptors often lay earlier and produce larger clutches and broods (e.g., Dijkstra et al. 1980, 1990; Beukeboom et al. 1988; Aparicio 1994; Korpimäki and Wiehn 1998; Lehikoinen et al. 2011; Catry et al. 2017).

The tawny owl is a medium-sized nocturnal opportunistic predator inhabiting almost the whole of Europe excluding northern areas (Cramp and Simmons 1988). It breeds in tree cavities that can be successfully substituted with nest boxes (e.g., Roulin et al. 2009). The diet composition of the tawny owl has been studied across the whole of Europe (e.g., Sunde et al. 2001; Zawadzka and Zawadzki 2007; Obuch 2011). Although, rodents are generally the most common tawny owl prey, some populations or individuals show high proportions of other components (especially birds and amphibians). Similarly, the representation of the two most available rodent groups in tawny owl diet (*Apodemus* mice and *Microtus/Myodes* voles) is variable and probably reflects their availability in the field (Obuch 2011). More recently, there is a growing body of evidence that *Apodemus* mice and not *Microtus/Myodes* voles are the main prey of several Central European owl species (Marchesi et al. 2002; Roulin et al. 2009; Zárybnická et al. 2013; Chausson et al. 2014).

The main aim of this study is to reveal the role of main prey in the ecology of the tawny owl population in Central Europe. To assess the importance of different prey across

Europe, (1) we performed a meta-analysis of diet composition of Tawny Owl. Further, (2) we analyzed the diet composition of tawny owl in our study area (Central Bohemia) and tested the effect of prey availability on diet composition. We also assessed (3) the effect of prey availability on the number of breeding pairs. Finally, (4) we tested the effect of diet composition on breeding performance both between-years (i.e., clutch size, brood size and number of fledglings) and within a year (i.e., the relationship with laying date).

Methods

Study area

The study was conducted between the towns of Mělník and Mnichovo Hradiště (district Mladá Boleslav) in Central Bohemia (50°30'N, 14°47'E, 190 km², 220–400 m a.s.l.). The landscape within the study area changes from southwest to northeast. The southwestern part of the area is situated in CHKO Kokořínsko along the river Pšovka, in the vicinity of the town Mšeno. The landscape has a canyon like character with typical eroded sandstone rocks covered mainly by forest (forests 46.7%, arable land 40.1%, permanent crops, orchards and meadows 11.4%, urban areas 1.3%, water surfaces 0.5%). The northeastern part of the area is located in the vicinity of the town Mnichovo Hradiště and is more developed and more used for agriculture than the former (arable land 39.8%, forests 33.1%, permanent crops, orchards and meadows 21.9%, urban areas 3.5%, water surfaces 1.7%). The forests within the study area consist mainly of acidophilus beech and pine-oak forests dominated by Scots Pine *Pinus sylvestris* (60%) and Norway Spruce *Picea abies* (20%).

During the years 2008–2014, a total of 60 nest boxes were installed within the study area. The nest boxes were made of spruce wood, the bottom measured 30 cm × 30 cm and height was 55 cm (back) and 45 cm (front). The entrance hole was 17.5 cm in diameter. Nest boxes were checked each year at the end of March to detect nest box occupancy. Occupied nest boxes were further checked at least three times to assess reproductive parameters and collect material for diet composition analyses. During the autumn, we repaired damaged nest boxes and prepared them (i.e., cleaning the leaf litter) for the next breeding season. The annual occupancy of nest boxes varied between 12 and 20% per year (mean ± SD, 15.7 ± 4.0, Table 1). When we recorded predation by martens (*Martes* sp.), the nest box was relocated during the following winter.

Table 1 Nest box occupancy and reproductive parameters of tawny owl during the years 2008–2014

Year	Number of available nest boxes	Number of occupied nest boxes (%)	Clutch size per nest box \pm SD	Brood size per nest box \pm SD	Number of fledglings per nest box \pm SD	Reproductive success (%)
2008	30	6 (20)	3.7 \pm 1.0	2.2 \pm 1.3	2.0 \pm 1.3	55
2009	50	6 (12)	3.3 \pm 0.8	2.0 \pm 1.4	1.8 \pm 1.2	55
2010	59	12 (20)	4.7 \pm 0.7	3.2 \pm 1.9	2.8 \pm 1.9	61
2011	58	7 (12)	2.7 \pm 1.1	1.4 \pm 1.4	1.3 \pm 1.1	47
2012	57	11 (19)	4.1 \pm 1.3	1.9 \pm 2.2	1.6 \pm 2.2	40
2013	57	7 (12)	3.4 \pm 1.3	2.9 \pm 1.8	2.9 \pm 1.8	83
2014	57	8 (14)	2.8 \pm 1.2	1.6 \pm 1.8	1.3 \pm 1.8	45

Food supply

The abundance of small mammals was assessed using the snap-trap capture method (Pelikán et al. 1972). The captures were carried out twice each year (2008–2014) during the turn of March and April and during the turn of September and October. The traps were laid out in four squares within the study area (two squares on meadows and two squares in forests). Each square covered an area of 100 m \times 100 m, a couple of traps were placed within a span of 10 m with a total of 242 traps at 121 points in each square. The traps were exposed for three nights and checked once a day in the morning to avoid data losses caused by scavengers. All caught mammals were determined to species ($n = 1267$ individuals).

Diet composition

Pellets and prey remains from the nest box bottom (i.e., rubble) were collected in the breeding period during three visits to nest boxes occupied by tawny owl. The first visit was carried out in order to check for nest box occupancy, the second visit took place during the presence of the chicks in the nest box and the third visit immediately after the chicks had fledged. The material from the nest boxes was put into a 5% solution of NaOH for 1 day (Schueler 1972). Feather remains were carefully picked up before the dissolving process. After the hair debris were dissolved, the samples were rinsed using a dense sieve under running water. Washed samples were then dried and bones were sorted into various categories including mammalian jaw bones and bird beaks, tarometatarsi, humeri and metacarpal bones. Small mammals were determined by identifying skulls using Anděra and Horáček (2005), and birds by feathers and beaks using a reference collection. Thrush-sized and sparrow-sized birds were determined using humeri and/or femuri. Number of individuals was assessed according to the maximal number of a particular bone from the left and right side of a prey body or according to the maximal number of parts that can be found on a prey body (e.g., humeri, femuri and number

of upper and lower incisors). We determined 2268 individuals to 38 taxa based on 24,134 bone and feather remains from fledglings' pellets found in 39 nest boxes (mean \pm SD, 58.1 \pm 38.0) of which 1916 individuals were rodents. In 604 cases (31.5%), only upper or lower incisors were present, and individuals were considered as non-determined rodents. For the purpose of further analyses, diet components were classified into seven main groups: Birds, Muridae—mainly *Apodemus* sp. mice (less frequently also *Mus musculus*, *Rattus norvegicus*), Arvicolidae—mainly *Microtus/Myodes* sp. voles (less frequently also *Arvicola terrestris*), Soricidae—mainly *Sorex* sp. (*Sorex araneus*, *Sorex minutus*, rarely also *Neomys fodiens*), Gliridae (*Glis glis*, *Muscardinus avelanarius*), and non-determined rodents and amphibians [Table S1 in Electronic Supplementary Material (ESM)].

Reproductive success

We estimated reproductive success based on visits to nest boxes during the breeding season. We recorded the number of eggs and chicks in the nest box and the number of fledged young. During the study period, we recorded a total of 57 nesting attempts of tawny owl (mean \pm SD, 8.1 \pm 2.4 per year). From these attempts, 39 were successful (at least one fledgling was produced) with a total of 114 fledglings produced (mean \pm SD, 2.9 \pm 1.4 per nest). During nest box visits we determined the age of chicks to assess approximate laying date (i.e., day from 1 January of particular year).

