Turkish Journal of Zoology

Volume 48 | Number 1

Article 7

1-4-2024

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Recommended Citation

HORVATH, GYOZO F. and HORVÁTH, ADRIENN (2024) "Diet and reproductive outputs of common barn-owl (Tyto alba) during the common vole (Microtus arvalis) outbreak and crash," *Turkish Journal of Zoology*: Vol. 48: No. 1, Article 7. https://doi.org/10.55730/1300-0179.3160
Available at: https://journals.tubitak.gov.tr/zoology/vol48/iss1/7

Turkish Journal of Zoology

http://journals.tubitak.gov.tr/zoology/

Research Article

Turk J Zool
(2024) 48: 54-76
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doi:10.55730/1300-0179.3160

Diet and reproductive outputs of common barn-owl *(Tyto alba)* during the common vole *(Microtus arvalis)* outbreak and crash

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Received: 18.07.2023 • **Accepted/Published Online:** 22.12.2023 • **Final Version:** 04.01.2024

Abstract: In this paper, we investigated the relationship between the breeding parameters and food composition of the common barn-owl (*Tyto alba*) comparing the outbreak and subsequent crash periods of the common vole (*Microtus arvalis*) as the barn owl's main prey. For the analyses, data of 29 (2014 outbreak: 6, 2016 crash: 8; 2019 outbreak: 7, 2021 crash: 7) breeding pairs of barn owls were selected. First, we examined the differences between the breeding parameters (clutch size, number of hatchlings and fledglings), the main and alternative prey taxa (common vole and Apodemus genus), the two derived indices (trophic level index, Microtinae/Murinae ratio) between the given outbreaks and subsequent crashes as well as the cumulative data of the two demographic periods. In addition, we analysed the difference in rank-abundance distribution of prey composition comparing the outbreak and crash. We investigated the relationships between breeding parameters and demographic periods, the main and alternative prey taxa and the two derived indices using generalized linear mixed models (GLMM). The clutch size was significantly higher in both outbreaks than the crash periods, while the number of hatchlings and fledglings differed only between the second outbreak and crash period. Regarding the cumulative data of outbreaks and crashes, the values of all three breeding parameters were significantly higher in the outbreak period of the common vole. Our results highlighted the main prey role of common voles during the outbreak, as well as the importance of the Apodemus genus during the crash period. GLMM analysis supported that all three breeding parameters were positively determined by the ommon vole's abundance in the diet of barn owls in outbreak and crash periods, while the reproductive output was positively influenced common by the frequency of the Apodemus genus as potential alternative prey in the crash period.

Key words: Food composition, breeding parameters, common barn-owl, common vole, demographic period

1. Introduction

The common barn-owl (*Tyto alba* Scopoli, 1769), as a cosmopolitan species, has successfully adapted to the conditions of different habitats (Taylor, 2004; Frey et al., 2011; Roulin 2020). However, despite the adaptation of this synanthropic owl species, population declines have been observed since the 1980s (Colvin, 1985; de Bruijn, 1994; Taylor, 2004; Heath et al., 2000[1]; Toms et al., 2001). The disappearance of living and nesting sites caused by intensive agricultural cultivation and the instability of the agricultural landscape (Ramsden, 1998; Taylor, 2004; Martin et al., 2010; Hindmarch et al., 2012; Latorre et al., 2022), as well as the treatment of its hunting areas with various rodenticides, resulted in the decline of the species (Gray et al., 1994; Newton et al., 1991, 1997[2]; Albert et al., 2010; Geduhn et al., 2016). In addition to the above, weather conditions also have a significant impact on the barn owl's populations, as colder than average winters lead to a decrease in the nesting population (Marti, 1994; Taylor, 2004; Martínez and López, 1999; Altwegg et al., 2006; Chausson et al., 2014). Winter mortality has been proven to be one of the most important key factors in the demographic change of common barn-owl populations, both at the local and regional scales (Marti and Wagner, 1985; Altwegg et al., 2006; Tóth et al., 2009).

In addition to the abiotic factors, the availability and quantity of the potential food resource as a biotic factor is the most studied and evaluated effect in the relationship between food habits and the reproductive output of barn owls (Gubanyi et al., 1992; Taylor, 2004; Klok and de

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[1] Heath M, Borggreve C, Peet N, Hagemeijer W (2000). European Bird Populations: Estimates and Trends. Birdlife International, Cambridge, United Kingdom, 160 p

[2] Newton I, Wyllie I, Dale L (1997). Mortality causes in British barn owls (Tyto alba), based on 1,101 carcasses examined during 1963–1996. In: Duncan JR, Johnson DH, Nicholls TH, (editors). Biology and conservation of owls of the Northern Hemisphere: 2nd International symposium. Saint Paul, MN, USA. p. 8.

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Roos, 2007; Frey et al., 2011; Charter et al., 2015; Horváth et al., 2020). It is a known fact that raptors and owls show numerical and/or spatial as well as functional responses depending on the variation and density fluctuation of their main prey (Korpimäki and Norrdahl, 1991; Salamolard et al., 2000; Millon and Bretagnolle, 2008; Baudrot et al., 2016; Luka and Riegert, 2018; Sharikov et al., 2019; Dostál et al., 2021). The reproductive output and population dynamics of these avian predators are strongly affected by multiannual cyclic or irregular fluctuations of small mammals, especially herbivorous voles (Korpimäki et al., 2002; Klok and de Roos, 2007; Pavluvčík et al., 2015; Tulis et al., 2015; Adejumo, 2019; Fay et al., 2020; Avotins et al., 2023). The relationship, according to which a greater number of voles as main prey positively affects the clutch size, was also shown for the barn owl, along with other birds of prey that are typically characterized as vole-eating predators (Korpimäki and Norrdahl, 1991; Jędrzejewski et al., 1994; Salamolard et al., 2000; Solonen et al., 2015; Horváth et al., 2020; Korpimäki, 2020).

In temperate zones of the Nearctic and Paleartic regions, the food habits of the common barn-owl are mainly determined by the abundance fluctuations of agricultural pest rodents, such as different microtine voles (Colvin and MacLean, 1986; Marti, 1988; Taylor, 2004; Kitowski, 2013; Petrovici et al., 2013; Purger, 2014; Veselovský et al., 2017). Considering this predator-prey interaction, several studies demonstrated a negative correlation between vole (Microtus spp.) abundance in the diet and the food-niche breadth of the common barn-owl (Milchev et al., 2006; Marti, 2010; Hindmarch and Elliott, 2015; Milchev, 2015; Horváth et al., 2018).

The common vole (*Microtus arvalis*) is the most abundant and widespread microtine rodent and a major agricultural pest in Europe that causes significant crop damage during population outbreaks (Bryja et al., 2001; Bernard et al., 2010; Jacob and Tkadlec, 2010[3]; Luque-Larena et al. 2013; Jacob et al., 2014; Paz et al., 2016; Horváth et al., 2020; Jacob et al., 2020; Wymenga et al., 2021). Numerous studies in Europe have also demonstrated that the numbers of the common vole, as the main prey species of the common barn-owl, significantly affects the nesting of this species (e.g., Benedek et al., 2007; Pavluvčík et al., 2015). For instance, the nesting success of owls increased with the higher abundance of the common vole (de Jong, 1997; Taylor, 2004; Klok and de Roos, 2007; Pavluvčík et al., 2015), while less nesting pairs was observed in the collapse phase (Benedek et al., 2007). Pavluvčík et al. (2015) showed a positive correlation between the number of eggs laid by barn owls and the abundance of the common vole. However, the studies of the barn owl's diet analysis conducted in Mediterranean countries highlighted the importance of Apodemus species and mice (Murinae) in general since, in this geographical region, mouse species are the dominant main prey in drier areas. Nevertheless, the voles as main prey species in the Mediterranean region are also important for the barn owl primarily in agricultural areas (Pezzo and Morimando, 1995; Varuzza et al., 2001; Bontzorlos et al., 2005; Tores et al., 2005; Shehab and Al Charabi, 2006; Charter et al., 2009; Paspali et al., 2023).

In our earlier study, we already analysed and evaluated the relationship between the food composition and breeding parameters of the common barn-owl in the demographic phases of the common vole during its earlier population cycle (2015–2020). The results suggested that the number of fledglings was significantly higher in the increase phase than during the vole crash phase. In addition, the clutch size of barn owls was ultimately determined by the availability and consumption of the common vole as their main prey, while other small mammal prey categories did not affect the clutch size. Considering the alternative prey role, our results pointed out that only murid rodent prey categories (Apodemus spp., Muridae) were the potential alternative prey groups for barn owls during the crash phase of the common vole in the investigated region (Horváth et al., 2020).

Based on the synthesis of monitoring data of several European countries, the increase in common vole abundance in end of the earlier population cycle led to a pan-European synchronized outbreak in the territory of several countries in 2019 (Jacob et al., 2020). The results of further monitoring in Hungary detected a crash of the common vole population in 2021 (unpublished data), which marked the beginning of a new population cycle of this pest rodent.

According to the above results of the earlier study and new monitoring data, the present study aims (1) to examine the differences in the reproductive output and diet composition of the common barn-owl between two outbreaks and two subsequent crashes of the common vole as their main prey, (2) to analyse the difference in rank-abundance distribution of prey composition comparing the outbreak and crash, and (3) to evaluate the relationships between the relative abundance of the main or potential alternative prey categories in the diet and the variation of breeding parameters comparing the vole's outbreak and crash period.

2. Material and methods

2.1. Study area

The study was conducted in the south-eastern part of the Transdanubian region in Southern Hungary, in Baranya

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[3] Jacob J, Tkadlec E (2010). Rodent outbreaks in Europe: dynamics and damage. In: Singleton G, Belmain S, Brown PR, Hardy B (editors.). Rodent outbreaks: Ecology and impacts. Los Banos, Philippines, The International Rice Research Institute (IRRI): pp. 207-224.

