

Variation in the diet and breeding biology of the Common Barn-owl (*Tyto alba*) in a demographic cycle of Common Vole (*Microtus arvalis*) between two outbreaks^x

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Abstract In the present study, we analysed the variation of breeding parameters and the diet composition of the Common Barn-owl (*Tyto alba*) in three different demographic phases of the Common Vole (*Microtus arvalis*) in a complete population cycle between two outbreaks. The study was conducted in the south-eastern part of the Transdanubian region in South Hungary. For the analysis, we used data of 81 randomly selected first clutches from 2015 to 2019, a time period which represented a full demographic cycle of the Common Vole after the 2014 outbreak with an exceptionally high peak. We tested the impact of prey abundance and diversity of diet composition as continuous predictors as well as the demographic phase of Common Vole and the mesoregion as categorical explanatory variables on the measured reproductive outputs as response variables using Generalized Linear Models (GLM). Considering the breeding parameters, the number of fledglings, and fledging and reproductive success were significantly higher in the increase phase than during the vole crash phase. Based on GLM models, our results demonstrated that the clutch size of the Common Barn-owl is determined ultimately by the availability and consumption rate of the Common Vole as main prey, while other small mammal prey categories did not affect the clutch size. These results support the finding that the clutch size of vole-eating raptors and owls, which begin breeding periods in early spring predicts the vole abundance in this early spring period. Considering the other investigated small mammal prey groups, the alternative prey role was confirmed only in case of the Murid rodent prey categories (*Apodemus* spp., Muridae).

Keywords: reproductive output, food consumption, alternative prey, outbreak

Összefoglalás Jelen tanulmányban a gyöngybagoly (*Tyto alba*) szaporodásbiológiai paramétereinek és táplálék-összetételének változását vizsgáltuk a mezei pocok (*Microtus arvalis*) egy teljes populációciklusában elkülönülő három demográfiai fázis során. A vizsgálat Dél-Magyarországon, a Dunántúl dél-keleti részén, Baranya megyében valósult meg. Az elemzéshez a 2015–2019 közötti időszakból 81 rétegzett random mintavétellel kiválasztott első költés adatait használtuk fel, amely reprezentálta a mezei pocok 2014-ben jellemző kiugró gradációját utáni teljes demográfiai ciklust. Általánosított lineáris modellek (GLM) alkalmazásával teszteltük a zsákmányabundancia, a táplálék-összetétel diverzitása, mint folytonos prediktorok, valamint a mezei pocok demográfiai fázisai és a mezorégiók, mint kategóriális magyarázó változók szaporodási kimenetekre gyakorolt hatását. A kirepült fiókák száma, valamint a kirepülési és szaporodási siker szignifikánsan magasabb volt a mezei pocok növekvő fázisában, mint az összeomlás időszakában. A GLM modellek alapján eredményeink azt mutatták, hogy a gyöngybagoly fészekalj méretét kizárólag a mezei pocok, mint fő zsákmány elérhetősége és fogyasztási aránya befolyásolta, míg más kisemlős zsákmánykategóriák nem voltak hatással a fészekalj méretre. Ezek az eredmények alátámasztották azt a megállapítást, hogy a szaporodásukat kora tavasszal megkezdő pocokfogyasztó ragadozó madarak és baglyok fészekalj mérete előrejelzi a kora tavaszi időszakban jellemző pocokabundanciát.

A figyelembe vett egyéb kisemlős zsákmánycsoportok tekintetében csak az egérfélék zsákmánykategóriái (*Apodemus* spp., Muridae) esetén bizonyítottuk e csoportok alternatív zsákmány szerepét.

Kulcsszavak: reprodukciós kimenet, táplálékfogyasztás, alternatív zsákmány, gradáció

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Introduction

Raptors and owls show both numerical and functional responses depending on the variation of their food supply, particularly the density fluctuation of their main prey (Korpimäki & Norrdahl 1989, 1991, Salamolard *et al.* 2000, Tome 2003, Reif *et al.* 2004, Millon & Bretagnolle 2008, Tóth 2014, Baudrot *et al.* 2016). The reproductive output and population dynamics of these avian predators are strongly affected by multi-annual periodic (cyclic) or irregular fluctuation of small mammals, especially herbivorous voles (Korpimäki *et al.* 2002, Klok & de Roos 2007, Pavlůvčik *et al.* 2015, Zárýbnická *et al.* 2015, Fay *et al.* 2020). Vole-eating raptors and owls show a rapid demographic response to the dramatic change of their main prey abundance, therefore, the breeding parameters of these diurnal and nocturnal birds of prey are considered as potential indicators to forecast the general abundance of voles (Solonen *et al.* 2015).

The Common Barn-owl was characterized as an opportunistic nocturnal raptor because it hunts various easily available prey species or groups depending on their density (Campbell *et al.* 1987, Taylor 1994, Bellocq 2000, Paspali *et al.* 2013, Charter *et al.* 2015). According to many studies, this owl species is a typical small mammal specialist (Marti 1988, Bonvicino & Bezerra 2003, Charter *et al.* 2009), which was also confirmed by a recent biogeographical assessment of the cosmopolitan Common Barn-owl group's (*Tyto alba* species complex) trophic ecology at global scale (Romano *et al.* 2020). However, Barn Owls frequently select a given prey species and/or group, and based on their functional response, switch easily between prey items in their foraging strategy (Yom-Tov & Wool 1997, Tores *et al.* 2005, Romano *et al.* 2020). According to the 'alternative prey hypothesis', if the main prey species declines in the given year, generalist predators can show dietary shifts and switch to alternative prey (Angelstam *et al.* 1984), which was detected in case of raptors (Reif *et al.* 2001, Riegert *et al.* 2009, Kreiderits *et al.* 2016, Dementavičius *et al.* 2020) and different owls (Korpimäki *et al.* 1990, Jędrzejewski *et al.* 1994, Sasvári *et al.* 2000, Riegert *et al.* 2009), including also the Common Barn-owl (Roulin 2004a, Tores *et al.* 2005, Charter *et al.* 2015, Baudrot *et al.* 2016).

In temperate ecosystems, Bernard *et al.* (2010) reported how the dietary response of Common Barn-owl can be affected by the density of prey species and demonstrated that the frequency of a given prey in the diet depends also on the population density or availability of other species. The feeding behaviour of Barn Owls is generally opportunistic (Bernard *et al.* 2010), but complex patterns of prey selection with switching mechanism to alternative

prey were reported by studies particularly in arid environments, where food intake results supported that the Common Barn-owl is a rather selective opportunistic predator (Heywood & Pavey 2002, Tores *et al.* 2005, McDowell & Medlin 2009, Romano *et al.* 2020).