Statistical analyses

Meta-analysis of literature data was performed in Canoco 5 software, using redundancy analysis (RDA) that is suitable for calculating inter-correlated variables (Šmilauer and Lepš 2014). The data unit was each study (Table S2 in ESM). Log-transformed percentages of the numbers of the following prey were used as response variables: *Apodemus* mice, *Myodes* and *Microtus* voles, Gliridae dormice, insectivores, other mammals (mainly bats), birds, insects, amphibians and other groups (mainly lizards, fish and invertebrates apart

from insects—e.g., crayfishes and slugs). The number of determined prey items in each study was used as a covariate. We tested the effect of latitude and longitude on diet composition, statistical significances were obtained using Monte-Carlo permutation tests.

Multivariate data on the effect of environmental factors on diet composition were calculated using variance partitioning by principal coordinate analysis of neighbour matrices (PCNM) in Canoco 5 software (ter Braak and Šmilauer 2012), the method recently recommended by Marrot et al. (2015). This multivariate analysis enabled us to separate the effect of space predictors (i.e., geographical position of nest box) from the effect of primary predictors (Legendre and Legendre 2012). Moreover, this analysis is suitable for calculating inter-correlated variables, such as proportions of diet items (i.e., when the proportion of one item increases, the proportion of other items decreases), since all these variables enter the analysis simultaneously. The analysis included nine steps: (1) primary predictor test (i.e., preliminary test of the overall effect of primary predictors on the dataset), (2) primary predictor selection by partial redundancy analysis (RDA) using forward selection based on partial Monte-Carlo permutation tests, (3) principal coordinate analysis (PCoA) based on Euclidean distances (i.e., finding the main space predictors based on coordinates), (4) PCNM for all predictors (i.e., preliminary test of the overall effect of space predictors on the dataset), (5) PCNM selection (i.e., the choice of space predictors based on coordinates using forward selection and partial Monte-Carlo permutation tests), (6) spatial effects analysis (i.e., assessing the amount of variability explained by space predictors), (7) primary predictor effects analysis (i.e., assessing the amount of variability explained by primary predictors), (8) joint effects analysis (i.e., assessing the amount of variability explained by both predictor types) and (9) removal of spatial effects (Šmilauer and Lepš 2014). The data unit was represented by each nesting attempt. Response variables were represented as percentages of the numbers of each main diet component (*Apodemus* mice, *Microtus/Myodes* voles, Gliridae, Rodentia unidentified, insectivores, birds and amphibians) that were log-transformed prior to analysis as recommended by Šmilauer and Lepš (2014). As a covariate we used the total number of identified prey items in the nest box. Nest box ID and year were used as random factors to eliminate biases in occupancy rate among nest boxes during the study period. The following factors were used as explanatory variables: spring, autumn and total yearly abundance of main small mammal groups (*Microtus/Myodes* voles, *Apodemus* mice, *Sorex* shrews—individuals/ha) and also their abundances in the previous year. Statistical significance was obtained by Monte-Carlo permutation tests.

Partial regressions between number of breeding pairs and abundance of prey in the field were computed for each

prey species separately using regressions in Statistica 12 software. We used proportion of occupied nest boxes as the dependent variable and abundance of a particular prey species in the field (individuals/ha) as the independent variable. Using the same method, we analyzed relationships between abundance of *Apodemus* mice in the field (independent variable) and its proportion in the diet and clutch size (dependent variables), and between laying date (dependent variable) and clutch size and brood size (independent variables).

The effect of diet composition on breeding parameters (laying date, clutch size, brood size and number of fledglings) was tested using scores from the first and second ordination axes (from the above mentioned PCNM analysis) that represented the main gradients in our dataset (i.e., gradient of unidentified rodents—*Microtus/Myodes* and Gliridae on first ordination axis, and gradient *Apodemus* mice—birds and insectivores on second axis). A diet item was considered to be associated with an ordination axis when the value of its regression coefficient reached at least 0.6. Further, we built a GLM model (dependent variable—laying date) and GLMM models (dependent variables—clutch size, brood size and number of fledglings) with scores from the first and second ordination axes, year and nest box ID as independent variables. In GLMM models, we used previous reproductive stage as covariates (i.e., laying date in the analysis of clutch size, clutch size in the analysis of brood size and brood size in the analysis of number of fledglings) to eliminate their influence on subsequent breeding stages. Since data on laying date did not significantly differ from Gaussian distribution (Kolmogorov–Smirnov test, $P=0.226$), we used identity link function in the GLM analysis. In GLMMs, we used log link function for Poisson distributions. We used forward selection of independent variables using AIC criterion and showed only significant results.

Results

Food supply

Between the years 2008–2014, we caught 1267 individual small mammals. *Microtus* voles were the most frequently captured small mammals (87.2%, represented almost exclusively by the common vole *M. arvalis*), other groups of small mammals were less common (*Myodes* voles 4.7%, *Sorex* shrews 4.3% and *Apodemus* mice 3.7%). The total yearly abundance (pooled spring and autumn abundance) of *Microtus arvalis* showed peaks in 2008, 2011 and 2014, while the abundance of *Apodemus* mice and *Myodes* voles showed increased abundances in 2010 and 2012. *Sorex* shrews had low between-year variability in abundance with a maximum in 2012 (Fig. 1).

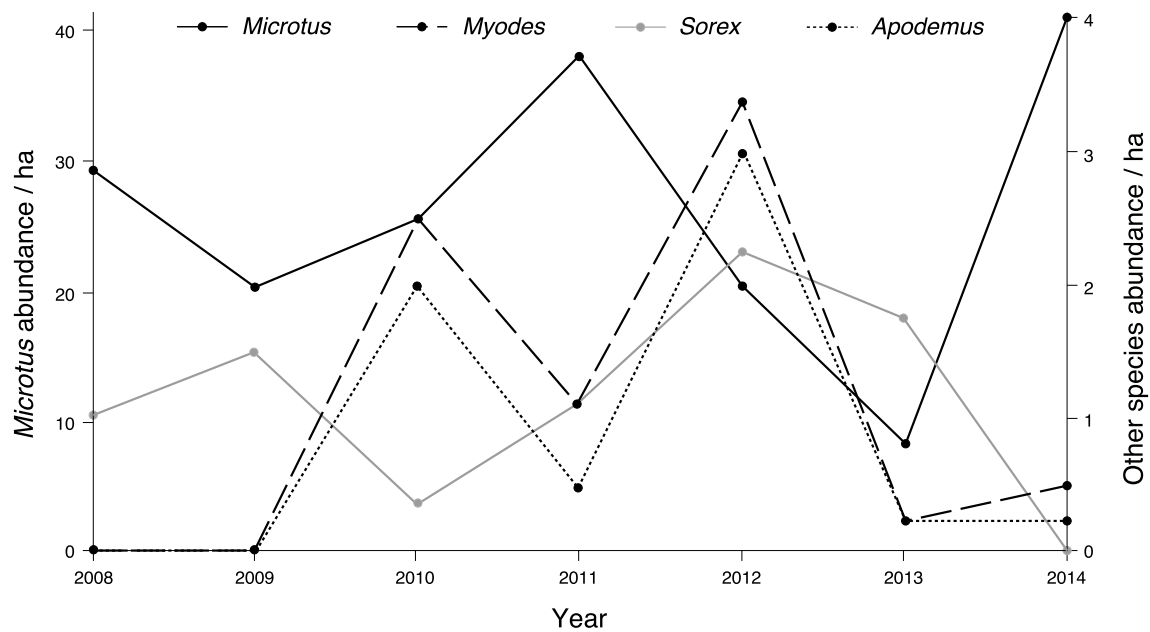


Fig. 1 Changes in abundances of small mammals in the field during the years 2008–2014