County (4429.6 km^2) (45°53′ N, 18°20′ E) (Figure 1). The climate and weather conditions characteristic of the county (short, mild winter; small temperature fluctuations; high number of hours of sunshine; high average temperature) create suitable climatic conditions for the barn owl population survival and stability as well as a successful conservation management program. In addition, the dense small-village-type settlement system of the county is also favourable from the point of view of the breeding of barn owls, since most of the villages have church towers suitable for placing nest boxes (Bank et al., 2019).

2.2. Nesting pairs and breeding parameters

In Baranya County, the breeding biology monitoring of barn owls started in the early 1990s, which was closely connected with the local common barn-owl protection program, namely the installation of nest boxes suitable for this owl species by the Baranya County Group of BirdLife Hungary. Within the framework of this program, more than 160 nesting boxes were placed in Baranya County in the last 30 years, based on which it became possible to monitor the nesting parameters of barn owl pairs in a long term. Sampling for breeding parameters started in the first half of April every year and lasted until mid-October. This monitoring interval covered the period of the barn owls' first and, depending on the weather and food supply, also the possible second annual clutches (Bank et al., 2019). In this study, to analyse the relationships of the feeding ecology and reproductive outputs during two outbreaks and subsequent crashes, data of 29 (2014 outbreak: 6, 2016 crash: 8; 2019 outbreak: 7, 2021 crash: 7) barn owl breeding pairs belonging to 27 different settlements were randomly selected from the area of Baranya County (Figure 1).

In case of all nesting pairs, clutch size, brood size at hatching and fledging were recorded, which breeding parameters are appropriate to measure the numerical response of barn owls. During the analysis, all successful clutches were taken into account together; we did not separate the first and second breeding periods.

2.3. Pellet collection and processing

Parallel to breeding biology monitoring, the trophic ecological analyses of barn owls were realized based on the regular pellet collections in cooperation between the Baranya County Group of BirdLife Hungary and the University of Pécs and later in the framework of the Hungarian Biodiversity Monitoring System (HBMS) at the local and the country level (Horváth et al., 2019). Considering the four years of the two outbreaks and two crashes, the number of pellet samples belonging to the 29 nest locations was 67, which represented a total of 1622 (outbreak 2014: 398, crash 2016: 501; outbreak 2019: 485, crash 2021: 238) pellets.

Pellets were processed by the dry technique that is, the individual pellets were broken down by hand (Schmidt, 1967) and prey items were identified to the lowest

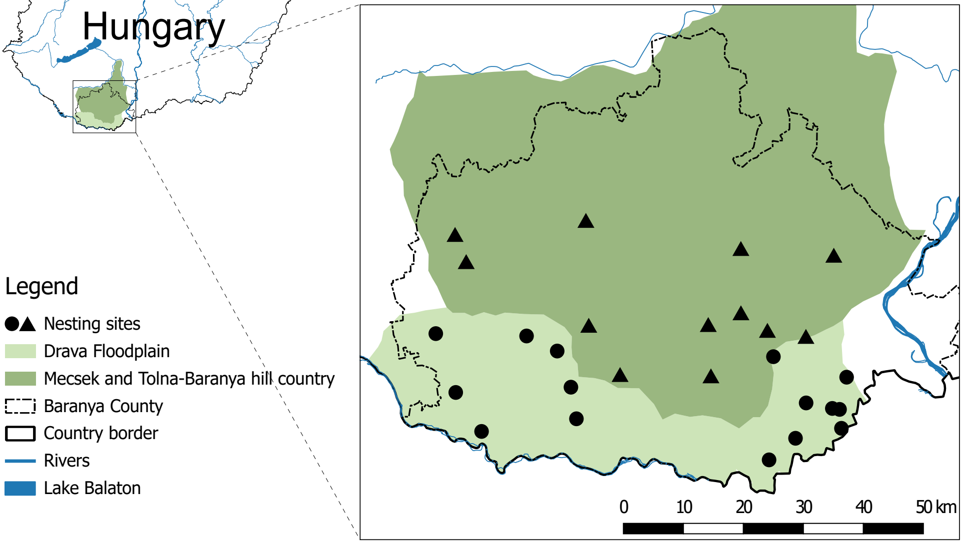

Figure 1. Study area in Baranya County (Hungary), showing the location of sampled nesting pairs (settlements).

taxonomical level. Small mammals and bats were identified based on skeletal parameters (features of skull, mandible and teeth), following published literature (Schmidt, 1967; März, 1972; Yalden, 1977; Niethammer and Krapp, 1978, 1982, 1990; Yalden and Morris, 1990), while birds were identified by their skulls, bills, feet, pelvises and feathers (Kessler, 2015), and frogs (Anura) by their skulls and bones of postcranial skeleton (Schaefer, 1932). Insects were identified by pieces of exoskeletons. If major skeletal elements were missing, prey items were identified to genus (small mammals, birds), to order (frogs) and to class (birds) level (Horváth et al., 2020, 2022). The numbers of prey were estimated as the minimum number of individuals (MNI), which was determined according to the number of the same anatomical parts of bones for small mammals (Klein and Cruz-Uribe, 1984; Torre et al., 2015; Tulis et al., 2015) and skulls, mandibles and long bones for birds, as well as skulls, remnants of ilium or frontoparietal bones for frogs.

Furthermore, the percent frequency of occurrence (MNI%) was calculated from the total number of prey found in all the pellets. The ratio of insectivores to rodents as an environmental (Paspali et al., 2013) or trophic level index (TLI) (Prete et al., 2012) and the ratio of Microtinae/Murinae (MMR) were also calculated. The first index is a suitable indicator of possible biotope alteration (Mazzotti and Caramori, 1998; Paspali et al., 2013), while the MMR is a suitable environmental index for the indication of the agronomic value (Prete et al., 2012) of intensively cultivated landscapes.

2.4. Statistical analysis

First, we analysed the difference in reproductive output values, the relative abundance of the main (common vole) and potential alternative prey taxa (Apodemus spp.) and the value of trophic indices (TLI, MMR) in comparison of different outbreak and crash years (2014 vs. 2016 and 2019 vs. 2021), as well as between the cumulative data of the two outbreak (2014 and 2019) and two crash (2016 and 2021) periods. After the analysis of normality and homogeneity of variance of the breeding parameters by the Shapiro-Wilk and Levene tests, log(x+1) transformed breeding data and arcsin-square root transformed relative frequency data of prey abundance were used for analysis.

The values of transformed breeding parameters and relative frequency of prey abundance were presented as mean ± SE standard error and range separately for samples of different outbreaks and crashes as well as for cumulative samples of outbreak and crash periods. The significance of the differences between means was evaluated using one-way ANOVA with Tukey's HSD multiple post hoc comparison of the different outbreak and crash years and Student's *t*-test between the two cumulated outbreak and crash periods. Since the normality condition for the two trophic indices (TLI, MMR) was not fulfilled even after data transformation, nonparametric Kruskal-Wallis median test with Dunn's procedure for post hoc comparisons was used to evaluate the quantitative difference between the outbreak and crash years, while Mann-Whitney nonparametric U test was performed to analyse the difference of the cumulative results between the outbreak and crash period (Zar 2010). Considering the relative abundance of prey taxa, chi-square test was applied with the command prop.test in R to evaluate the difference of abundance distribution.

In the second step, we assessed the prey consumption of barn owls in the periods of two outbreaks and the subsequent collapses that mark the ends and beginnings of common vole population cycles. Abundance distributions of detected prey categories in the given outbreak and crash periods and cumulative data of two outbreaks and two crashes were visualized by generating rank-abundance curves (RAC) in package 'goeveg' (Goral et al. 2018) using relative frequency data at the log-scale. To compare the rank abundance curve (RAC) of the outbreak and crash periods' prey composition, 'codyn' package (Hallet et al. 2018) with RAC-difference () function was used (Hallet et al. 2016, Avolio et al. 2019). We calculated three quantified comparative indices such as species richness difference (1), evenness difference (2) and rank difference (3) between the outbreak and crash, as well as between two cumulated outbreak and crash periods. Based on the applied function, species richness difference (S.D.) measures the length difference of the RAC, where S.D. is a ratio value between −1 and 1, thus larger values indicate greater changes in species richness. The evenness difference (E.D.) measures the difference of two prey compositions' evenness, whose value varies between −1 and 1, where larger negative values indicate greater decreases in evenness. Finally, rank difference (R.D.) compares the rank of prey items at which R.D. is a ratio between 0 and 0.5, where 0.5 occurs when there is a maximum rank change between the two prey assemblages (Avolio et al. 2019).

In the third step, before the regression modelling, the differences in reproductive output values and prey abundance distribution among the four years and between the cumulated data of the outbreak and crash periods were tested using nonparametric permutational multivariate analysis of variance (PERMANOVA) with the Bray-Curtis dissimilarity index (Anderson 2001). It was performed with the adonis2() function in package 'vegan' (Oksanen et al. 2022[4]) and 9999 permutations were run to test for statistically measurable overall differences between the

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[4] Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, et al. (2022). Package 'vegan': Community Ecology Package [online]. Website https://cran.r-project.org/web/packages/vegan/index.html [accessed 11 October 2022]

samples. Pairwise comparisons between sampled years and cumulated data were carried out with the FDR p-value adjustment method (Benjamini & Hochberg 1995). Taking these results into account, Generalized Linear Mixed Models (GLMMs) were performed to analyse and evaluate the relationship between the three considered breeding parameters as response variables, the period (outbreak, crash) as an explanatory variable, the abundance of the main and potential alternative prey taxa and trophic indices as continuous predictor variables, and their interaction. The localities of 'nesting pairs' were included in all models as a random factor. To avoid overdispersion, functions from the packages 'AER' (Kleiber and Zeileis, 2008, 2022[5]) and 'DHARMa' (Hartig and Lohse, 2022[6]) were used to test for this problem. Regarding the count data of reproductive parameters as response variables, a negative binomial error distribution with a log-link function was used to correct for overdispersion from a standard Poisson distribution (Zuur et al., 2009) with glmer() function and 'lme4' package (Bates et al., 2023) within the R platform to build the GLMM models. We created two groups of models. In the first case, we ran three models, which included the years, the demographic period, their interaction and the random factor. For the second model group, we also took into account the frequency values of the main and alternative prey taxa and the two derived indices, as well as the interaction of these continuous and the explanatory variables, so for the second model group, we ran 4×4 models for all response variables.