The food consumption of the Common Barn-owl is mainly determined by changes in the density of agricultural pest rodents such as different *Microtus* vole species, both in temperate zones of Nearctic and Palearctic regions and the Mediterranean (Colvin & MacLean 1986, Marti 1988, Taylor 1994, Shehab & Al Charabi 2006, Charter *et al.* 2009, Kitowski 2013, Petrovici *et al.* 2013, Purger 2014, Veselovský *et al.* 2017). Due to their preference and high rates of consumption, several studies demonstrated negative correlation between vole (*Microtus* spp.) frequency and food-niche breadth of the Common Barn-owl (Milchev *et al.* 2006, Marti 2010, Hindmarch & Elliott 2015, Milchev 2015, Horváth *et al.* 2018). As vole specialists, the breeding success of Barn Owls increases with the proportion of voles (*Microtus* spp.) in the diet (Gubanyi *et al.* 1992, De Bruijn 1994, Taylor 1994, Klok & de Roos 2007, Bernard *et al.* 2010, Charter *et al.* 2018).

Considering the European agricultural landscape, the Common Vole (*Microtus arvalis* Pallas, 1778) is the most abundant and widespread microtine rodent species, and due to high overshoots of carrying capacity (Bryja *et al.* 2001, Jacob & Tkadlec 2010), Common Voles cause significant damage during outbreaks (Lambin *et al.* 2006, Jacob *et al.* 2014, 2020). Population dynamics of the Common Vole is characterized by multiannual fluctuation with 3–5 year-long population cycles in agricultural fields (Tkadlec & Stenseth 2001, Lambin *et al.* 2006, Cornulier *et al.* 2013, Luque-Larena *et al.* 2013, Jacob *et al.* 2014, 2020) and it shows typical well-defined and separable demographical phases, such as long intervals of low abundance (crash phase), increase phase and short intervals of peak phase (outbreak) (Tkadlec & Stenseth 2001, Lambin *et al.* 2006).

Earlier studies of the Common Barn-owl's breeding biology had already reported that the reproductive output of owls were larger in the peak phase during the outbreak than in the non-outbreak periods of the Common Vole (Schönfeld & Girbig 1975, Kaus 1977, Baudvin 1979, De Bruijn 1994). These results suggested that population fluctuation of Common Barn-owls correlated with changes of vole density. Klok and de Roos (2007) demonstrated that the fluctuating change in the breeding success of the Common Barn-owl correlated with the dynamics of voles as main prey. Based on the analysis of the vole fluctuation effect in a simple predator-prey model system, this study suggested that population persistence of the Common Barn-owl is affected by poor-years with low abundance of voles (Klok & de Roos 2007). Furthermore, the increase in productivity of Common Barn-owls was demonstrated in the Czech Republic, which study confirmed a significant linear relationship between the annual productivity and Common Vole abundance (Pavluvčik *et al.* 2015).

Size-dependent predation of the Common Barn-owl was reported and discussed in more studies (Kotler *et al.* 1988, Yom-Tov & Wool 1997, Bellocq 1998), which confirmed that the prey size is an important trait of the profitability (Ille 1991). Therefore, we hypothesized that large body mass rodent (LBMR) species, such as European Water Vole (*Arvicola amphibius*), Brown Rat (*Rattus norvegicus*) and Black Rat (*R. rattus*) may be a possible alternative prey group for the Barn Owls to compensate for the lack and/or lower availability of the main prey species, especially during its crash phase. In addition, considering the importance

of the Common Vole as main prey abundance, we predicted that the reproductive output of the Barn Owl reaches its maximum in the peak phase.

According to the above predictions, the present study aims to examine the differences in reproductive output and food intake of the Common Barn-owl among the demographic phases of the Common Vole as main prey (1) and to analyse the relationships between the consumption rate of the main or potential alternative prey categories and variation of the owls' breeding parameters between two vole outbreaks (2).

Material and methods

Study area and sample collection

The study was conducted in the south-eastern part of the Transdanubian region in Southern Hungary, in Baranya County (4,429.6 km²) (45°53' N, 18°20' E) (*Figure 1*). Due to significant Mediterranean and sub-Mediterranean climate effects, the environmental conditions of this county are favourable for Common Barn-owls. Moreover, the county is characterized by a large number of villages (number of settlements is 301), and four mesoregions are distinguished in the total area of Baranya. However, the largest territorial coverage of the county is represented by two mesoregions: the Drava floodplain (DFP) and the Mecsek and Tolna-Baranya hill country (MTBHC). The area of the Drava floodplain includes the erstwhile flood basin of the Drava, altitude varies between 89 and 212 meters, its area size is 1,300

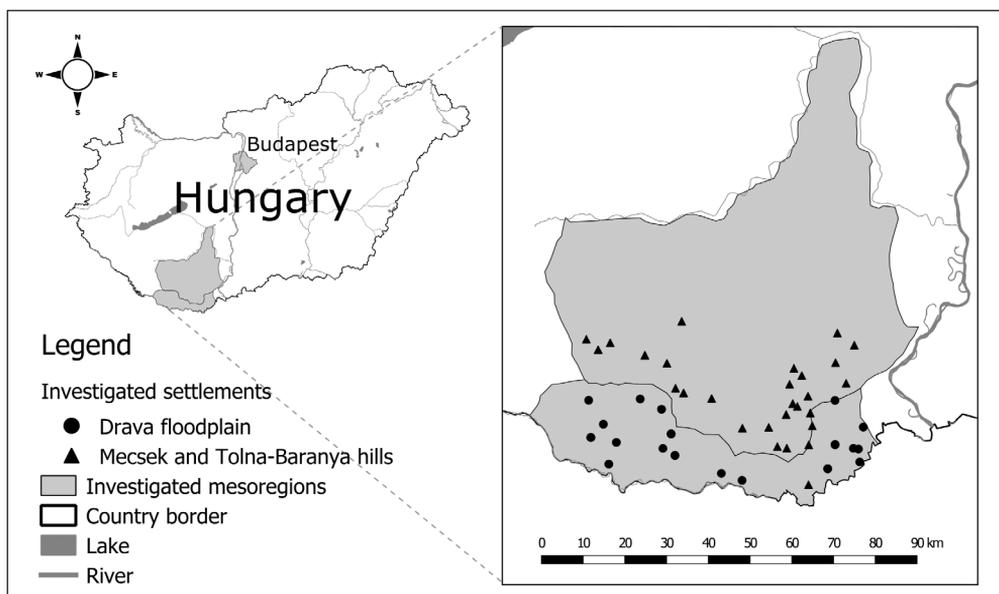


Figure 1. Study area in the South-Transdanubian region, Hungary, showing the location of the two mesoregions and the investigated nesting pairs within the examined landscape