Diet composition

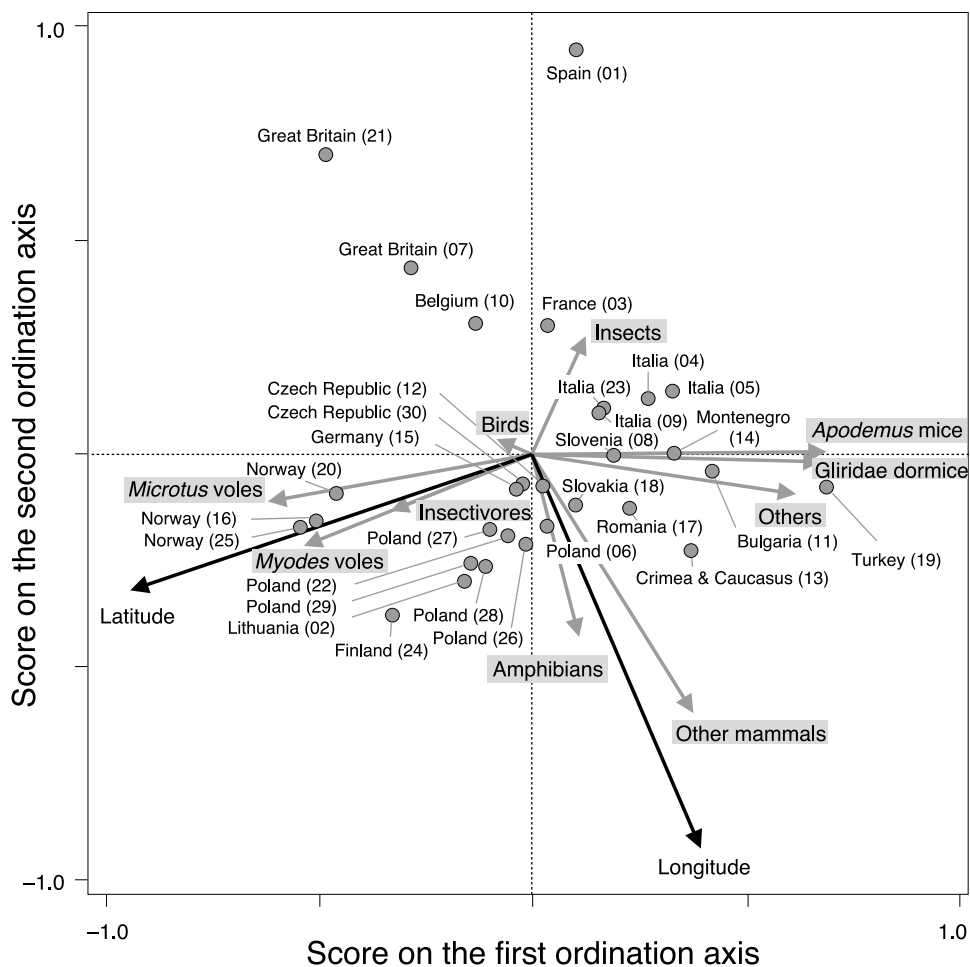
Meta-analysis of literature data showed that the diet of tawny owl in Europe can be divided into four main groups based on their positions within the ordination space (Fig. 2). First, the group including *Apodemus* mice, Gliridae dormice and other groups, proportions of which showed positive correlations with the first ordination axis (regression coefficients; *Apodemus* mice: 0.98, Gliridae dormice 0.97, other groups 0.88). Second, proportions of *Myodes*/*Microtus* voles and insectivores that were negatively correlated with the first ordination axis (regression coefficients; *Microtus* voles – 0.90, *Myodes* voles – 0.77, insectivores – 0.49). Third, other mammals and amphibians, proportions of which were independent of the above mentioned groups and were negatively correlated with the second ordination axis (regression coefficients; other mammals – 0.76, amphibians – 0.84). Fourth, birds and insects, proportions of which were independent of the above mentioned prey groups and did not correlate with any ordination axis (Fig. 2). Latitude and longitude significantly affected the diet of tawny owl within its European range (RDA analysis; latitude: $F = 7.80$, $P = 0.004$, longitude: $F = 3.10$, $P = 0.008$). Latitude was negatively correlated with the first ordination axis (regression coefficient – 0.64) and longitude was negatively correlated with the second ordination axis (regression coefficient – 0.47). In Northern Europe, the diet of tawny owl is mainly dominated by insectivores, *Myodes* and *Microtus* voles. Towards the South, we recorded an increased proportion of *Apodemus* mice, and Gliridae dormice. Proportions of insects and birds

were not related to latitude. Towards the East, we recorded increased proportions of amphibians and other mammals (e.g., *Rattus norvegicus*).

In the diet of our tawny owls rodents dominated (84.5%), alternative prey were birds (12.1%), frogs (2.2%) and insectivores (1.2%) represented by three Soricidae species (*Sorex araneus*, *S. minutus* and rarely *Neomys fodiens*). 31.5% of rodents were unidentified. Within determined rodents *Apodemus* mice represented the most dominant prey item (66.9%), *Myodes* (17.3%) and *Microtus* voles (9.4%) were less represented. Other rodents (*Mus* mice, water vole *Arvicola terrestris*, rat *Rattus norvegicus* and Gliridae dormice, mainly *Glis glis* and *Muscardinus avellanarius*) formed a minor proportion of the rodent prey (<4%). The proportion of main mammal groups varied between years, *Apodemus* mice formed 36.8–72.6% of determined mammals. When the proportion of *Apodemus* mice in the diet decreased, the representation of *Microtus* voles (23.3% in 2009 and 2011, yearly median 8.0%), *Myodes* voles (24.1% in 2011, yearly median 16.9%) and insectivores (14.0% in 2009, yearly median 2.2%) increased.

Representation of birds in the diet was variable with maxima in 2009 (42.4%) and 2011 (38.8%), reaching median 24.2%. The thrush-sized (33.2%) and sparrow-sized birds (37.2%) dominated among bird prey items. The most frequently caught determined species was Blackbird *Turdus merula* (9 ex., 3.3%). We also determined three individuals of Great Spotted Woodpecker *Dendrocopos major*, two individuals of Eurasian Jay *Garrulus glandarius* and one unidentified parrot species (Psittaciformes, Table S1 in ESM).

Fig. 2 The effect of latitude and longitude on the diet composition of tawny owl in Europe. Meta-analysis of literature data (RDA analysis, I and II ordination axes explain 34.0% of variability). Data taken from: (1) Adánez (2000); (2) Balčiauskienė et al. (2006); (3) Baudvin and Jouaire (2006); (4) Capizzi (2000); (5) Capizzi and Luiselli (1998); (6) Grzedzicka et al. (2013); (7) Kirk (1992); (8) Kuhar et al. (2006); (9) Marchesi et al. (2006); (10) Delmee et al. (1979); (11, 12, 13, 14, 16, 17, 18, 19) Obuch (2011); (15) Uttendörfer (1939, 1952); (20) Overskaug et al. (1995); (21) Petty (1999); (22) Romanowski and Zmihorski (2009); (23) Sergio et al. (2007b); (24) Solonen and Karhunen (2002); (25) Sunde et al. (2001); (26) Wiacek et al. (2009); (27) Zalewski (1994); (28) Zawadzka and Zawadzki (2007); (29) Zmihorski and Osojca (2006) and (30) this study



In two nest boxes, we determined individuals of amphibians (unspecified frogs, Anura) that formed up to 33.0% of the diet by numbers. Finally, we found one maxilla of a small predatory fish.