To rank and evaluate the importance of candidate models, Akaike Information Criterion corrected for small sample size, AICc was used. The lowest AICc value was assigned to the best-approximating model, in addition, models with ΔAICc < 2 were also considered to have significant support (Burnham and Anderson, 2002). Akaike model weights (*w*i) were included to represent the probability of best fit among all candidate models (Burnham and Anderson, 2002). Model selection was performed using the package 'AICcmodavg' (Mazerolle 2023[7]). Analysis of deviance table (Type III Wald χ^2 test) was used to test the effect of predictors and their interactions (Dobson and Barnett, 2008), and the results of the fitted regression models were visualized in the package 'effects' (Fox et al., 2022[8]). All statistical analyses were conducted in the R v. 4.2.3 (R Development Core Team, 2023). Statistical tests were considered significant at the level $p \leq 0.05$ in all analyses (Sokal and Rohlf, 1995).

3. Results

The breeding parameter values of 29 common barn-owl pairs from the two detected outbreak (2014, 2019) and the subsequent crash (2016, 2021) periods were used for the analysis. The average transformed values of clutch size varied (Table 1) and significantly differed among years ($F_{3, 25} = 21.592$, $p < 0.001$). According to post hoc Tukey HSD tests, the mean clutch size was significantly larger in the two outbreaks than in the subsequent crashes (outbreak$_{2014}$ vs crash$_{2016}$: $p < 0.01$; outbreak$_{2019}$ vs crash$_{2021}$: $p < 0.001$),

Table 1. Average values (±SE, range) of the barn owls' breeding parameters (log(x+1) transformed data.

Breeding parameter	Clutch size			Hatchlings			Fledglings		
Periods	$\bar{x}$	±SE	Range	$\bar{x}$	±SE	Range	$\bar{x}$	±SE	Range
Outbreak$_{2014}$	0.971	0.022	0.93-1.08	0.875	0.042	0.78-1.04	0.810	0.049	0.602-1.0
Crash$_{2016}$	0.844	0.012	0.78-0.90	0.763	0.028	0.60-0.85	0.633	0.032	0.48-0.78
Outbreak$_{2019}$	1.008	0.023	0.90-1.08	0.972	0.017	0.90-1.04	0.876	0.041	0.69-1.0
Crash$_{2021}$	0.793	0.029	0.69-0.09	0.608	0.063	0.30-0.78	0.608	0.063	0.30-0.78
Outbreak$_{2014, 2019}$	0.989	0.016	0.90-1.08	0.924	0.025	0.78-1.04	0.843	0.032	0.60-1.0
Crash$_{2016, 2021}$	0.819	0.016	0.69-0.90	0.691	0.037	0.30-0.85	0.621	0.032	0.30-0.78

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[5] Kleiber C, Zeileis A. (2022). Package 'AER': Applied Econometrics with R [online]. Website http://CRAN.R-project.org/package=AER [accessed 12 October 2022]

[6] Hartig F, Lohse L (2022). Package 'DHARMa': Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models [online]. Website https://cran.r-project.org/web/packages/DHARMa/DHARMa.pdf [accessed 12 October 2022]

[7] Mazerolle MJ (2023). Package 'AICcmodavg': Model Selection and Multimodel Inference Based on (Q)AIC(c) [online]. Website https://cran.pau.edu.tr/web/packages/AICcmodavg/AICcmodavg.pdf [accessed 20 March 2023]

[8] Fox J, Weisberg S, Friendly M, Hong J, Andersen R et al. (2022). Package 'effects'. Effect Displays for Linear, and Other Models [online]. Website https://cran.rproject.org/web/packages/effects/effects.pdf [accessed 13 October 2022]

but clutch size did not differ between the two outbreaks (outbreak$_{2014 \text{ vs } 2019}$: p = 0.635) and the two crashes (crash$_{2016 \text{ vs } 2021}$: p = 0.377). Considering the number of hatchlings and fledglings, the variation of average values significantly differed between the outbreaks and crashes (hatchlings: $F_{3\ 25}$ = 14.599, p < 0.001; fledglings: $F_{3\ 25}$ = 7.869, p < 0.001). In case of both parameters, the distribution of values showed a similar pattern (Table 1). The mean of hatchlings and fledglings did not differ between the earlier outbreak and the subsequent crash (Tukey HSD test - outbreak$_{2014}$ vs. crash$_{2016}$: p = 0.218), while the value of these two breeding parameters was larger in the second outbreak than in the subsequent crash (Tukey HSD test - outbreak$_{2019}$ vs. crash$_{2021}$: p < 0.001). The average values of hatchlings and fledglings were not different between the two outbreaks (Tukey HSD test - outbreak$_{2014 \text{ vs. } 2019}$: p = 0.354), however, the mean of both parameters was larger in the first than in the second crash period (Tukey HSD test - crash$_{2016 \text{ vs. } 2021}$: p < 0.001). In the case of cumulative data of the two outbreak and two crash periods, the average value of all three breeding parameters was greater during the outbreak than the crash period (clutch size: t = 7.466, df = 27, p < 0.001; hatchlings: t = 5.041, df = 27, p < 0.001; fledglings: t = 4.825, df = 27, p < 0.001) (Table 1, Figure 2).

Based on the common barn-owl's pellet samples, 30 animal taxa and 3623 prey items were identified. For both periods, common voles were the main prey with the highest relative abundance (MMI%) (outbreak: 60.35%, crash: 36.34%), which demonstrated a significant inhomogeneity in common vole abundance in the barn owls' consumption (Table 2) (χ^2 = 205.640, df = 1, p < 0.001). Regarding both demographic periods, Apodemus spp. appeared with the second highest abundance (outbreak: 18.16%, crash: 28.26%) (Table 2). Based on the significant inhomogeneity in its relative abundance distribution, the barn owls consumed Apodemus spp. as alternative prey with larger frequency during the crash than outbreak period (χ^2 = 52.133, df = 1, p < 0.001). During the outbreaks, the Striped field mouse (*Apodemus agrarius*) occurred with an abundance of 2.60%, while during the crash periods, it accounted for 7.00% of the food composition, which resulted in significant inhomogeneity in the food composition of barn owls for this species as well (Table 2) (χ^2 = 39.987, df = 1, p < 0.001). These larger mouse species, especially the striped field mouse, are generalists, so they appear in several habitat types, thus increasing the probability of predation, and in terms of cost-benefit, they are optimal prey for barn owls.

Rank-abundance distributions of barn owls' prey composition varied across different years of outbreak and crash periods, as shown by the shape and length of curves (Figure 3). Although according to the expected result, the number of prey was larger in the crash period than in the outbreak of the common vole as main prey, the length of rank-abundance curves (RAC) was very similar in the first outbreak$_{2014}$ and the consecutive crash$_{2016}$, which was confirmed by the close to zero positive value of the species richness difference index (S.D.) (Table 3). In this first outbreak, the eudominant common vole had the highest relative abundance, and Apodemus spp. was the second most frequent prey. On the contrary, the Apodemus group was the first in rank order as potential alternative prey in the crash$_{2016}$, but in comparison, the proportion of the common vole did not decrease significantly. Regarding the evenness difference (E.D.), the low value of this index showed that both abundance distributions were characterized by similar evenness, which was indicated by the similar slope of the two RACs. Thus, the calculated E.D. value did not prove the expected decrease during the outbreak period (Table 3). In case of the rank comparison of the two prey compositions, the rank change was 33% between the outbreak$_{2014}$ and the crash$_{2016}$. The RACs of the second outbreak and crash showed a different pattern, since the length of RACs were smaller and the slope of RACs were higher than in the first time period. The calculated values of S.D. and E.D. were similarly small and close to zero, but in case of S.D., it was negative value (Table 3), which indicated that the species richness was higher in the outbreak$_{2019}$ than during the crash$_{2021}$. Nonetheless, the rank change was larger (40%) in this crash following the outbreak than in the first time period (Figure 3). In case of the outbreak$_{2014 \text{ vs. } 2019}$ and crash$_{2016 \text{ vs. } 2021}$ comparisons, the results show larger difference than between the outbreaks and crashes. The shape and length of RACs differed between the two outbreaks, and the calculated negative values of S.D. demonstrated that the prey richness of barn owls' diet was larger in the first than in the second outbreak (Table 3). The calculated evenness difference (E.D.) showed that the evenness of the prey composition was larger in the first outbreak than in the second period, which presented that due to the higher consumption of the main prey (Table 3), the decrease in evenness expected during the outbreak was more typical in the period of the second outbreak (Figure 3). Regarding the rank change between the two outbreaks, the calculated value of the rank difference index demonstrated a 31% rank change in the second outbreak (Figure 3). The difference between the two periods is even more pronounced in the comparison of the two crashes. The negative values of species richness end evenness differences demonstrated that these values were higher in the first than in the second crash period, which was determined by the higher consumption rate of the main prey than the potential alternative prey (Table 3). The rank difference value was also greater in the comparison of the two crashes than in the case of the outbreak periods (Table 3). Compared to the period of