1. ábra A vizsgált terület Dél-Dunántúlon, Magyarországon, feltüntetve a két középtáj és a vizsgált költőpárok elhelyezkedését a vizsgált tájegységben belül

km². The climate of this mesoregion is moderately warm and moderately humid. The number of sunny hours increases from west (2,000) to east (2,080), while the annual amount of precipitation increases from east to west: 630–680 mm in the east, while more than 720 mm in the west. The Mecsek and Tolna-Baranya hill country is situated north of the previous mesoregion and its area is 4,400 km². The number of sunny hours is between 1,400 and 1,450, and yearly mean precipitation is 680–720 mm. The Mediterranean climatic impact is typical in both regions. Due to different environmental conditions, these two landscapes were considered as explanatory variables for our analysis.

In the present study, data on the reproductive output come from the long-term monitoring program of nest box breeding Common Barn-owls. The continuous survey of the reproductive parameters has been conducted since the mid-90s in our studied region by the Baranya County Group of BirdLife Hungary during the last 25 years (Bank *et al.* 2019). Detailed data of nest box installation and control protocol can be found in Bank *et al.* (2019). Pellet collections and diet analyses were also conducted parallel to the breeding biology monitoring.

For the analysis, we used data from 2015 to 2019, a time period which represented a full demographic cycle of the Common Vole after the 2014 outbreak with an exceptionally high peak (see Luque-Larena *et al.* 2015, Rodríguez-Pastor *et al.* 2017 in Spain, plant protection engineers personal communication of Bóly Co.'s crop production sector in Hungary) and included the crash (2015–2016), the increase (2017–2018) and the peak (outbreak) (2019) phase. The 2019 peak phase indicated a pan-European synchronous population outbreak of the Common Vole (Jacob *et al.* 2020). Considering the years, the mesoregions, the first and second annual clutches and the presence/absence of pellet collection per nesting site, a stratified random procedure of sample selection was used to ensure a proportionate sampling effort in the 5-year period. Because the number of successful second clutches was low for randomly selected pairs, only the data of the first clutches were considered in the analysis. From the total of 389 clutches, where the complete reproductive history was known, 81 first clutches (N = 30 in crash phase, N = 30 in increase phase and N = 21 in peak phase) were taken into account for the analysis. The average number of first clutches per year was 16.2 ± 2.45 SE (range: 9–21). The randomly selected sample consisted of data from 46 different localities (settlements) and 53 nest boxes.

Pellets were processed by the dry technique, the individual pellets were broken down by hand and prey items were identified to the lowest possible taxonomical level. Small mammals were identified based on skeletal parameters (features of skull, mandible and teeth; März 1972, Yalden 1977, Yalden & Morris 1990). Three different *Apodemus* species, the Wood Mouse (*Apodemus sylvaticus*), the Yellow-necked Wood Mouse (*A. flavicollis*) and the Pygmy Field Mouse (*A. uralensis*) were categorized commonly as *Apodemus* spp. When the Striped Field Mouse (*A. agrarius*) was not separable from the *Sylvaemus* group (*Apodemus* spp.) the individuals were determined as 'unidentified *Apodemus*'. The sibling species of the genus *Mus* were determined according to Macholán (1996) and Kryštufek & Macholán (1998). Birds were identified by their skulls, bills, feet, pelvises and feathers, and frogs (Anura) by their skulls and bones of the postcranial skeleton. Prey items were identified to genus (small mammals, birds), to order (frogs), and to class (birds) level if major skeletal elements were missing.

Data analysis

For each of the selected Barn Owl pairs, the reproductive output was evaluated by six parameters: 1) clutch size (number of eggs in a clutch), 2) brood size at hatching, 3) brood size at fledging, 4) hatching success (the percentage of eggs that hatched within each clutch), 5) fledging success (the percentage of young that fledged from each brood), and 6) reproductive success (the percentage of fledged young per eggs from each successful nest) (see Bank *et al.* 2019).

Considering the food consumption of the owls, we focused our analysis on small mammal prey taxa (98.75% of prey MNI – 9,966 out of 10,092 prey specimens). Prey numbers were estimated as the minimum number of individuals (MNI) which we determined based on the same anatomical parts of bones for small mammals (McDowell & Medlin 2009, Torre *et al.* 2015, Tulis *et al.* 2015). The percent frequency of occurrence (MNI %) was calculated for the total number of prey at the prey species and group level found in the pellet sample of each nesting pair.

To analyse the relationship between the breeding performance and diet composition of Common Barn-owls the following prey categories of small mammals were considered: Common Vole (*M. arvalis*) (*Mar*) as main prey species, Lesser White-toothed Shrew (*Crocidura suaveolens*) (*Csu*), Bicolored White-toothed Shrew (*Crocidura leucodon*) (*Cle*) and Striped Field Mouse (*A. agrarius*) (*Aag*) at species level, *Sorex*, *Crocidura*, *Apodemus* spp. (excluding the Striped Field Mouse) at genus level, and Soricidae, Muridae at the highest taxonomic level as possible alternative prey categories. In addition, the cumulative proportion of large body mass rodent (LBMR) species and Shannon diversity (H') of prey composition were calculated and used as predictors in our analysis.

In the first step, breeding parameters and derived percentage values of successes, as well as the proportion (MMI%) of the prey categories were presented as range and mean \pm SE per breeding pair for the total sample and sample groups based on demographic phases of the Common Vole and the two mesoregions, respectively. After analysis of normality by Shapiro-Wilk test (Zar 2010), nonparametric statistics were used to evaluate the results. Boxplots (median, 25–75% percentiles and min-max values) were used to present the variation of the Barn Owls' reproductive output and their small mammal consumption. Mann-Whitney's U-test and Kruskal-Wallis test (followed by Dunn's post hoc test for multiple comparisons) were used to compare the values of breeding parameters and relative abundances (MMI%), as well as Shannon diversity (H') of prey composition between the two mesoregions and among the demographic phases of Common Vole, respectively (Zar 2010).