We found a significant effect of single space predictor on diet composition (PCNM, principal coordinate PCO.4, 2.8% of explained variability, $F=3.3$, $P=0.039$), but more variability was explained by primary predictor abundance of *Apodemus* mice in the field (16.8% of explained variability, $F=4.01$, $P=0.028$). Abundance of *Apodemus* mice in the field was negatively correlated with the second ordination axis (regression coefficient 0.96, Fig. 3a). We also found a positive relationship between the proportion of *Apodemus* mice in the diet and their abundance in the field (regression, $R^2=0.50$, $F=12.63$, $\beta=0.23$, $P=0.001$, Fig. 3b). Proportion of *Apodemus* mice was negatively correlated with the second ordination axis and proportions of birds and insectivores (mainly *Sorex* sp.) showed a positive correlation with this ordination axis. Proportions of *Microtus/Myodes* voles and Gliridae were positively correlated with the first ordination axis and unidentified rodents showed a negative relationship with this ordination axis. These two main gradients

of diet composition were independent of each other. Proportions of amphibians did not show significant correlation with any ordination axis (Table 2; Fig. 3a).

Population size

Based on the dataset from 7 years, we did not find significant relationships between the number of breeding pairs and the abundance of *Apodemus* mice in the field (regression, $R^2=0.30$, $F=2.18$, $\beta=0.55$, $P=0.199$), *Microtus/Myodes* voles (regression, $R^2=0.01$, $F=0.04$, $\beta=0.09$, $P=0.854$) nor *Sorex* shrews in the field (regression, $R^2=0.01$, $F=0.06$, $\beta=-0.11$, $P=0.818$).

Reproduction

During the years 2008–2014, the studied Tawny Owls produced 208 eggs and 127 young (57 breeding attempts). Tawny owl pairs produced (mean \pm SD) 3.7 ± 1.2 eggs, 2.2 ± 1.8 hatchlings and 2.0 ± 1.8 fledglings per nest. The mean clutch size, brood size and number of fledglings varied among years (clutch size 2.7–4.7, brood size 1.4–3.2 and

Fig. 3 The effect of **a** abundance of *Apodemus* mice on diet composition of tawny owls in the Czech Republic. Spatial effects were removed by PCNM analysis, I and II ordination axes explain 60.1% of variability. In the graph we show results after removing spatial effects. **b** The relationship between abundance of *Apodemus* mice in the field and its proportion in the diet of tawny owl

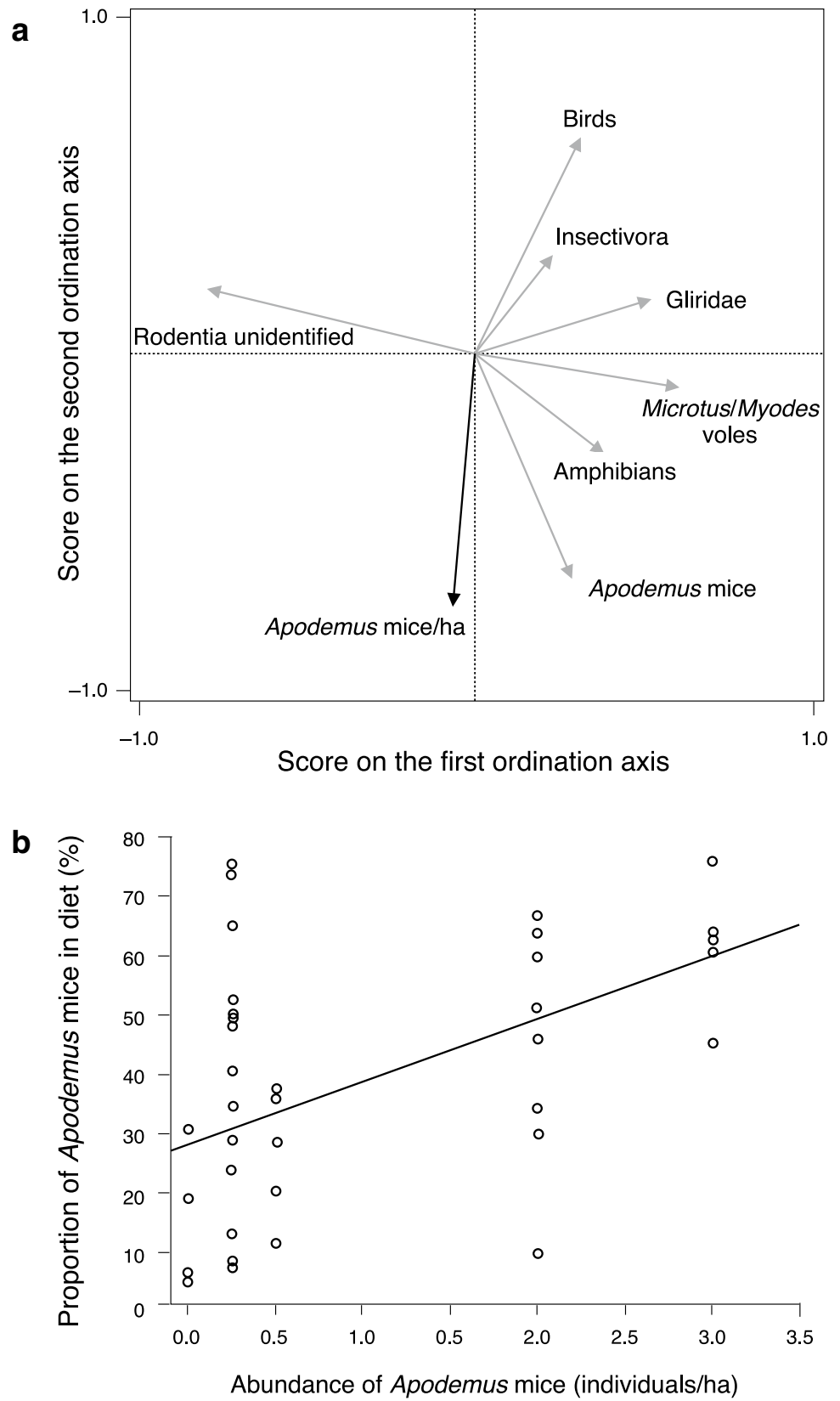


Table 2 Regression coefficients for the proportions of main diet items with first and second ordination axes based on PCNM analysis of diet composition of tawny owl

Prey item	First axis	Second axis
Birds	0.21	0.84
<i>Apodemus</i> mice	0.24	-0.92
<i>Microtus/Myodes</i> voles	0.89	-0.26
Gliridae	0.65	0.22
Rodentia unidentified	-0.86	0.26
Insectivora	0.45	0.85
Amphibians	0.26	-0.30

Values above 0.6 are in bold

number of fledglings 1.3–2.9 per breeding pair). The largest clutches and broods were produced in 2010 and the highest numbers of fledglings were recorded in 2013. The lowest reproductive parameters were found in 2011 (Table 1).