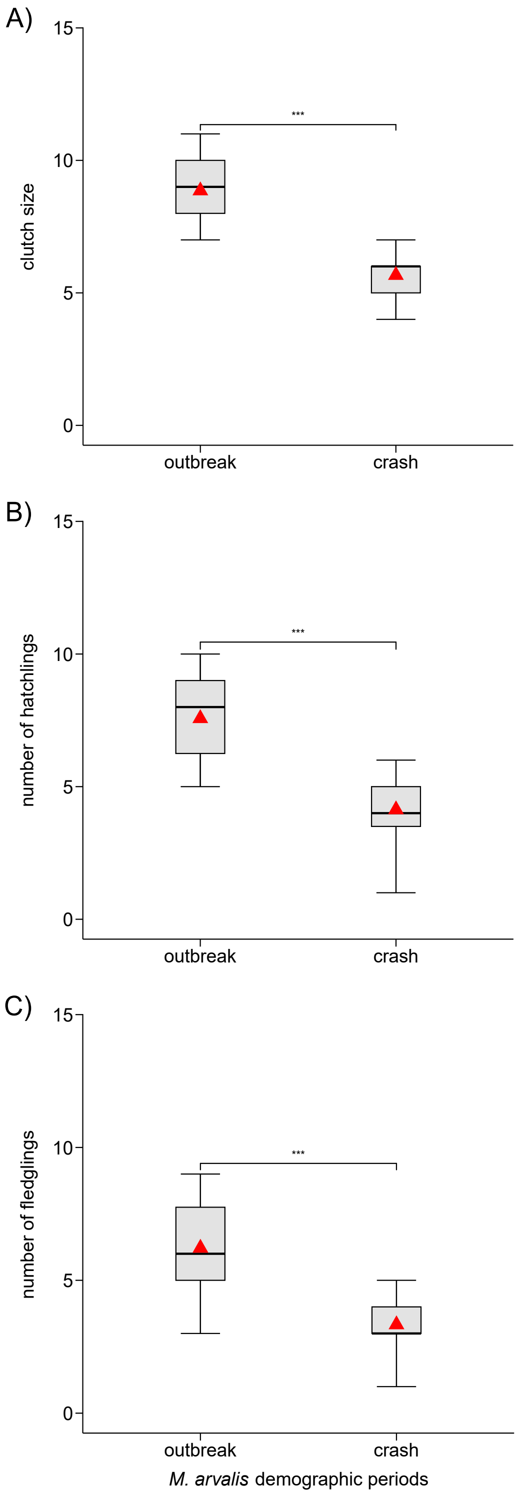

Figure 2. Box plots of barn owls' breeding parameters (A: clutch size; B: number of hatchlings; C: number of fledglings). The bottom and top limits of each box are the lower and upper quartiles; error bars equal ±1.5 times the interquartile range; the horizontal black band within each box is the median; and the red triangle is the mean.

Table 2. The food composition of the common barn-owl in the two different demographic periods of the common vole (MNI: minimum number of individuals, MNI%: percentage frequency of occurrence).

Demographic period / years	Outbreak						Crash					
	2014		2019		Total		2016		2021		Total	
Prey taxa	MNI	MNI%	MNI	MNI%	MNI	MNI%	MNI	MNI%	MNI	MNI%	MNI	MNI%
Talpa europaea	0	0	1	0.12	1	0.05	0	0	6	1.13	6	0.38
Sorex araneus	15	1.24	4	0.48	19	0.93	5	0.47	3	0.56	8	0.50
Sorex minutus	7	0.58	8	0.97	15	0.74	1	0.09	0	0.00	1	0.06
Crocidura suaveolens	81	6.68	38	4.60	119	5.84	53	5.03	26	4.90	79	4.98
Crocidura leucodon	68	5.61	8	0.97	76	3.73	31	2.94	11	2.07	42	2.65
Neomys fodiens	2	0.17	0	0.00	2	0.10	18	1.71	0	0.00	18	1.14
Neomys anomalus	1	0.08	0	0.00	1	0.05	13	1.23	0	0.00	13	0.82
Neomys sp.	0	0.00	0	0.00	0	0.00	3	0.28	0	0.00	3	0.19
Clethrionomys glareolus	2	0.17	1	0.12	3	0.15	6	0.57	0	0.00	6	0.38
Microtus agrestis	5	0.41	1	0.12	6	0.29	4	0.38	1	0.19	5	0.32
Microtus arvalis	642	52.97	588	71.19	1230	60.35	295	27.99	281	52.92	576	36.34
Microtus subterraneus	3	0.25	2	0.24	5	0.25	21	1.99	0	0.00	21	1.32
Arvicola amphibius	8	0.66	1	0.12	9	0.44	26	2.47	11	2.07	37	2.33
Rattus norvegicus	3	0.25	0	0.00	3	0.15	4	0.38	0	0.00	4	0.25
Rattus rattus	3	0.25	0	0.00	3	0.15	0	0.00	0	0.00	0	0.00

Table 2. (Contiued)

Rattus sp.	2	0.17	1	0.12	3	0.15	25	2.37	18	3.39	43	2.71
Apodemus agrarius	25	2.06	28	3.39	53	2.60	76	7.21	35	6.59	111	7.00
Apodemus sp.	247	20.38	123	14.89	370	18.16	320	30.36	128	24.11	448	28.26
Apodemus indet.	46	3.80	0	0.00	46	2.26	81	7.69	0	0.00	81	5.11
Mus spicilegus	10	0.83	6	0.73	16	0.79	9	0.85	1	0.19	10	0.63
Mus musculus	16	1.32	2	0.24	18	0.88	7	0.66	1	0.19	8	0.50
Mus sp.	15	1.24	10	1.21	25	1.23	23	2.18	4	0.75	27	1.70
Micromys minutus	8	0.66	1	0.12	9	0.44	20	1.90	2	0.38	22	1.39
Muscardinus avellanarius	1	0.08	1	0.12	2	0.10	6	0.57	0	0.00	6	0.38
Aves indet.	1	0.08	0	0.00	1	0.05	4	0.38	1	0.19	5	0.32
Hirundinidae sp	0	0.00	0	0.00	0	0.00	0	0.00	1	0.19	1	0.06
Passer domesticus	1	0.08	0	0.00	1	0.05	1	0.09	0	0.00	1	0.06
Passeriformes sp.	0	0.00	0	0.00	0	0.00	0	0.00	1	0.19	1	0.06
Pelobates fuscus	0	0.00	0	0.00	0	0.00	1	0.09	0	0.00	1	0.06
Insecta	0	0.00	2	0.24	2	0.10	1	0.09	0	0.00	1	0.06
Total:	**1212**		**826**		**2038**		**1054**		**531**		**1585**	

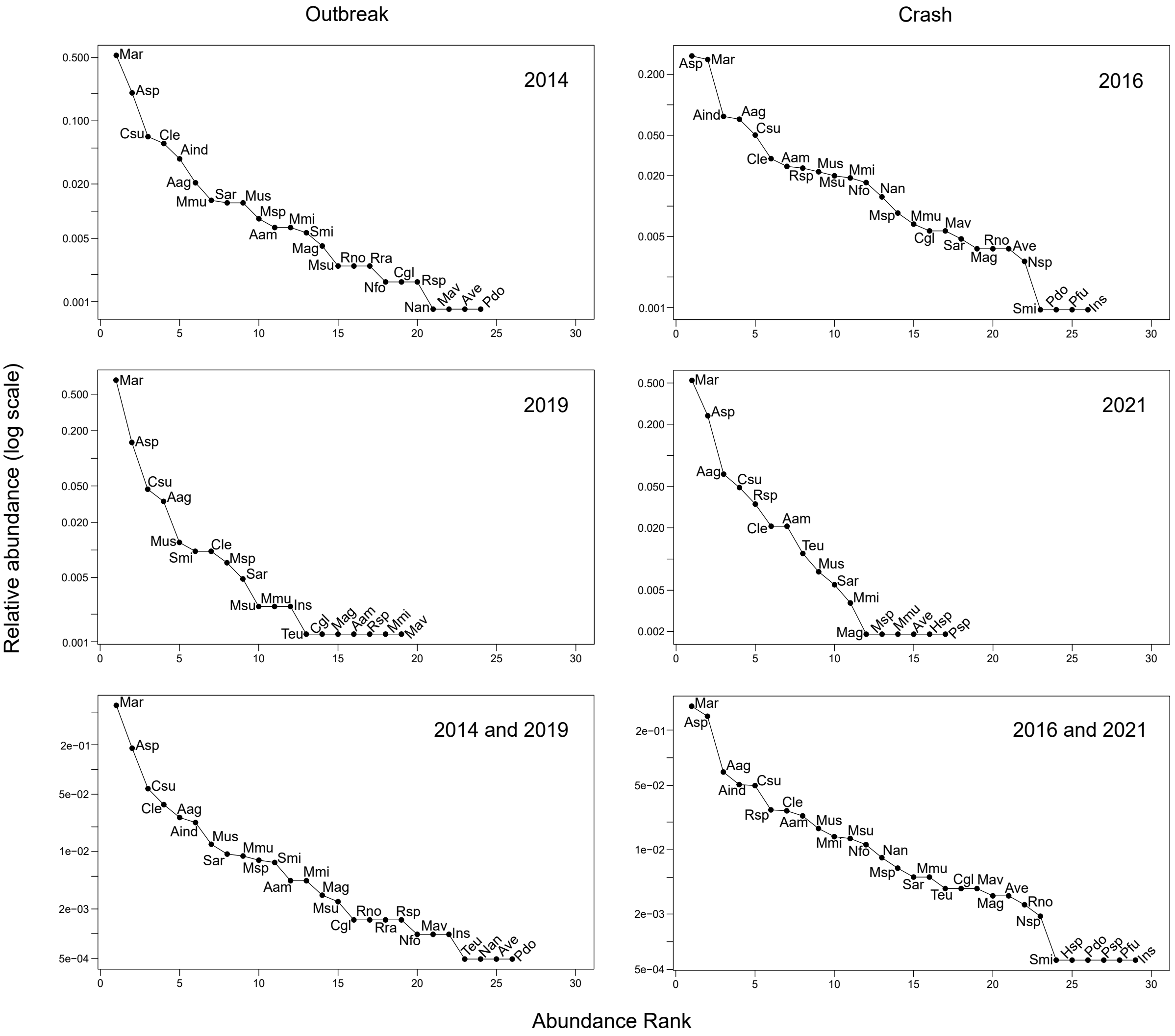

Figure 3. Rank abundance curves of the prey composition of the common barn-owl in different outbreak and crash years, and cumulative results of these two periods.