Second, we tested the impact of prey abundance ($Prey_i$) and prey diversity (H') as continuous predictors as well as the Common Vole's demographic phase (Phase) and the mesoregion (Region) as categorical explanatory variables on the reproductive outputs as response variables (Y_i) using Generalized Linear Models (GLM). Based on the interaction of predictors, three models were built in case of each breeding parameters of the Common Barn-owls (M1: $Y_i \sim Prey_i \times Phase$; M2: $Y_i \sim Prey_i \times Region$; M3: $Y_i \sim Prey_i \times Phase \times Region$). In case of count data (clutch and brood size, number of fledglings), a quasi-Poisson error distribution with a log-link function was used to correct for overdispersion from a standard

Poisson distribution (Zuur *et al.* 2009), while in case of breeding successes as derived percentage data a quasi-binomial error distribution with logit-link function was used for analysis. In case of both error distributions, ‘glm()’ function and “lme4” packages (Bates *et al.* 2015) were used to build the GLM models. Functions from the packages ‘AER’ (Kleiber & Zeileis 2008, 2009) and ‘DHARMA’ (Hartig 2017) were used to test for overdispersion. To rank and evaluate the importance of candidate models, a Quasi-Akaike Information Criteria with a correction for small sample sizes (QAICc) was used. The lowest QAICc value was assigned to the best-approximating model, in addition, models with $\Delta\text{QAICc} < 2$ were also considered to have significant support (Burnham & Anderson 2002). Akaike model weights (w_i) were included to represent the probability of best fit among all candidate models (Burnham & Anderson 2002). The package “MuMIn” (Barton 2016) was used to implement the model selection. Analysis of deviance table (Likelihood Ratio (LR) χ^2 for Type III analysis) was used to test the effect of predictors and their interactions (Dobson & Barnett 2018), and the results of the fitted regression models were visualized in the package ‘effects’ (Fox *et al.* 2017). All statistical analyses were conducted in the R version 3.4.0 environment (R Core Team 2019). Statistical tests were considered significant at the level $P \leq 0.05$ in all analyses (Sokal & Rohlf 1997).

Results

Regarding the breeding parameters of the investigated first clutches, the average number of eggs was 6.91 ± 0.15 (range 4–12), the mean number of hatchlings was 5.91 ± 0.20 (range 0–10) and the average number of fledglings was 4.26 ± 0.21 (range 0–9) in the 5 studied years. The clutch size (Kruskal-Wallis test: $H(2, N = 81) = 1.28$, n.s.) and the brood size did not differ ($H(2, N = 81) = 3.29$, n.s.), while the number of fledglings significantly varied among the demographic phases of the Common Vole (Kruskal-Wallis test: $H(2, N = 81) = 10.52$, $P = 0.0066$). The number of fledglings was significantly higher in the increase phase than during the crash phase (post hoc Dunn test: $z = 3.004$, $P = 0.0079$) (Figure 2a). Considering the breeding successes, the mean of hatching success was $86.29 \pm 2.36\%$ (range 0–100%), the mean of fledging success was $70.19 \pm 3.13\%$ (range 0–100%) and the reproductive success was $62.81 \pm 2.98\%$ (range 0–100%) during the total demographic cycle of the Common Vole. We did not find significant difference in hatching success ($H(2, N = 81) = 5.58$, n.s.), however, the fledging ($H(2, N = 81) = 7.42$, $P = 0.0244$) and the reproductive success ($H(2, N = 81) = 9.83$, $P = 0.0073$) significantly varied among the vole phases. In both cases, the success was significantly higher during the increase than in the crash phase of the Common Vole (post hoc Dunn test – fledging success: $z = 2.61$, $P = 0.0027$; breeding success: $z = 3.12$, $P = 0.0054$), similar to the number of fledglings (Figure 2b). Based on the statistical analysis of overall data, the value of breeding parameters (Mann-Whitney U-test: $Z = 1.05 - 0.26$, n.s.) and successes ($Z = 0.67 - 1.73$, n.s.) did not show significant difference between the two mesoregions. As evaluated based on demographic phases of the Common Vole, the number of fledglings (Mann-Whitney U-test: $Z = 2.37$, $P = 0.017$) and the reproductive success ($Z = 2.27$, $P = 0.022$) differed significantly only in the increase phase, while

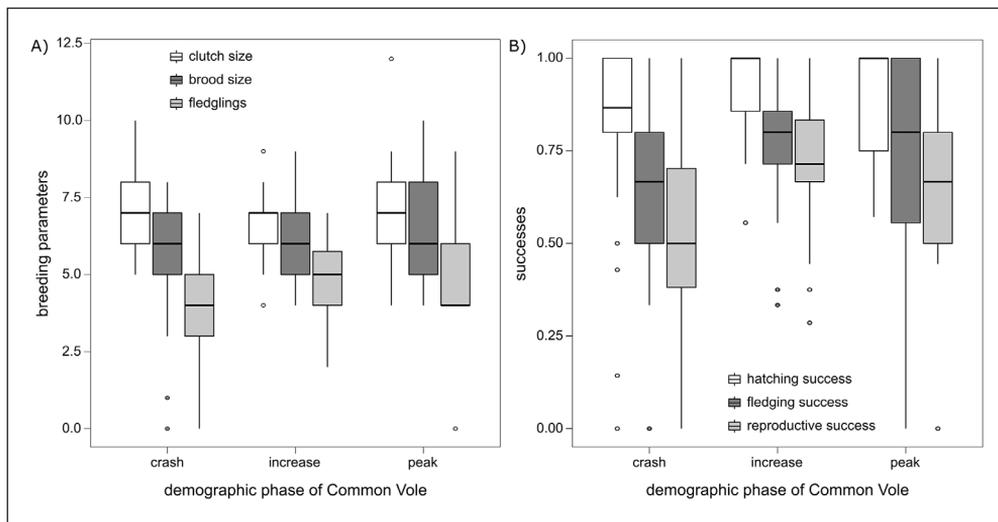


Figure 2. Variation in the values of breeding parameters (A) and breeding biology successes (B) (median, 25–75% percentiles, min-max) in the demographic phases of Common Vole

2. ábra A költési paraméterek (A) és sikerek (B) értékeinek (medián, 25–75% percentilis, minimum-maximum) változása a mezei pocok demográfiai fázisaiban