We confirmed negative relationships between laying date and clutch size (regression, $R^2=0.39$, $F=6.66$, $\beta=-0.13$, $P=0.014$, Fig. 4a) and brood size (regression, $R^2=0.31$, $F=3.87$, $\beta=-0.07$, $P=0.057$, Fig. 4b). The relationship between laying date and number of fledglings was indicative (regression, $R^2=0.07$, $F=2.9$, $\beta=-0.27$, $P=0.094$). Finally, we also found a positive correlation between the abundance of *Apodemus* mice in the field and clutch size (regression, $R^2=0.48$, $F=11.06$, $\beta=0.21$, $P=0.002$, Fig. 4c).

Scores from the second ordination axis of PCNM analysis on diet composition (i.e., gradient of proportions of birds and *Apodemus* mice) showed a positive relationship with laying date (Table 3). Particularly, we recorded a decreasing proportion of *Apodemus* mice and an increasing proportions of birds and insectivores in the diet during the course of the breeding season (Fig. 5a). These scores were also negatively correlated with clutch size (Fig. 5b) and indicatively negatively correlated with brood size (Fig. 5c; Table 3). Laying date also significantly differed among years (Table 3; Fig. 5d). Neither scores from the first ordination axis (i.e., gradient between unidentified rodents and *Microtus/Myodes* voles and Gliridae) nor nest box ID had a significant effect. None of the factors affected the number of fledglings.

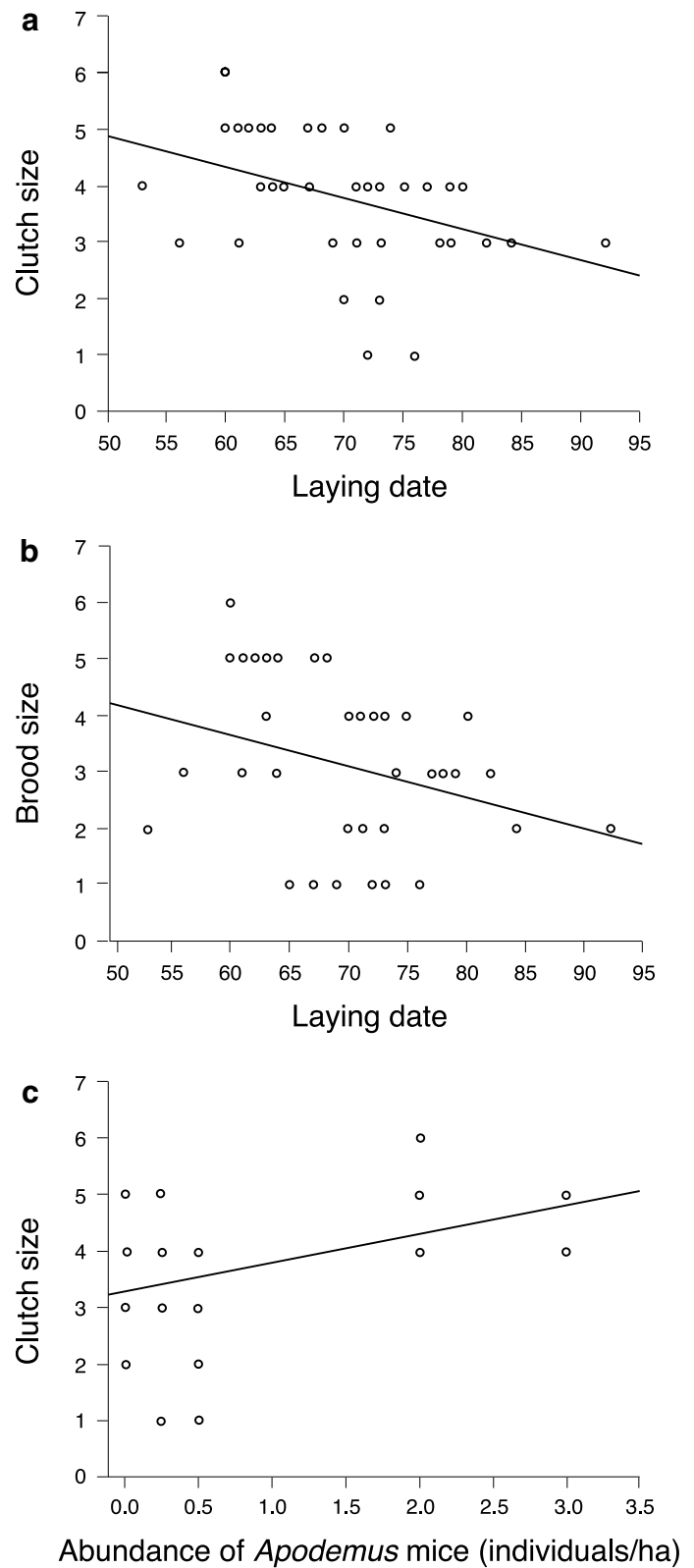
Discussion

The role of main prey types in the diet of tawny owl populations can substantially change with their geographic positions. Within Europe, *Microtus/Myodes* voles are common throughout the whole continent, but *Apodemus* mice have their northern range border in Southern Finland. Therefore, Central European populations are more likely to

include *Apodemus* mice in their diet compared to northern owls. In agreement, studies from Northern Europe (more than 54°N) consistently show an increased proportion of *Microtus/Myodes* voles compared to *Apodemus* mice (e.g., Overskaug et al. 1995; Petty 1999; Sunde et al. 2001). Similarly, Zmihorski et al. (2008) reported an increased proportion of Arvicolidae and a decreased proportion of Muridae in the diet of Tawny Owls along a NE gradient in the area around the Baltic Sea. Also our meta-analysis showed that the proportion of *Apodemus* mice decreases towards northern areas and owls there often feed on shrews and *Microtus/Myodes* voles.

In agreement with most others studies (e.g., Capizzi 2000; Balčiauskiene 2005; Balčiauskiene et al. 2005; Gryz et al. 2008), the dominant prey of our owls were rodents (84.5%). Within Europe, rodents in the diet of tawny owl are mainly represented by Muridae (mainly *Apodemus* mice) and Arvicolidae (mainly *Microtus* and *Myodes* voles) (e.g., Sunde et al. 2003; Balčiauskiene and Naruševičius 2006; Balčiauskas et al. 2011), which is also supported by our results (*Apodemus* mice 66.9% and *Microtus/Myodes* voles 26.7%). Moreover, *Apodemus* mice showed a positive relationship between their proportion in the diet and availability in the field. Such a relationship was not found for *Microtus/Myodes* voles nor *Sorex* shrews. The great importance of *Apodemus* mice in the diet of tawny owl has also been recently documented in Switzerland (Roulin et al. 2009). Moreover, it was documented that within Europe *Apodemus* mice represent the main prey for several owl species. For example, Zárbynická et al. (2013) showed that Boreal Owl diet in the Czech Republic is dominated by *Microtus* voles, but a functional response was found only for *Apodemus* mice. Similar results were also found in long-eared owl, a vole specialist in northern latitudes, but often feeding on *Apodemus* mice in Central Europe during vole scarcity (Riegert et al. 2009). Based on these results, we suggest that the availability of *Apodemus* mice drives the diet composition of these owls within their range. The suitability of *Apodemus* mice as a main prey is supported by the following: (1) *Apodemus* mice show mainly nocturnal activity compared to the cathemeral activity of *Microtus* voles (Halle and Stenseth 2000). Therefore, compared to, for example, diurnal vole specialists like Eurasian Kestrel (*Falco tinnunculus*) (Village 1990), owls are more likely to exploit *Apodemus* mice as prey. In agreement, Eurasian Kestrels in Central Europe during vole scarcity feed mainly on insects and *Apodemus* mice are not frequent prey (Riegert and Fuchs 2004). (2) Habitat preferences of *Apodemus* mice for wooded and ruderal habitats (Anděra and Horáček 2005) are consistent with the hunting habitat preferences of tawny owl (Kajtoch et al. 2015), long-eared owl (Lövy and Riegert 2013) and boreal owl (Zárbynická et al. 2015b).