Table 3. The comparison of rank abundance differences in prey composition between the years of outbreaks and crashes, as well as the two outbreak and crash periods.

Sample pairs	S.D.	E.D.	R.D.
Outbreak$_{2014}$ vs. Crash$_{2016}$	0.074	0.073	0.164
Outbreak$_{2019}$ vs. Crash$_{2021}$	–0.091	0.008	0.202
Outbreak$_{2014}$ vs. Outbreak$_{2019}$	–0.192	–0.015	0.154
Crash$_{2016}$ vs. Crash$_{2021}$	–0.310	–0.044	0.168
Outbreak$_{2014, 2019}$ vs. Crash$_{2016, 2021}$	0.074	0.037	0.164

S.D.: Species richness difference; E.D.: Evenness difference; R.D.: Rank difference the previous crash, the rank change of prey composition was 34% in the second crash period (Figure 3). Based on the cumulative values of the two outbreaks and the two crashes, the RAC analysis showed similar results as in the first outbreak and crash periods, thus, in accordance with the expected result, the species richness and evenness of the barn owls' prey composition were greater during the crash than during the outbreak (Figure 3, Table 3).

Considering the transformed relative frequency distribution of the main and alternative prey, the average abundance values of the common vole as main prey (Table 4) significantly differed among years (outbreak vs. subsequent crash, and between two outbreaks and two crashes) ($F_{3\ 25} = 8.039$, $p < 0.001$). The post hoc Tukey HSD test showed that the mean common vole abundance was significantly higher in the two outbreaks than the subsequent crashes (outbreak$_{2014}$ vs. crash$_{2016}$: $p < 0.05$; outbreak$_{2019}$ vs. crash$_{2021}$: $p < 0.05$), but the relative frequency of this prey did not differ between the two outbreaks (outbreak$_{2014\text{ vs. }2019}$: $p = 0.289$) and the two crashes (crash$_{2016\text{ vs. }2021}$: $p = 0.521$). In case of the potential alternative prey group (Apodemus genus), the variation of average relative frequency values significantly differed between the outbreaks and crashes ($F_{3\ 25} = 5.413$, $p < 0.01$). The mean Apodemus abundance significantly differed between the earlier outbreak and the subsequent crash (Tukey HSD test - outbreak$_{2014}$ vs. crash$_{2016}$: $p < 0.05$), while the relative frequency of this alternative prey did not differ between the second outbreak and the subsequent crash (Tukey HSD test - outbreak$_{2019}$ vs. crash$_{2021}$: $p = 0.078$). Similarly, the abundance of the Apodemus prey group was not significantly different between the two outbreaks (Tukey HSD test - outbreak$_{2014\text{ vs. }2019}$: $p = 0.880$) and between the two crash periods (Tukey HSD test - crash$_{2016\text{ vs. }2021}$: $p = 0.766$). In the case of cumulative data from the two outbreak and crash periods, the average value of main prey abundance was significantly higher during the outbreak than in the crash ($t = 4.110$, $df = 27$, $p < 0.001$) (Figure 4A), while the relative frequency of the Apodemus genus as alternative prey was significantly higher during the crash than the outbreak period ($t = 3.876$, $df = 27$, $p < 0.001$) (Table 4, Figure 4B). In case of trophic indices, the variation of the calculated MMR values significantly differed between outbreak and crash years ($H(3, N = 29) = 13.704$, $p < 0.01$) (Table 5); however, the distribution of the TLI values did not differ among the sampling years ($H(3, N = 29) = 5.935$, $p = 0.115$) (Table 5). The post hoc Dunn's multiple comparison of MMR values demonstrated a different result than expected. The value of this trophic index was not different between the two outbreaks and the subsequent crash periods, but a significant difference was detected between the crash in 2016 and the outbreak in 2019, when its value was the highest (post hoc test: $z = 3.554$, $p < 0.01$).

In case of the distribution of breeding parameters and prey consumption, the results of PERMANOVA confirmed that in both cases the data distribution was statistically more dependent on outbreak and crash periods (breeding parameters: $R^2 = 0.534$, $F = 33.565$, $p < 0.001$; prey consumption: $R^2 = 0.244$, $F = 9.643$, $p < 0.001$) than the different outbreak and crash years (breeding parameters: $R^2 = 0.068$, $F = 2.133$, $p = 0.109$; prey consumption: $R^2 = 0.123$, $F = 2.436$, $p < 0.05$). Based on these results, the outbreak and crash periods were included in the GLMM models as a more significant explanatory variable than years.

Considering all breeding parameters, the results of the first GLMM model group demonstrated that the M2 model (breeding parameters ~ period + (1|loc)) was the best, which included only the demographic period of the

Table 4. Average values (±SE, range) of the main and alternative prey (arcsin transformed relative frequency).

Prey	*M. arvalis*			Apodemus spp.		
Periods	$\bar{x}$	±SE	Range	$\bar{x}$	±SE	Range
Outbreak$_{2014}$	0.971	0.022	0.93–1.08	0.875	0.042	0.78–1.04
Crash$_{2016}$	0.844	0.012	0.78–0.90	0.763	0.028	0.60–0.85
Outbreak$_{2019}$	1.008	0.023	0.90–1.08	0.972	0.017	0.90–1.04
Crash$_{2021}$	0.793	0.029	0.69–0.09	0.608	0.063	0.30–0.78
Outbreak$_{2014, 2019}$	0.989	0.016	0.90–1.08	0.924	0.025	0.78–1.04
Crash$_{2016, 2021}$	0.819	0.016	0.69–0.90	0.691	0.037	0.30–0.85

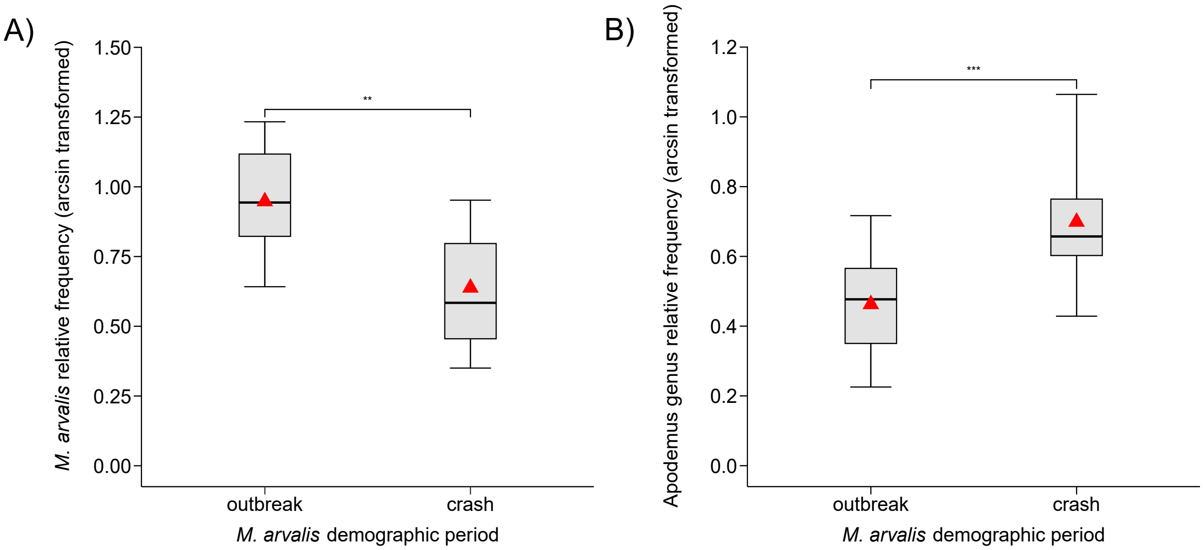

Figure 4. Box plots of the relative frequency of the main and alternative prey taxa. The bottom and top limits of each box are the lower and upper quartiles; error bars equal ±1.5 times the interquartile range; the horizontal black band within each box is the median; and the red triangle is the mean.

Table 5. Median values (lower-upper quartile, range) of the two trophic indices.

Trophic index	Microtinae/Murinae ratio (MMR)			Trophic level index (TLI)		
Periods	median	Lower - upper Quartile	Range	median	Lower - upper Quartile	Range
Outbreak$_{2014}$	4.625	2.018–7.000	1.78–10.71	0.018	0.000–0.041	0.00–0.25
Crash$_{2016}$	0.528	0.416–1.016	0.03–2.07	0.096	0.026–0.216	0.00–0.26
Outbreak$_{2019}$	4.625	2.017–7.000	1.77–10.71	0.018	0.000–0.041	0.00–0.25
Crash$_{2021}$	1.185	0.777–1.816	0.14–3.48	0.075	0.029–0.125	0.01–0.17
Outbreak$_{2014, 2019}$	2.624	1.621–6.055	0.92–10.71	0.048	0.018–0.203	0.00–0.31
Crash$_{2016, 2021}$	0.777	0.425–1.535	0.14–3.48	0.075	0.027–0.174	0.00–0.26

common vole ($AIC_c = 119.67–125.54$; $\Delta AIC_c = 0.00$; $w = 0.63–0.89$). The effect (χ^2) test supported our assumption that the demographic period significantly influences the breeding parameters ($\chi^2 = 12.842 – 14.749$, $p < 0.001$), the values of the regression coefficient confirmed that the crash period had a negative effect on the breeding parameters (clutch size: $B = –0.447 \pm 0.125$ SE, $z = –3.584$, $p < 0.001$, number of hatchlings: $B = –0.605 \pm 0.158$ SE, $z = –3.840$, $p < 0.001$; number of fledglings: $B = –0.623 \pm 0.171$ SE, $z = –3.638$, $p < 0.001$).