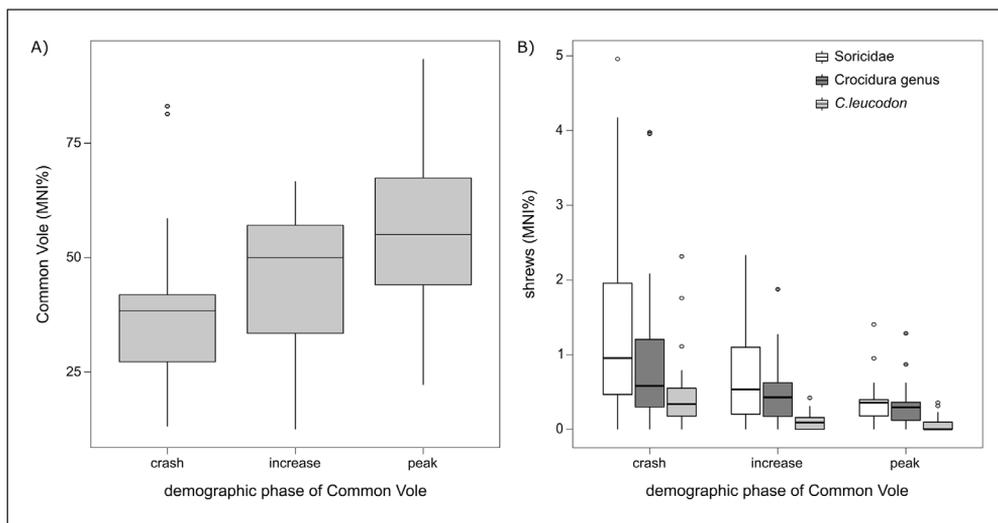


Figure 3. Variation in the relative abundance of Common Vole (A) and shrews (B) (median, 25–75% percentiles, min-max) in the demographic phases of Common Vole

3. ábra A mezei pocok (A) és a cickányok (B) gyakorisági értékeinek (medián, 25–75% percentilis, minimum-maximum) változása a mezei pocok demográfiai fázisaiban

for the other two demographic phases showed no significant differences in the reproductive output values between the two mesoregions.

Considering the small mammal prey categories, the mean of Common Vole's relative abundance (MNI %) in the food was $44.94 \pm 1.97\%$ (range 12.5–93.37%) for its whole demographic cycle. The proportion of this main prey significantly varied among the demographic phases ($H(2, N = 81) = 15.29, P = 0.0005$). The prey consumption data of Common Barn-owls reflected that the MNI % of this *r*-strategist prey was significantly higher during the peak than in the crash phase (post hoc Dunn test: $z = 3.88, P < 0.0003$), but in the other two pairings of demographic phases there was no significant difference (post hoc Dunn test: $z = 1.88 - 2.2, n.s.$) (Figure 3a). Due to the high range overlap of the Common Vole's consumption rate in its whole demographic cycle, the relative abundance (DFP: = $45.45 \pm 2.64\%$, range: 14.81–93.37%; MTBHC: = $44.34 \pm 2.98\%$, range: 12.5–83.05%) did not differ between the two mesoregions (Mann-Whitney U-test: $Z = 0.27, n.s.$). As regards the relative abundance of potential alternative prey categories and prey diversity for the whole 5-year period, the mean \pm SE and range values per breeding pair are summarized in Table 1. Larger proportion values (MMI %) were detected in case of some potential alternative prey categories, such as Muridae, *Apodemus* spp. Soricidae, *Crocidura* and Bicolored White-toothed Shrew (*C. leucodon*) (in descending order). However, significant differences of the relative abundances among the demographic phases of the Common Vole were only detected in case of the three shrew categories (Soricidae: Kruskal-Wallis test: $H(2, N = 81) = 13.66, P = 0.0011$; *Crocidura*: $H(2, N = 81) = 9.75, P = 0.0076$; *C. leucodon*: $H(2, N = 81) = 31.16, P < 0.0001$). The total abundance of shrews (Soricidae) and the *Crocidura* genus were higher in the crash phase than during the outbreak (post hoc Dunn test: $z = 2.98 - 3.60, P < 0.01$), while the proportion of consumption of the Bicolored White-toothed Shrew was higher in the collapse ($z = 4.99, P < 0.0001$) and increase phase ($z = 4.27, P < 0.0001$) than in the peak phase (Figure 3b). Distribution of means (\pm SE) and the range intervals of the relative abundances (MMI %) from the total dataset are summarized in comparison of the two mesoregions (Table 2). Although the rate of consumption of each prey category varied in a different range of percent values in the owls' diet, we did not find significant differences between the two mesoregions

Table 1. Average values (\pm SE, range) of the potential alternative prey categories' proportion (MMI %), prey diversity for the whole 5-year dataset
1. táblázat A potenciális alternatív zsákmány kategóriák arányának (MMI %), valamint a zsákmány diverzitás átlaga (\pm SE, Min-Max) a teljes 5 éves adatkészletből

Prey categories/ Shannon H'	Mean ()	\pm SE	Range
Species level			
<i>Crocidura suaveolens</i>	4.90	0.98	0–21.98
<i>Crocidura leucodon</i>	4.68	0.92	0–23.16
<i>Apodemus agrarius</i>	7.49	0.58	1.69–13.57
Genus level			
<i>Sorex</i>	1.29	0.32	0–6.67
<i>Crocidura</i>	9.59	1.79	0–39.78
<i>Apodemus</i> spp.	22.62	2.98	4.39–45.38
Higher taxa			
Soricidae	13.22	2.11	0–49.59
Muridae	43.98	2.91	15.25–77.33
LBMR*	3.74	0.87	0–21.05
Shannon diversity (H')	1.82	0.07	0.72–2.51

*: LBMR: large body mass rodents / nagy testtömegű rágcsálók

Table 2. Average value (\pm SE, range) of the potential alternative prey categories' proportion (MMI%), prey diversity according to mesoregions for the whole 5-year dataset

2. táblázat A potenciális alternatív zsákmány kategóriák arányának (MMI%), valamint a zsákmány diverzitás átlaga (\pm SE, Min-Max) a középtájak bontásában a teljes 5 éves adatkészletről

Prey categories/ Shannon H'	Drava floodplain (DFP) (N = 44)			Mecsek and Tolna-Baranya hill country (MTBHC) (N = 37)		
	Mean ()	\pm SE	Range	Mean ()	\pm SE	Range
Species level						
<i>Crocidura suaveolens</i>	4.35	0.64	0–7.14	3.56	0.79	0–21.99
<i>Crocidura leucodon</i>	2.37	0.61	0–23.16	2.15	0.52	0–17.58
<i>Apodemus agrarius</i>	8.65	0.74	0–25	7.38	0.84	0–25
Genus level						
<i>Crocidura</i>	6.72	1.11	0–39.78	5.72	1.16	0–39.56
<i>Apodemus</i> spp.	21.69	1.49	2.41–41.15	25.39	2.11	4.39–59.26
Higher taxa						
Soricidae	9.05	1.41	0–49.59	8.21	1.44	0–41.76
Muridae	40.02	2.22	4.82–71.61	43.23	2.64	12.5–77.33
LBMR*	2.81	0.59	0–21.05	2.99	0.77	0–25
Shannon diversity (H')	1.62	0.07	0.34–2.51	1.53	0.07	0.72–2.43

*: LBMR: large body mass rodents / nagy testtömegű rágcsálók

neither in proportion of prey categories (Mann-Whitney U-test: $Z = 0.21 - 1.31$, n.s.), nor in Shannon diversity ($Z = 0.97$, n.s.) values. Difference of alternative prey abundance and Shannon H' were tested between the two mesoregions in case of each demographic phase of the Common Vole. Significant differences were detected in case of four alternative prey categories and the Shannon H' during the crash phase of the Common Vole (Table 3). In contrast, we did not find significant differences between the two regions in the increase and the peak phase.