Fig. 4 Regression relationships between laying date (i.e., day from 1 January) and **a** clutch size ($P=0.014$) and **b** brood size ($P=0.057$) and **c** the relationship between abundance of *Apodemus* mice in the field and clutch size ($P=0.002$). For all relationships, $n=39$ nesting attempts

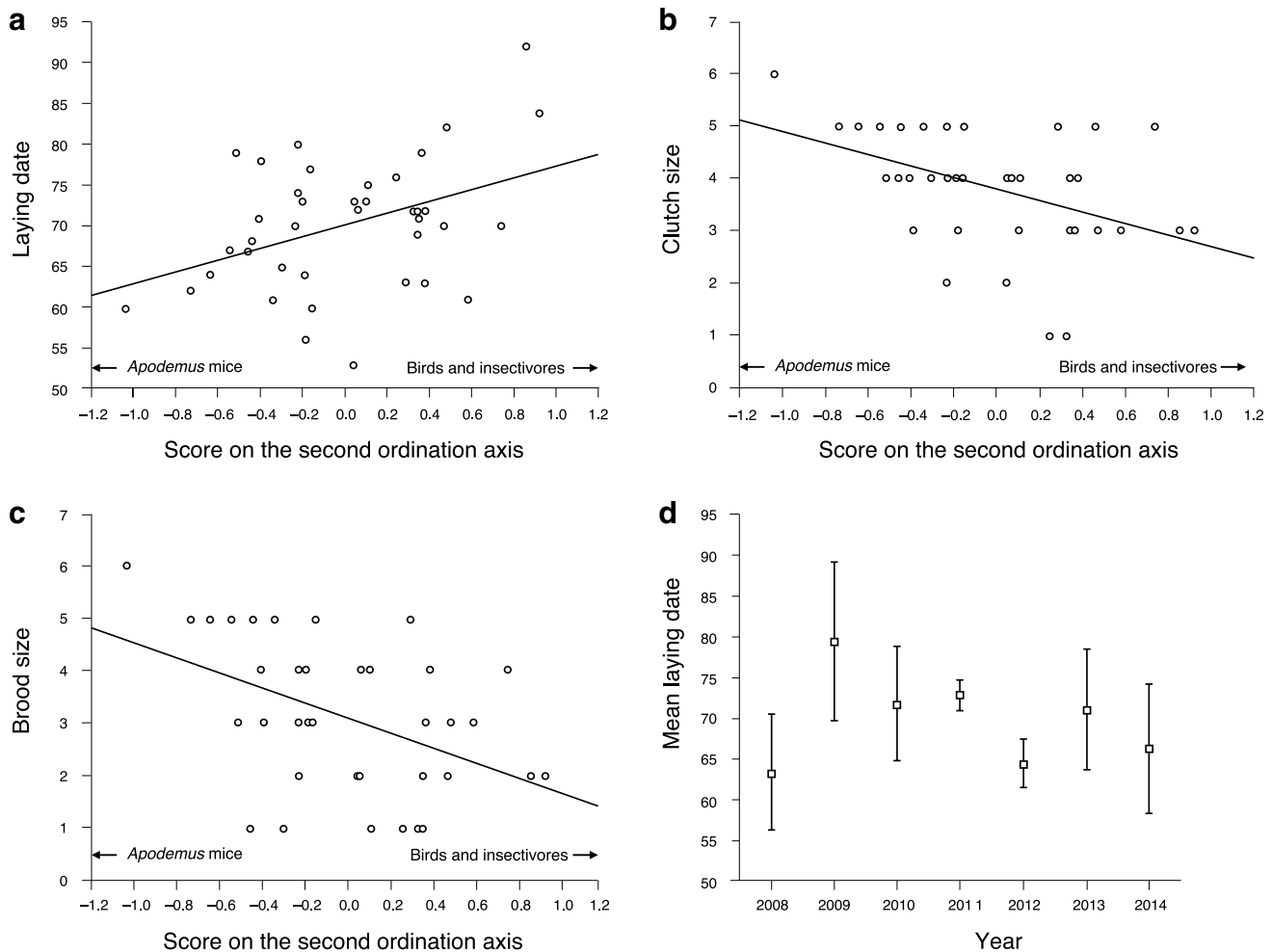


Representations of other components of tawny owl diet considerably vary across the European continent, but in general, proportions of birds (12.1%), insectivores (1.2%)

and amphibians (2.2%) in the diet of our tawny owls are comparable with other studies (e.g., Kirk 1992; Kekkonen et al. 2008; Grzedzicka et al. 2013). Across the years of

Table 3 The effect of diet composition and year on laying date and reproductive parameters of tawny owl GLM (F values) and GLMM (Chi values) analyses

Method	Dependent variable	Covariate	Independent variable	df	Percentages of explained variability	Beta	F/Chi	P
GLM	Laying date		Score on the second ordination axis	37	16.0	0.66	7.05	0.012
			Year	31	33.6		2.60	0.036
GLMM	Clutch size	Laying date	Score on the second ordination axis	37	6.8	-0.45	8.12	0.004
	Brood size	Clutch size	Score on the second ordination axis	37	2.4	-0.16	3.15	0.076

**Fig. 5** The relationships between scores from the second ordination axis of PCNM analysis on diet composition (i.e., gradient of proportion of birds, insectivores and *Apodemus* mice in the diet as indicated

by arrows above horizontal axes) and **a** laying date (regressions, $P=0.012$), **b** clutch size ($P=0.004$) and **c** brood size ($P=0.076$). **d** Mean laying dates (\pm SD) during the study period ($P=0.036$)

study, *Apodemus* mice were replaced by different prey including birds, insectivores and *Microtus/Myodes* voles in relation to their abundance in the field. Interestingly, in one year we recorded an increased proportion of frogs (11%). In this year (2013), two of six pairs settled nearby water streams. In the territory of one tawny owl pair, the water surface developed during the breeding period,

which consequently led to the occurrence of frogs in the diet. Similar results were shown by Zmihorski and Osójka (2006) who reported a high proportion of amphibians in the diet of tawny owls mainly occurring in pairs breeding near water surfaces. Based on our meta-analysis the proportion of amphibians increases towards the East, but their representation is probably influenced by the presence of

an aquatic environment in the home ranges of individual pairs. A similar latitudinal trend was also recorded for other mammals, this was probably caused by the different faunal composition of rodents in Southeast Europe compared to other parts of Europe (e.g., *Chionomys*, *Dinaromys*). The role of Gliridae in the diet of our owls was of rather minor importance, but based on the results of the meta-analysis their proportion in tawny owl diet increased at low latitudes.

We did not find a positive relationship between abundance of *Apodemus* mice, *Microtus/Myodes* voles or *Sorex* shrews in the field and the number of breeding tawny owl pairs. These results are in contrast with some studies in Central Europe (e.g., Roulin et al. 2009), but agree with others (e.g., Zárybnická et al. 2013, 2015a). In our study, we cannot distinguish whether the absence of a numerical response was caused by the breeding strategy of tawny owls, low number of caught *Apodemus* mice in the field or relatively short study period (7 years).