In case of the second model group, we first tested the impact of the common vole as the main prey of barn owls on clutch size. As a result of the model selection, we accepted the M1 model (Table 6). The effect test of variables confirmed the significant impact of common vole frequency ($\chi^2 = 7.355$, $p < 0.01$). The positive importance of this main prey species on clutch size is well illustrated by the GLMM effect plot and is also proven by the estimated value of the significant regression coefficient ($B = 0.754 \pm 0.278$ SE, $z = 2.712$, $p < 0.01$) (Figure 5A). Considering

Table 6. The model parameters of the best candidate GLMM models for each breeding parameters. These models were chosen according to the lowest AICc, the ΔAICc value < 2 and model weight.

response variables / GLMM models	K	AIC_c	ΔAIC_c	w_t
clutch size				
M. *arvalis* (Mar)				
~Mar+(1|loc) (M1)	4	128.84	0.00	0.57
Apodemus genus				
~Apodemus+(1|loc) (M1)	4	129.37	0.00	0.56
~period×Apodemus+(1|loc) (M3)	6	129.84	0.47	0.44
Microtinae/Murinae ratio (MMR)				
~MMR+(1|loc) (M1)	4	127.79	0.00	0.68
~period×MMR+(1|loc) (M3)	6	129.26	1.46	0.32
trophic level index (TLI)				
~period×TLI+(1|loc) (M3)	6	130.49	0.00	0.88
number of hatchlings				
M. *arvalis* (Mar)				
~period×Mar+(1|loc) (M3)	6	127.83	0.00	0.60
Apodemus genus				
~period×Apodemus+(1|loc) (M3)	6	128.80	0.00	0.92
Microtinae/Murinae ratio (MMR)				
~period×MMR+(1|loc) (M3)	6	128.12	0.00	0.66
trophic level index (TLI)				
~period×TLI+(1|loc) (M3)	6	129.81	0.00	0.98
number of fledglings				
M. *arvalis* (Mar)				
~Mar+(1|loc) (M1)	4	121.40	0.00	0.52
Apodemus genus				
~period×Apodemus+(1|loc) (M3)	6	120.47	0.00	0.91
Microtinae/Murinae ratio (MMR)				
~MMR+(1|loc) (M1)	4	119.14	0.00	0.63
trophic level index (TLI)				
~period×TLI+(1|loc) (M3)	6	125.06	0.00	0.97

K: Number of model parameters; AIC_c: Akaike Information Criterion corrected for small sample size; ΔAIC_c: AIC_c differences; w_t: Akaike weights

the Apodemus genus as a potential alternative prey group, M1 was accepted as the best model by model selection, in which only the relative frequency of the Apodemus genus was included as a continuous variable (Table 6). The χ^2 test showed a significant effect of the Apodemus prey group ($\chi^2 = 6.627$, $p < 0.05$). The GLMM plot shows a significant negative linear relationship between this alternative prey group and clutch size, which is also supported by the value of the regression coefficient ($B = -0.975 \pm 0.379$ SE, $z = -2.574$, $p < 0.05$) (Figure 5B). In the case of the M3 model, the ΔAIC_c value was also below 2, so we took into account the result of this model as well, which included the interaction of the frequency of the Apodemus genus and the demographic period (Table 6). Thus, the explanatory power of the two best models was 99.96%. The importance of the interaction was significant ($\chi^2 = 4.654$, $p < 0.05$). The impact of alternative prey taxa on clutch size was significantly negative in the outbreak period ($B = -0.798 \pm 0.257$ SE, $z = -3.108$, $p < 0.01$), but the effect of the Apodemus prey group was different in the

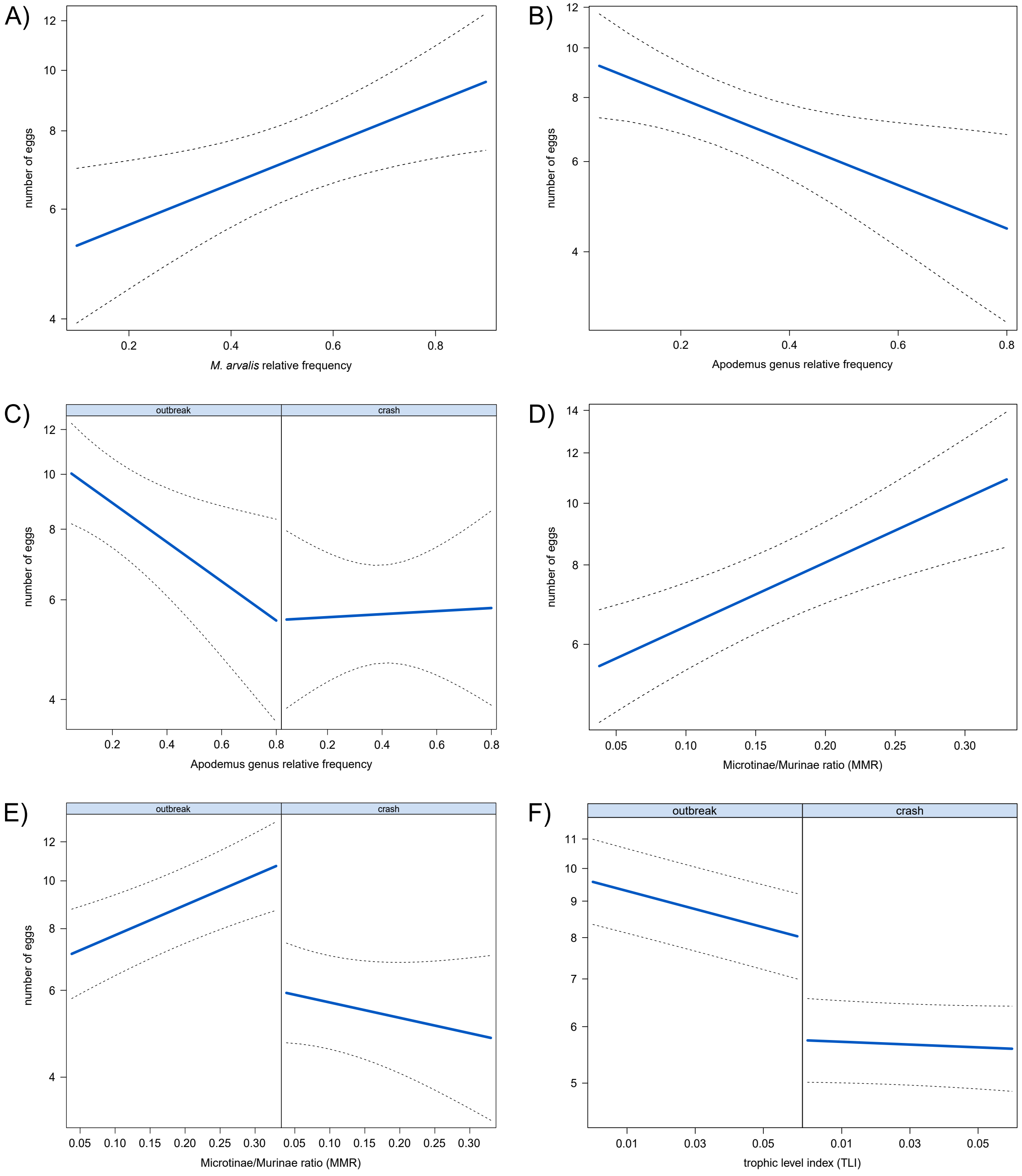

Figure 5. GLMM diagrams illustrating the effect of the main and alternative prey taxa and the two derived indices on clutch size (A: Common vole, B–C: Apodemus genus, D–E: Microtinae/Murinae ratio, F: Trophic level index).

outbreak and the crash periods based on the estimated regression coefficient of the interaction (B = 0.860 ± 0.358 SE, z = 2.402, $p < 0.05$) (Figure 5C). Based on our results, the M1 model had the highest explanatory power in the case of the MMR index (Table 6). The χ^2 test confirmed our assumption, according to which the values of the MMR index significantly influenced the clutch size (χ^2 = 22.272, $p < 0.001$). The value of the estimated regression coefficient confirmed that the MMR index had a positive effect on clutch size (B = 2.315 ± 0.491 SE, z = 4.719, $p < 0.001$), because the higher value of the index is the result of the higher consumption of common voles (Figure 5D). The M3 model was also taken into account because its ΔAIC_c value was below 2 and the explanatory power of the two best models was close to 100% (w_{cum} = 99.98%) (Table 6). The importance of the demographic period × MMR interaction was supported by the effect test (χ^2 = 12.968, $p < 0.001$). The MMR interaction had a significant positive effect in the outbreaks (B = 1.403 ± 0.321 SE, z = 4.378, $p < 0.001$). Furthermore, the estimated regression coefficient of the interaction was significant, according to which the influence of the Microtinae/Murinae ratio on clutch size differed between periods (B = −2.122 ± 0.534 SE, z = −3.972, $p < 0.001$) (Figure 5E). Finally, for TLI, the M3 model containing the interaction of this index as a continuous predictor and the demographic period proved to be the best model based on the model selection (Table 6). The importance of the interaction of these variables was confirmed (χ^2 = 8.059, $p < 0.01$). The estimated regression coefficient of TLI was significant, the trophic level index had a negative effect on clutch size in the outbreak period (B = −2.929 ± 0.463 SE, z = −6.330, $p < 0.001$). However, the impact of TLI was significantly different between periods (B = 2.481 ± 0.874 SE, z = 2.839, $p < 0.01$) (Figure 5F).