As regards the GLM analysis, clutch size was affected by the abundance of the Common Vole as the main prey. Based on model selection parameters, M2 was the best approximating model (Table 4), the result of which showed the significant main effect of vole proportion ($\chi^2 = 4.22$, $P = 0.04$), while the mesoregion and the

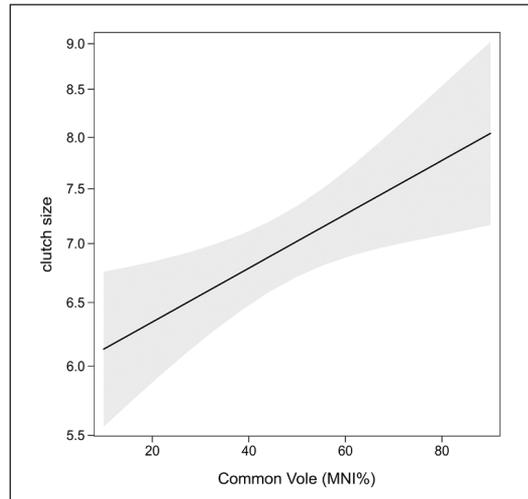


Figure 4. Relationship between clutch size and relative abundance of the Common Vole (*M. arvalis*) based on main effect of the M2 model

4. ábra A fészekalj méret és a mezei pocok relatív abundancia közötti összefüggés az M2 modell főhatása alapján

Table 3. Results of alternative prey abundance analysis (Mann-Whitney U test) in comparison of the two mesoregions (DFP vs TBHC) during the crash phase of the Common Vole

3. táblázat Az alternatív zsákmány abundancia elemzés eredménye (Mann-Whitney U teszt) a két középtáj (DFP vs TBHC) összehasonlításában a mezei pocok összeomlási fázisában

Prey categories/ Shannon H'	U	Z	P value
Species level			
<i>Crocidura suaveolens</i>	50	2.56	<0.05
<i>Crocidura leucodon</i>	90	0.89	n.s.
<i>Apodemus agrarius</i>	105	0.27	n.s.
Genus level			
<i>Sorex</i>	49	2.59	<0.01
<i>Crocidura</i>	60	2.14	<0.05
<i>Apodemus</i> spp.	99	0.52	n.s.
Higher taxa			
Soricidae	50	2.56	<0.05
Muridae	101	0.44	n.s.
LBMR	84	1.14	n.s.
Shannon diversity (H')	29	3.43	<0.001

*: LBMR: large body mass rodents / nagy testtömegű rágcsálók

interaction of these two predictors were not determining factors of clutch size. Considering the estimation of regression coefficient, the consumption rate of the Common Vole positively affected the clutch size (Table 5, Figure 4).

Brood size was affected by the proportion of the Common Vole and the Shannon diversity based on the best-fitted M2 model (Table 4). In case of each three continuous predictors, the significant main effect was confirmed by Type III test (Mar: $\chi^2 = 6.51$, $P = 0.0108$; H': $\chi^2 = 8.73$, $P = 0.0031$).

Similar to clutch size, significant positive relationships were confirmed by the estimated parameters between brood size and the relative abundance (MNI%) of the Common Vole (Table 5, Figure 5a). In contrast, a significant negative regression was detected between the prey diversity and the brood size (Table 5,

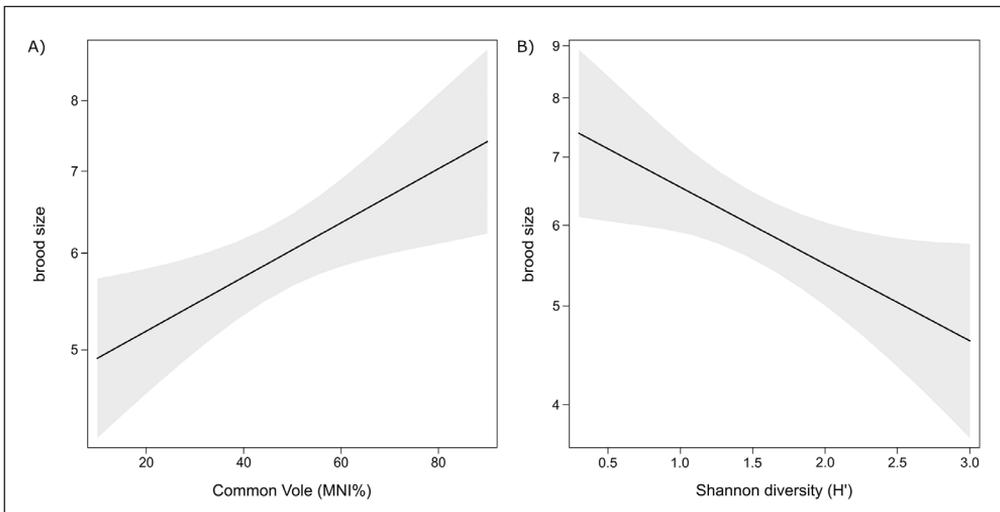


Figure 5. Relationship between brood size and relative abundance of the Common Vole (*M. arvalis*) (A) and Shannon diversity (B) based on main effects of the M2 model

5. ábra A fészekalj méret és a mezei pocok relatív abundancia (A), valamint a Shannon diverzitás (B) közötti összefüggés az M2 modell főhatásai alapján

Table 4. Quasi-Akaike's rank value of the candidate GLM models with count breeding parameters (For the abbreviations of the predictor variables see Material and Methods)

4. táblázat Az alkalmazott modellek Quasi-Akaike's rang értékei a számolt szaporodási paraméterek esetén (A magyarázó változók rövidítését lásd a Material and Methods fejezetben)