We found a negative relationship between the proportion of *Apodemus* mice in the diet and laying date (i.e., the earlier the owl breeds the more *Apodemus* mice occur in its diet) and clutch size that is consistent with the results of a study from Switzerland (Roulin et al. 2009). We also found a positive relationship between the proportion of *Apodemus* mice in the diet (expressed by scores from ordination axis) and breeding parameters (clutch size and brood size). These results suggest that unavailability of the main prey in the late breeding phase forces breeders to switch to alternative prey (i.e., birds or insectivores). As shown by several studies, laying date can be used as a good measure of individual quality (reviewed by Sergio et al. 2007a).

Our results document the great importance of *Apodemus* mice in the feeding ecology of tawny owl in Central Europe, independent of the availability of other prey groups. The role of *Apodemus* mice in the diet of tawny owl in Central and Southern Europe is also supported by meta-analysis of literature data. *Apodemus* mice availability further influences breeding performance. Although, Tawny Owls are flexible in prey choice, our data suggests that on average the abundance of *Apodemus* mice is important in shaping its breeding performance.

Acknowledgements This work has been supported by the Student Grant Agency at the Faculty of Science of the University of South Bohemia (SGA 2011/004) and Grant Agency of University of South Bohemia (GAJU 144/2010/P, 159/2013/P and 151/2016/P). We would like to thank Kateřina Luková (Mašková), Josef Luka and Dr. Jan Procházka for assistance in the field, and CHKO Kokořínsko for cooperation during installation of nest-boxes. We also thank two anonymous referees and Dr. David Serrano for valuable comments that improved the previous draft. The study was approved according to the law 246/1992 by the Ministry of Education, Youth and Sports under permission No. 1515-28569/2012-30.

References

- Adánez AV (2000) Análisis comparativo de la dieta de ambos sexos en el cárabo común *Strix aluco* en la Península Ibérica. *Ardeola* 47:203–213 (in Spanish with English abstract)
- Anděra M, Horáček I (2005) Poznáváme naše savce. Sobotáles, Praha (in Czech)
- Aparicio JM (1994) The seasonal decline in clutch size: an experiment with supplementary food in the Kestrel, *Falco tinnunculus*. *Oikos* 71:451–458
- Balčiauskas L, Balčiauskienė L, Alejunas P (2011) Northern Birch mouse (*Sicista betulina*) in Lithuania, findings in the diet of tawny owl (*Strix aluco*). *Acta Zool Acad Sci H* 57:277–289
- Balčiauskienė L (2005) Analysis of tawny owl (*Strix aluco*) food remains as a tool for long-term monitoring of small mammals. *Acta Zool Litu* 15:85–89
- Balčiauskienė L, Naruševičius V (2006) Coincidence of small mammal trapping data with their share in the tawny owl diet. *Acta Zool Litu* 16:93–101
- Balčiauskienė L, Juškaitis R, Atkočaitis O (2005) The diet of the tawny owl (*Strix aluco*) in south-western Lithuania during the breeding period. *Acta Zool Litu* 15:13–20
- Balčiauskienė L, Jovaišas A, Naruševičius V, Petraška A, Skuja S (2006) Diet of tawny owl (*Strix aluco*) and Long-eared owl (*Asio otus*) in Lithuania as found from pellets. *Acta Zool Litu* 16:37–45
- Baudvin H, Jouaire S (2006) Le régime alimentaire d'une population forestière de Chouettes hulottes (*Strix aluco*) en Bourgogne. *Rev Sci Bourgogne-Nat* 4:85–89 (in French)
- Beukeboom L, Dijkstra C, Daan S, Meijer T (1988) Seasonality of clutch size determination in the Kestrel *Falco tinnunculus*: an experimental approach. *Ornis Scand* 19:41–48
- Bowman J, Badzinski DS, Brooks RJ (2010) The numerical response of breeding Northern saw-whet owls *Aegolius acadicus* suggests nomadism. *J Ornithol* 151:499–506
- Brommer J, Pietiäinen H, Kolunen H (2002) Reproduction and survival in a variable environment: ural owls (*Strix uralensis*) and three-year vole cycle. *Auk* 119:544–550
- Capizzi D (2000) Diet shifts of the tawny owl *Strix aluco* in central and northern Italy. *Italian J Zool* 67:73–79
- Capizzi D, Luiselli L (1998) A comparative study of the variability of owl diets in three localities of Central Italy. *Revue d'Ecologie (La Terre et la Vie)* 53:367–385
- Catry T, Moreira F, Alcazar R, Rocha PA, Catry I (2017) Mechanisms and fitness consequences of laying decisions in a migratory raptor. *Behav Ecol* 28:222–232
- Chausson A, Henry I, Ducret B, Almasi B, Roulin A (2014) Tawny owl *Strix aluco* as an indicator of barn owl *Tyto alba* breeding biology and the effect of severity on barn owl reproduction. *Ibis* 156:433–441
- Cramp S, Simmons KEL (1988) The birds of the Western Palearctic Volume II. Oxford University Press, Oxford
- Delmee E, Dachy P, Simon P (1979) Etude comparative du régime alimentaire d'une population forestière de Chouettes hulottes (*Strix aluco*). *Le Gerfaut* 69:45–99 (in French)
- Dijkstra C, Vuursteen L, Daan S, Masman D (1980) Clutch size and laying date in the Kestrel *Falco tinnunculus*: effect of supplementary food. *Ibis* 124:210–213
- Dijkstra C, Bult A, Bijlsma S, Daan S, Meijer T, Zijlstra M (1990) Brood size manipulations in the Kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *J Anim Ecol* 59:269–285
- Gilg O, Sittler B, Sabard B, Hurstel A, Sané R, Delattre P, Hanski I (2006) Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos* 113:193–216