Regarding the number of hatchlings, in the case of the common vole, the best model (M3) included the interaction of the relative frequency of this main prey and the demographic period (Table 6). The χ^2 test of the variables did not support the significant effect of this interaction (χ^2 = 3.698, n.s.). However, the main effect of the common vole's abundance proved to be significant (χ^2 = 7.991, $p < 0.01$). Despite that the difference in the effect characteristic of the crash phase compared to the outbreak was not significant based on the estimated regression slope of the interaction, the value of the regression coefficient confirmed that the main prey had a positive effect on the number of hatchlings during the outbreak period (B = 1.142 ± 0.404 SE, z = 2.827, $p < 0.01$) (Figure 6A). With respect to the Apodemus genus as an alternative prey, based on the model selection, we accepted the M3 as the best model, in which the main effects of the Apodemus genus and the period and their interaction were included (Table 6). The effect test of the variables supported the importance of the interaction (χ^2 = 3.886, $p < 0.05$). Based on the parameter estimation, we calculated a significant positive regression coefficient value for the interaction (B = 1.939 ± 0.984 SE, z = 1.971, $p < 0.05$), which indicated the opposite effect of Apodemus in the two demographic periods (Figure 6B). When the MMR index was incorporated into the models, the M3 model had the highest model weight, which included the period × MMR index interaction (Table 6). The effect test showed that the interaction had a significant effect (χ^2 = 32.067, $p < 0.001$). The MMR index had a significant effect on the number of hatchlings in the outbreak (B = 2.145 ± 0.515 SE, z = 4.166, $p < 0.001$). According to the slope of the interaction, the difference between the effects in the two periods was also significant (B = −4.426 ± 0.782 SE, z = −5.663, $p < 0.001$) (Figure 6C). In the case of the TLI, the M3 model containing the interaction of the trophic level index and the period was the best model based on the model selection (Table 6).

The importance of this interaction was confirmed by the χ^2 test (χ^2 = 72.221, $p < 0.001$). The significant estimated regression coefficient confirmed that the trophic level index had a significant negative effect on the number of hatchlings during the outbreak period (B = −7.394 ± 0.987 SE, z = −7.494, $p < 0.001$). Moreover, the positive regression coefficient of the interaction demonstrated that the impact of TLI significantly differed in the two periods (B = 9.699 ± 1.141 SE, z = 8.498, $p < 0.001$) (Figure 6D).

In the case of the number of fledglings, we first tested the effect of common voles as the main prey. Based on the model selection, the M1 was placed at the top of the model ranking with the highest model weight (Table 6). The χ^2 test also confirmed the significant importance of the abundance of common voles (χ^2 = 12.247, $p < 0.001$), which is also supported by the estimated value of the regression coefficient (B = 1.269 ± 0.363 SE, z = 3.500, $p < 0.001$) (Figure 7A). We also tested the effect of the Apodemus genus as an alternative prey, in which case, based on the model selection, we accepted the M3 model that included the Apodemus × period interaction (Table 6). The χ^2 test confirmed the importance of the interaction of these variables (χ^2 = 6.586, $p < 0.05$). The GLMM interaction plot shows a significant negative linear relationship between the alternative prey and the number of fledglings in the outbreak period, which is also supported by the estimated regression coefficient (B = −2.089 ± 0.658 SE, z = −3.172, $p < 0.01$). Based on the interaction's regression slope, the effect of Apodemus consumption was significantly different in the crash compared to the outbreak (B = 2.876 ± 1.121 SE, z = 2.566, $p < 0.05$) (Figure 7B). Considering the model group where the MMR index was incorporated into the models as a continuous variable, the best model included only this index (Table 6). The result of the χ^2 test confirmed our assumption that the MMR index significantly affects the number of fledglings (χ^2 = 23.592, $p < 0.001$). The value of the estimated regression coefficient confirmed that the

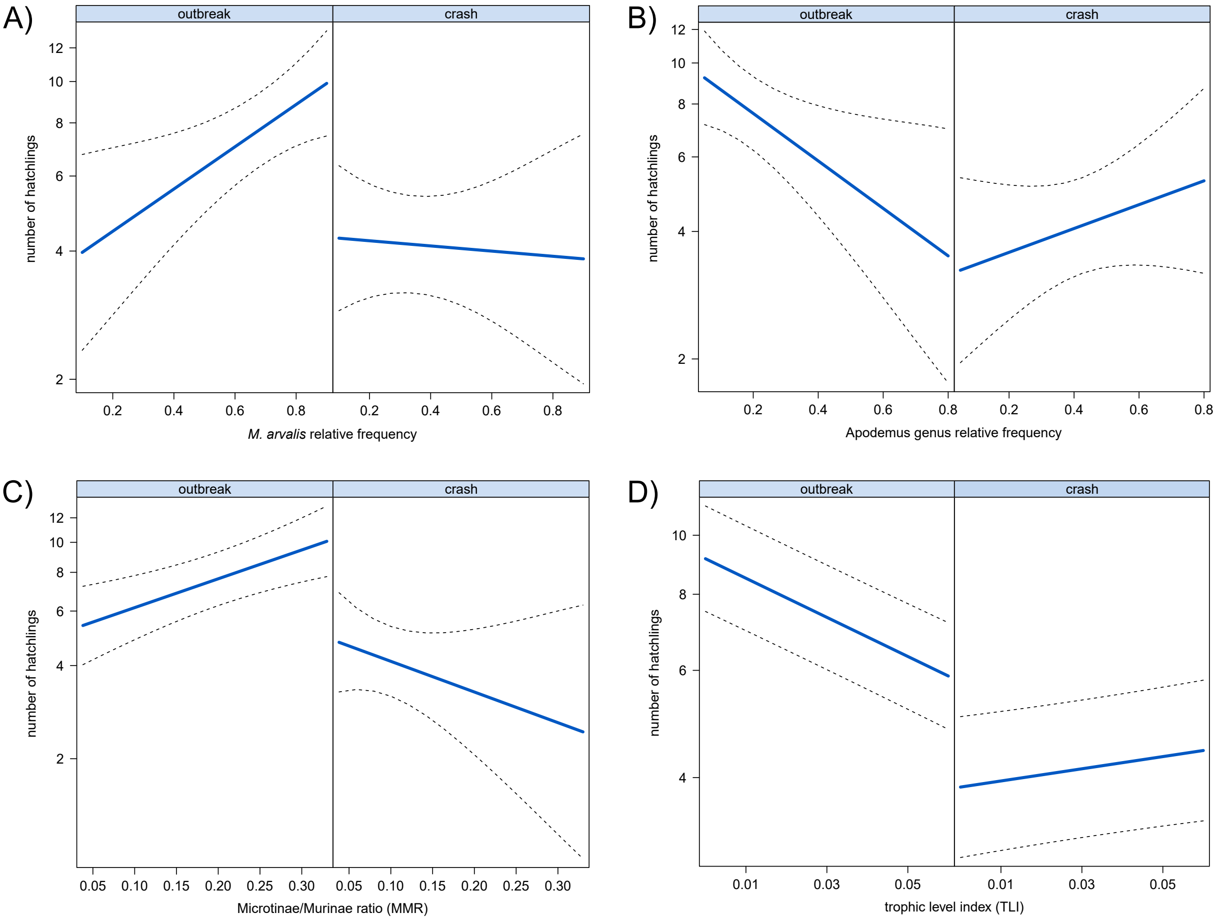

Figure 6. GLMM diagrams illustrating the effect of the main and alternative prey taxa and the two derived indices on the number of hatchlings (A: Common vole, B: Apodemus genus, C: Microtinae/Murinae ratio, D: Trophic level index).

MMR index has a positive effect on the development of this breeding parameter (B = 3.794 ± 0.781 SE, z = 4.857, $p < 0.001$) (Figure 7C). Finally, in case of the effect of the TLI index, the M3 model proved to be the best (Table 6). The importance of the demographic period × TLI index interaction was supported by the χ^2 test ($\chi^2 = 34.228$, $p < 0.001$). The interaction effect plot showed that TLI had a significant negative effect on the number of fledglings in the outbreak period (B = –4.096 ± 1.103 SE, z = –3.714, $p < 0.001$). The estimated regression coefficient was significant in the interaction of the two variables (B = 9.516 ± 1.627 SE, z = 5.850, $p < 0.001$), according to which the trophic index had a significantly different impact on the number of fledglings during the crash period (Figure 7D).

4. Discussion

In this paper, we investigated the relationship between the breeding parameters and diet composition of the common barn-owl, comparing the outbreak and crash periods of the common vole as the main prey of owls. For this analysis, we used a dataset of pellet samples from two consecutive outbreaks (2014, 2019) and two crash phases following these demographic peaks (2016, 2021). The studies investigating the breeding biology of barn owls highlighted that the reproductive outcome, population size, and survival were influenced by the quality of breeding sites and food composition, especially the availability and density of the main prey taxa as well as the fluctuation of their population (Taylor, 2004; Klok and de Roos, 2007; Charter et al., 2015; Pavluvčík et al., 2015).