Y_i /Predictor/Model (ID)	QAICc	Δ_i	w_i
clutch size			
<i>Microtus arvalis</i>			
~ Mar × Region (M2)	334.2	0.00	0.806
~ " × Phase (M1)	337.1	2.85	0.194
~ " × Phase × Region (M3)	348.8	14.54	0.001
brood size			
<i>Microtus arvalis</i>			
~ Mar × Region (M2)	347.9	0.00	0.685
~ " × Phase (M1)	349.5	1.55	0.314
~ " × Phase × Region (M3)	360.5	12.63	0.001
<i>Apodemus spp.</i>			
~ Asp × Phase (M1)	349.1	0.00	0.807
~ " × Region (M2)	351.9	2.89	0.191
~ " × Phase × Region (M3)	360.3	11.25	0.003
Muridae			
~ Muridae × Phase (M1)	349.3	0.00	0.726
~ " × Region (M2)	351.3	1.96	0.272
~ " × Phase × Region (M3)	360.5	11.18	0.003
Shannon diversity (H')			
~ H' × Region (M2)	347.4	0.00	0.821
~ " × Phase (M1)	350.5	3.05	0.179
~ " × Phase × Region (M3)	361.1	13.66	0.001
number of fledglings			
<i>Microtus arvalis</i>			
~ Mar × Region (M2)	340.2	0.00	0.724
~ " × Phase (M1)	342.2	2.01	0.265
~ " × Phase × Region (M3)	348.6	8.43	0.011
Shannon diversity (H')			
~ H' × Region (M2)	340.5	0.00	0.701
~ " × Phase (M1)	342.8	2.35	0.217
~ " × Phase × Region (M3)	344.8	4.30	0.082
LBMR			
~ LBMR × Phase (M1)	337.6	0.00	0.950
~ " × Phase × Region (M3)	344.0	6.41	0.039
~ " × Region (M2)	346.6	8.92	0.011

QAICc: Quasi-Akaike Information Criterion corrected for small sample size

Δ_i : QAICc differences

w_i : Akaike weights

Figure 5b). In addition, the brood size at hatching was influenced by the proportion of *Apodemus* spp. and total MNI% of Muridae, as alternative prey categories of the Common Barn-owl. The effect of both variables (Asp: $\chi^2 = 6.12$, $P = 0.0134$; Phase: $\chi^2 = 13.1$, $P = 0.0014$) and their interaction ($\chi^2 = 7.86$, $P = 0.0196$) of the best supported M1 model were significant (Table 4). Based on the interaction of model variables, the consumption of *Apodemus* spp. significantly affected the brood size during the crash phase of the Common Vole, while the relationship between the proportion of this prey and the number of nestlings was significantly negative in the peak phase and a weak negative relation was typical during the increase phase (Table 5, Figure 6a). A slight positive linear regression of the main effect of wood mice (*Apodemus* spp.) was indicated by the significant estimated parameter (Table 5). The obtained results were similar also in case of the total proportion of Muridae. Based on the analysis of deviance table of the best-fitted M1 model (Table 4), the effect of Phase ($\chi^2 = 9.58$, $P = 0.0083$) and Muridae \times Phase interaction ($\chi^2 = 6.05$, $P = 0.0485$) were

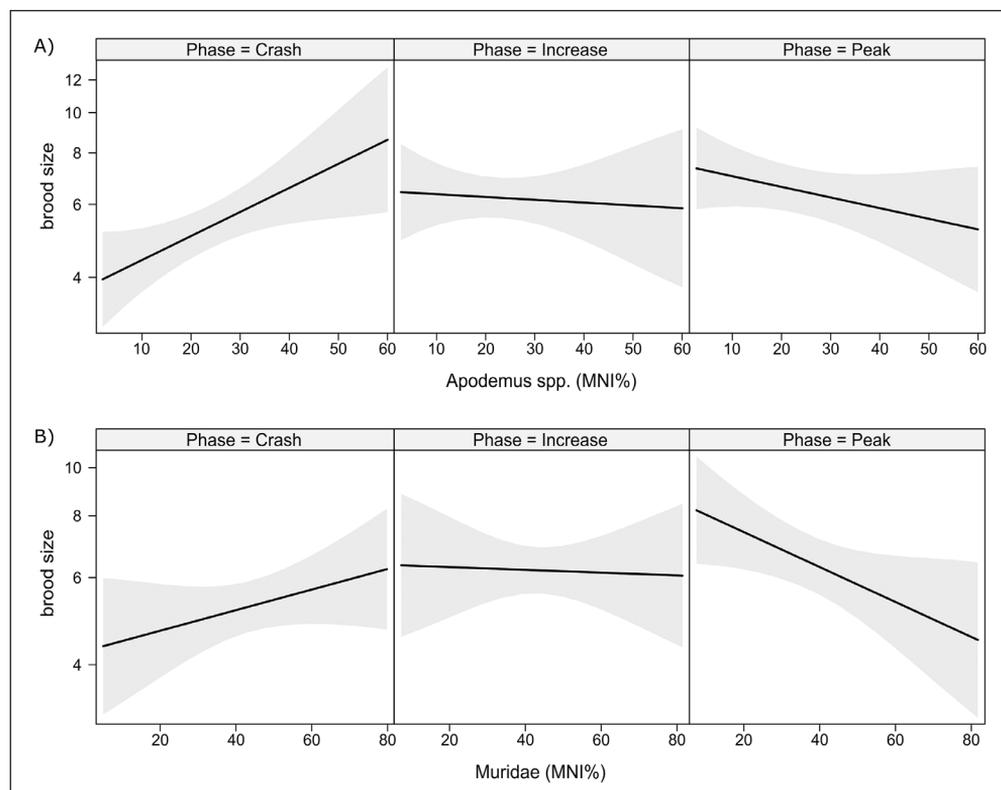


Figure 6. The interaction effect plot of the M1 model in case of *Apodemus* spp. (A) and Muridae (B) as potential alternative prey categories of the Common Barn-owl, showing the different impact of the two predictors on the variation of brood size during a given demographic phase of the Common Vole

6. ábra Az M1 modell interakciós hatás ábrái az *Apodemus* spp. (A) és a Muridae (B), mint a gyöngybagoly potenciális alternatív zsákmánykategóriái esetén, melyek a mezei pocok adott demográfiai fázisában mutatják e két prediktor különböző hatását a kikelt fiókák számának változására

Table 5. Results of regression coefficient estimation in case of the breeding parameters (GLM model/explanatory variables and their interaction), showing only the significant results (For the abbreviations of the predictor variables see Material and Methods)