- Gryz J, Krauze D, Goszczynski J (2008) The small mammals of Warsaw as inferred from tawny owl (*Strix aluco*) pellet analyses. *Ann Zool Fenn* 45:281–285
- Grzedzicka E, Krzysztof KUS, Nabielec J (2013) The effect of urbanization on the diet composition of the tawny owl (*Strix aluco* L.). *Pol J Ecol* 61:391–400
- Halle S, Stenseth NCh (2000) Activity patterns in small mammals—an ecological approach. *Ecological Studies* 141. Springer, Berlin
- Hone J, Sibly RM (2002) Demographic, mechanistic and density-dependent determinants of population growth rate: a case study in an avian predator. *Philos Trans R Soc Lond B* 357:1171–1177
- Jacobsen BV, Sonerud GA (1993) Synchronous switch in diet and hunting habitats as a response to disappearance of snow cover in Tengmalm's owl *Aegolius funereus*. *Ornis Fennica* 70:78–88
- Kajtoch L, Zmihorski M, Wieczorek P (2015) Habitat displacement effect between two competing owl species in fragmented forests. *Popul Ecol* 57:517–527
- Karell P, Ahola K, Karstinen T, Zolei A, Brommer JE (2009) Population dynamics in a cyclic environment: consequences of cyclic food abundance on tawny owl reproduction and survival. *J Anim Ecol* 78:1050–1062
- Kekkonen J, Kolunen H, Pietiäinen H, Karell P, Brommer JE (2008) Tawny owl reproduction and offspring sex ratios under variable food conditions. *J Ornithol* 149:59–66
- Kirk D (1992) Diet changes in breeding tawny owls (*Strix aluco*). *Journal of Raptor Research* 26:239–242
- Korpimäki E (1992) Diet composition, prey choice, and breeding success of long-eared owls: effects of multiannual fluctuations in food abundance. *Can J Zool* 70:2373–2381
- Korpimäki E (1994) Rapid or delayed tracking of multi-annual vole cycles by avian predators? *J Anim Ecol* 63:619–628
- Korpimäki E, Wiehn J (1998) Clutch size of Kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos* 83:259–272
- Kuhar B, Kalan G, Janžekovič F (2006) Diet of the tawny owl *Strix aluco* in the Kozjansko region (E Slovenia). *Acrocephalus* 27:147–154
- Legendre P, Legendre L (2012) *Numerical ecology*, 3rd edn. Elsevier, Amsterdam
- Lehikoinen A, Ranta E, Pietiäinen H, Byholm P, Saurola P, Valkama J, Huitu O, Henttonen H, Korpimäki E (2011) The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecologia* 165:349–355
- Lövy M (2007) *Potravní chování a složený potravy kalouse ušatého (Asio otus) v městském prostředí*. Master Thesis. University of South Bohemia, České Budějovice **(in Czech)**
- Lövy M, Riegert J (2013) Home range and land use of urban long-eared owls. *Condor* 115:551–557
- Marchesi L, Pedrini P, Sergio F (2002) Biases associated with diet study methods in the Eurasian eagle-owl. *J Raptor Res* 36:11–16
- Marchesi L, Sergio F, Pedrini P (2006) Implications of temporal changes in forest dynamics on density, nest-site selection, diet and productivity of tawny owls *Strix aluco* in the Alps. *Bird Study* 53:310–318
- Margalida A, Bertran J, Boudet J, Heredia R (2004) Hatching asynchrony, sibling aggression and cannibalism in the bearded vulture *Gypaetus barbatus*. *Ibis* 146:386–393
- Marrot P, Garant D, Charmantier A (2015) Spatial autocorrelation in fitness affects the estimation of natural selection in the wild. *Methods Ecol Evol* 6:1474–1483
- Millon A, Bretagnolle V (2008) Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. *Oikos* 117:1500–1510
- Obuch J (2011) Spatial and temporal diversity of the diet of the tawny owl (*Strix aluco*). *Slovak Raptor J* 5:1–120
- Overskaug K, Kristiansen E, Sunde P (1995) Sex-specific diet analysis of the tawny owl *Strix aluco* in Norway. *J Raptor Res* 29:137–140
- Pavluvčík P, Poprach K, Machar I, Losík J, Gouveia A, Tkadlec E (2015) Barn owl productivity response to variability of vole populations. *PLoS ONE* 10:e0145851
- Pelikán J, Zejda J, Holišová V (1972) Influence of prebaiting on the catch of small mammals. *Zool Listy* 21:209–225
- Petty SJ (1999) Diet of tawny owls (*Strix aluco*) in relation to field vole (*Microtus agrestis*) abundance in a conifer forest in northern England. *J Zool* 248:451–465
- Riegert J, Fuchs R (2004) Insects in the diet of urban Kestrels from central Europe: an alternative prey or constant component of the diet? *Ornis Fennica* 81:23–32
- Riegert J, Lövy M, Fainová D (2009) Diet composition of Common Kestrels *Falco tinnunculus* and long-eared owls *Asio otus* coexisting in an urban environment. *Ornis Fennica* 86:123–130
- Romanowski J, Zmihorski M (2009) Seasonal and habitat variation in the diet of the tawny owl (*Strix aluco*) in Central Poland during unusually warm years. *Biologia* 64:365–369
- Roulin A, Ducret B, Ravussin P-A, Bize P (2009) Importance des mulots *Apodemus* sp. dans le succès de reproduction de la chouette hulotte *Strix aluco* en Suisse romande. *Nos Oiseaux* 56:19–25 **(in French with English abstract)**
- Salamolard M, Butet A, Leroux A, Bretagnolle V (2000) Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology* 81:2428–2441
- Schueler FW (1972) A new method of preparing owl pellets: boiling in NaOH. *Bird-Banding* 43:142–142
- Sergio F, Blas J, Forero MG, Donazar JA, Hiraldo F (2007a) Sequential settlement and site dependence in a migratory raptor. *Behav Ecol* 18:811–821
- Sergio F, Marchesi L, Pedrini P, Penteriani V (2007b) Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? *Anim Behav* 74:1607–1616
- Sergio F, Marchesi L, Pedrini P (2008) Density, diet and productivity of long-eared owls *Asio otus* in the Italian Alps: the importance of *Microtus* voles. *Bird Study* 55:321–328
- Šmilauer P, Lepš J (2014) *Multivariate analysis of ecological data using Canoco 5*, 2nd edn. Cambridge University Press, Cambridge
- Solonen T, Karhunen J (2002) Effects of variable feeding conditions on the tawny owl *Strix aluco* near the northern limit of its range. *Ornis Fenn* 79:121–131
- Sunde P, Overskaug K, Bolstad JP, Øien IJ (2001) Living at the limit: ecology and behaviour of tawny owls *Strix aluco* in a northern edge population in central Norway. *Ardea* 89:495–508
- Sunde P, Bolstad MS, Moller JD (2003) Reversed sexual dimorphism in tawny owls, *Strix aluco*, correlates with duty division in breeding effort. *Oikos* 101:265–278
- ter Braak CJF, Šmilauer P (2012) *Canoco reference manual and user's guide: software for ordination, version 5.0*. Microcomputer Power, Ithaca
- Therrien J-F, Gauthier G, Korpimäki E, Bêty J (2014) Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian Arctic. *Ecology* 95:56–67
- Uttendörfer O (1939) *Die Ernährung der deutschen Tagraubvögel und Eulen und ihre Bedeutung in der heimischen Natur*. Neumann and Neudamm, Stuttgart **(in German)**
- Uttendörfer O (1952) *Neue Ergebnisse über die Ernährung der Greifvögel und Eulen*. E. Ulmer, Stuttgart **(in German)**
- Valkama J, Korpimäki E, Holm A, Hakkarainen H (2002) Hatching asynchrony and brood reduction in Tengmalm's owl *Aegolius funereus*: the role of temporal and spatial variation in food abundance. *Oecologia* 133:334–341
- Verhulst S, Nilsson J-Å (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philos Trans R Soc B* 363:399–410

- Village A (1990) *The Kestrel*. T & A D Poyser, London
- Wiacek J, Polak M, Niedźwiedz M (2009) The diet composition of the tawny owl *Strix aluco* in the Kozłówka Forest (eastern Poland). *Ann Univ Mariae Curie-Skłodowska* 64:75–81 (in Polish with English abstract)
- Zalewski A (1994) Diet of urban and suburban tawny owls in the breeding season. *J Raptor Res* 28:246–252
- Zárybnická M, Riegert J, Št'astný K (2013) The role of *Apodemus* mice and *Microtus* voles in the diet of the boreal owl in Central Europe. *Popul Ecol* 55:353–361
- Zárybnická M, Kloubec B, Obuch J, Riegert J (2015a) Fledgling productivity in relation to diet composition of boreal owl *Aegolius funereus* in Central Europe. *Ardeola* 62:163–171
- Zárybnická M, Riegert J, Št'astný K (2015b) Non-native spruce plantations represent a suitable habitat for boreal owl *Aegolius funereus* in the Czech Republic, Central Europe. *J Ornithol* 156:457–468
- Zawadzka D, Zawadzki J (2007) Feeding ecology of tawny owl (*Strix aluco*) in Wigry national park (North east Poland). *Acta Zool Litu* 17:234–241
- Zmihorski M, Osojca G (2006) Diet of the tawny owl (*Strix aluco*) in the Romincka forest (north east Poland). *Acta Zool Litu* 16:54–60
- Zmihorski M, Balčiauskiene L, Romanowski J (2008) Small mammals in the diet of the tawny owl (*Strix aluco*) in Central European lowland. *Pol J Ecol* 56:693–700