Based on our results, the common vole was the main prey, as described in several Central European studies (Horváth et al., 2005, 2018; Kitowski, 2013, Petrovici et al., 2013; Purger, 2014; Szép et al., 2017, 2018, 2019; Veselovský et al., 2017). In comparison of the outbreak and crash periods, there was a significant difference in the consumption of this main prey; during the demographic peak, the owls preyed on a significantly higher proportion

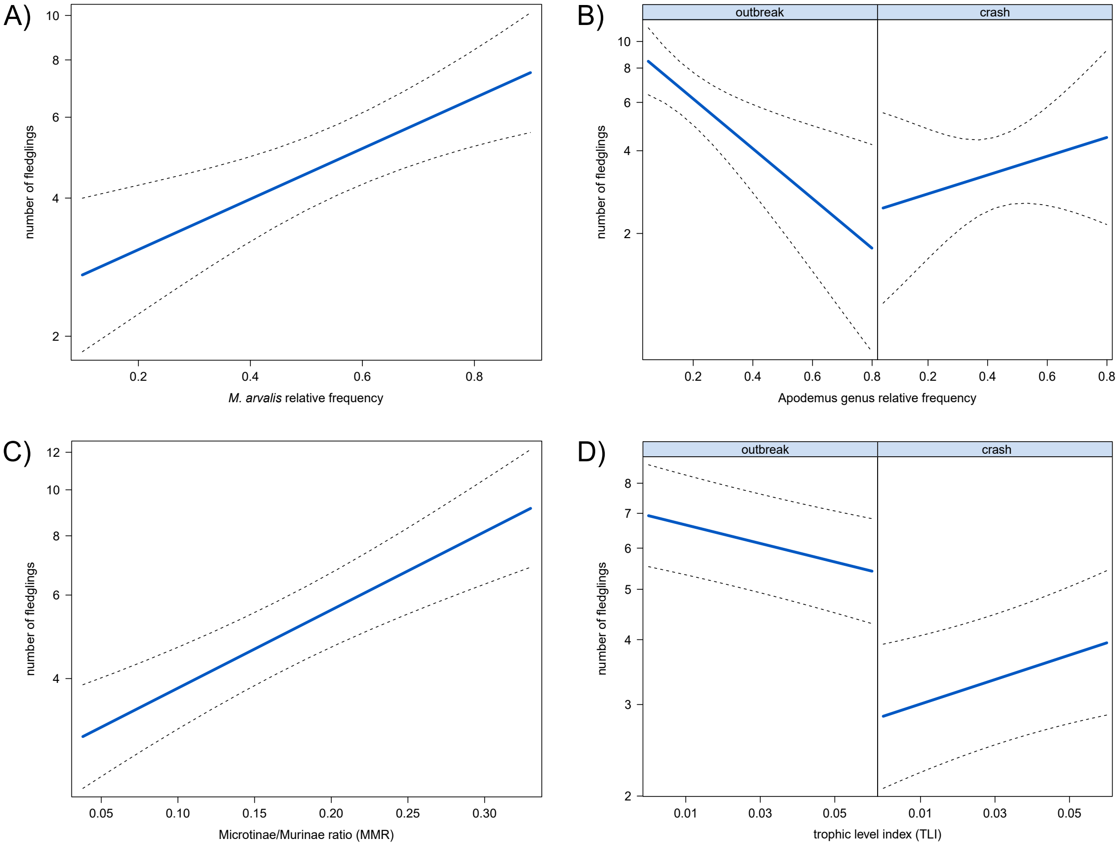

Figure 7. GLMM diagrams illustrating the effect of the main and alternative prey taxa and the two derived indices on the number of fledglings (A: Common vole, B: Apodemus genus, C: Microtinae/Murinae ratio, D: Trophic level index).

of common voles. It is already known that when the availability of the main prey decreases, the abundance of alternative prey species increases in the diet of barn owls (McDowell and Medlin, 2009; Charter et al., 2009; Marti, 2010; Horváth et al., 2020). In Baranya County, based on the previous studies (Szűcs et al., 2014, Horváth et al., 2020), the alternative prey are mainly the Apodemus species, which our results also supported because owls consumed more mice during the crash of the population of common voles.

Regarding the rank abundance analysis of prey composition, we found that the difference of RAC curves was greater between the two outbreaks and between the two crashes than in the comparison of the outbreaks and the subsequent crashes. We expected that the common vole frequency in the barn owls' diet is higher in the outbreak periods than in the crashes, while, on the contrary, the Apodemus frequency is higher in the crash periods than in the outbreaks. The rank order change of the main and alternative prey was not detected in the second crash period (2021). The common vole was the most frequent prey also in this period, suggesting that barn owls found areas richer in voles, which can be explained by the complex habitat selection of the common-barn owl (Séchaud et al., 2021), a characteristic spatial response observed in raptors as well (Dostal et al., 2021). These results pointed out the difference between each outbreak and crash period, which reflects the variability of the multiyear population cycle of common voles, determined by numerous biotic and abiotic factors as synchronizing and destabilizing effects of varying strength (Roos et al., 2022). Despite a smaller-than-expected decrease in vole consumption during the second crash phase, the drastic decline in breeding parameters confirmed the barn owls' negative numerical response.

We expected that there would be a significant difference between the barn owls' breeding parameters in comparison of the two demographic periods. This difference was shown in relation to the number of eggs, hatchlings, and fledglings, too; the values of all three parameters were higher during the period of the outbreak. It was described in several studies that the breeding of owls was highly influenced by the quantity of their main prey (e.g., Benedek et al., 2007; Charter et al., 2015; Pavluvčík et al., 2015); for example, the breeding success of owls increased as the frequency of common voles increased (de Jong, 1997; Taylor, 2004; Klok and de Roos, 2007; Pavluvčík et al., 2015), while there were fewer breeding attempts in the crash periods (Benedek et al., 2007). This relationship, that the higher availability of voles positively affects the clutch size, has also been shown in raptors that are typically characterized as vole-eating predators (Korpimäki and Norrdahl, 1991; Jędrzejewski et al., 1994; Salamolard et al., 2000; Korpimäki, 2020). Tores et al. (2005) described that the reproduction of barn owls was positively influenced by the large-scale availability of their main prey, the Levant vole (*Microtus guentheri*); however, when the vole population collapsed, the owls switched to consuming alternative prey, such as house mouse (*M. musculus*) and Tristram's jird (*Meriones tristrami*), and simultaneously reduced their reproduction rate. Our results showed that the Apodemus genus as an alternative prey group was important during the nesting of owls because the GLMM analysis clearly demonstrated that these mouse species substituted for the absence or lower availability of common voles in the crash periods in the investigated area because they positively influenced the number of hatchlings and fledglings.

In the 20th century, local populations of the barn owl began to decline due to increased agricultural cultivation and the loss of foraging habitat, including a lack of suitable breeding sites (Snow and Perrins, 1998; Mebs and Scherzinger, 2020; Taylor, 2004; Altwegg *et al.,* 2006, Askew *et al.,* 2007). Arlettaz et al. (2010) investigated whether the barn owl, as one of the top predators of agricultural areas, utilizes parcels planted with different plants as well as the so-called ecological compensation areas (ECAs). In order for owls to find suitable hunting areas, they increased the size of their home range. However, due to the increasing home range or the lack of suitable hunting areas, both the clutch size and the number of fledglings decreased (Arlettaz et al., 2010). Behaviour-specific analyses of barn owls' habitat selection and usage demonstrated that the habitat selection of this owl species is more specific and complex during breeding performance. Depending on this, agri-environment schemes (AES) habitat structures are also important for owls in addition to intensively cultivated areas (Séchaud et al., 2021). Almasi et al. (2015) found that both the intensity of agricultural cultivation and anthropogenic disturbance had a negative effect on the body weight of nestlings, suggesting that the intensity of agriculture negatively affects their fitness and the breeding performance of barn owls. Based on these, we expected to show a negative relationship between the breeding parameters and the Microtinae/Murinae ratio that indicates the intensity of agricultural cultivation (Contoli, 1980). On the contrary, our results showed that this index positively influenced the breeding parameters; however, it is important to note that the abundance of the eudominant common vole determines the value of this index, and the availability of this prey species has a positive effect on the reproduction of owls.

The Insectivora/Rodentia ratio (TLI) is an index that reflects the presence of different trophic levels (Prete et al., 2012; Paspali et al., 2013), and its higher value indicates a higher abundance of shrews. In outbreak periods, TLI negatively affected breeding parameters, while it had a positive effect on the number of hatchlings and fledglings during the crash phase of common voles. This is partly in accordance with the study of Benedek et al. (2007), which showed that in areas where the common vole population decreased, the owls consumed a higher proportion of shrews, proving the role of this small mammal group as alternative prey. However, during the decrease in the abundance of common voles, they observed fewer nesting attempts, the higher proportion of shrew consumption in their study area did not contribute to greater breeding success (Benedek et al., 2007). This result suggested that shrews may be potential alternative prey, but due to their low profitability, they are less important in forming the rapid numerical response of barn owls. On the contrary, we found that the higher consumption rate of shrews reflected in the TLI index positively influenced the number of hatchlings and fledglings, which suggested that in periods of absence or lower availability of the main prey, not only Apodemus species but also shrews represent a significant alternative prey group, facilitating the reproduction of barn owls.

In summary, despite the fact that the rank-abundance distribution in the diet of barn owls differed to a higher extent between the two outbreaks and the two crashes, we have clearly proven the difference in the food composition and the reproductive outputs of the common barn-owl during the outbreaks and the following crash periods. We highlighted the main prey role of the Common vole and its eudominant character in the prey composition during the outbreaks, and we showed the importance of the Apodemus genus as an alternative prey during the crash periods. Our results justified that the food composition of common barn-owls and the population cycle of their main prey determine the successful reproductive outputs of barn owls. Furthermore, based on the relationship between the consumption rate of the main prey and breeding parameters, it was possible to measure the rapid numerical response (reflected mainly in clutch size) of barn owls that depended on the higher availability of the main prey during the outbreaks and its lower frequency of occurrence during the crash periods. To reveal more information about the interaction between barn owls and its main prey, further research is required on the different effects of outbreaks and crashes of varying intensities in the multiannual population cycle of the main prey.

Acknowledgement

We thank the members of the Baranya County Group of BirdLife Hungary and the enthusiastic volunteers of the 'Foundation for Natural Resources in Baranya' who provided their generous help in the monitoring of the nest boxes. Also, we express our special thanks to László Bank, who made the breeding parameters available to us. The pellet analysis of the common barn owl was supported by the Foundation for Natural Resources in Baranya, the Hungarian Biodiversity Monitoring System, and the Duna-Dráva National Park Directorate. We are thankful for the volunteers and university students for their dedicated work in helping us disassemble and process the owl pellets.

Conflict of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Research ethics

All procedures performed in this study did not involve animal handling and were in accordance with the 1964 Helsinki Declaration and its later amendments.

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