5. táblázat A regressziós koefficiens becslés eredményei a számolt szaporodási paraméterek esetén (GLM modell/magyarázó változók és ezek interakciói), csak szignifikáns eredményeket mutatva (A magyarázó változók rövidítését lásd a Material and Methods fejezetben)

Model (ID)	Variable/Interaction	B	± SE	t	P
clutch size					
~ Mar × Region (M2)	Mar	0.003	0.002	2.067	< 0.05
brood size					
~ Mar × Region (M2)	Mar	0.006	0.003	2.582	< 0.05
~ Muridae × Phase (M1)	Phase-Peak	0.696	0.226	3.081	< 0.01
	Muridae × Phase-Peak	-0.013	0.005	-2.449	< 0.05
~ Asp × Phase (M1)	Asp	0.013	0.005	2.484	< 0.05
	Phase-Increase	0.512	0.203	2.525	< 0.05
	Phase-Peak	0.653	0.187	3.486	< 0.001
	Asp × Phase-Peak	-0.019	0.007	-2.753	< 0.01
~ H' × Region (M2)	H'	-0.276	0.092	-3.001	< 0.01
number of fledglings					
~ Mar × Phase (M2)	Mar	0.013	0.004	3.700	< 0.05
	Region-MTBHC	0.679	0.260	2.615	< 0.05
	Mar × Region-MTBHC	-0.012	0.005	-2.318	< 0.05
~ H' × Phase (2)	H'	-0.471	0.129	-3.647	< 0.001
	Region-MTBHC	-0.674	0.322	-2.092	< 0.05
	H' × Region-MTBHC	0.501	0.202	2.482	< 0.05
~ LBMR × Phase (M1)	Phase-Increase	0.479	0.147	3.258	< 0.01
	Phase-Peak	0.491	0.146	3.353	< 0.01
	LBMR × Phase-Peak	-0.130	0.053	-2.452	< 0.05

significant, but the main effect of Muridae was not an important predictor of brood size variation. As shown in the regression plot, proportion of Muridae significantly and positively affected the number of nestlings during the crash phase, while a significant negative relationship was detected between these variables in the peak phase, and the effect plot showed a weak regression with a non-significant negative slope (*Table 5, Figure 6b*).

The number of fledglings was affected by the proportion of Common Vole and by prey diversity (H') based on the best supported M2 model (*Table 4*). In case of the main prey, the effect of both model parameters and their interaction were significant (Mar: $\chi^2 = 13.03$, $P = 0.0003$; Region: $\chi^2 = 6.79$, $P = 0.0092$; Mar × Region: $\chi^2 = 5.35$, $P = 0.021$). Considering the significant negative regression coefficient, the number of fledglings was influenced negatively by MTBHC compared to DFP region (*Table 5*). Based on the effect plot of the interaction, the proportion of the Common Vole significantly affected the number of fledglings in the DFP region but had no significant effect in the other mesoregion (MTBHC) (*Figure 7a*).

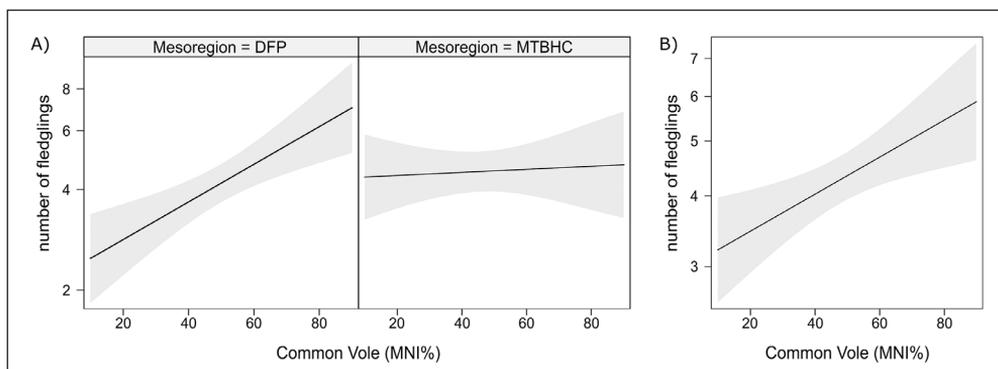


Figure 7. The interaction effect plot of the M2 model in case of the Common Vole, showing the different impact of this predictor on the variation of number of fledglings in the two investigated mesoregions (A) and the relationship between relative abundance of the Common Vole and number of fledglings based on the main effect of the M2 model (B)

7. ábra Az M2 modell interakciós hatás ábrái a mezei pocok esetén, melyek a két vizsgált középtájban mutatják e prediktor különböző hatását a kirepült fiókák számának változására (A), valamint a mezei pocok relatív abundancia és a kirepült fiókák száma közötti összefüggés az M2 modell főhatása alapján (B)

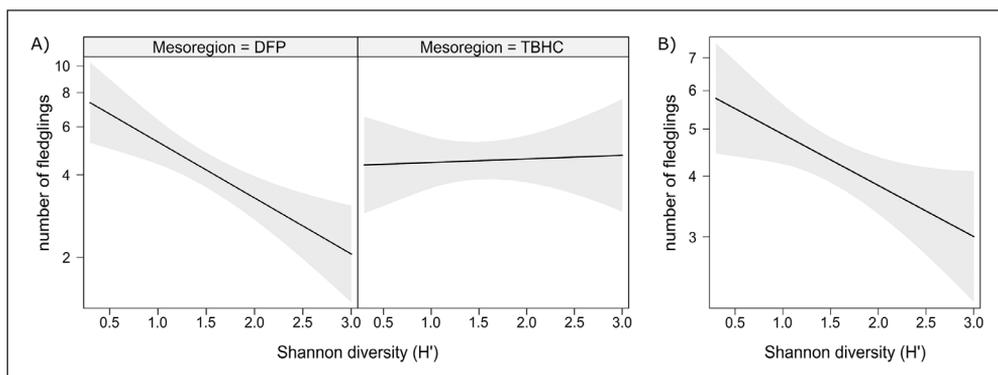


Figure 8. The interaction effect plot of the M2 model in case of Shannon diversity, showing the different impact of this predictor on the variation of number of fledglings in the two investigated mesoregions (A) and the relationship between Shannon diversity and number of fledglings based on the main effect of the M2 model (B)

8. ábra Az M2 modell interakciós hatás ábrái a Shannon diverzitás esetén, melyek a két vizsgált középtájban mutatják e prediktor különböző hatását a kirepült fiókák számának változására (A), valamint a Shannon diverzitás és a kirepült fiókák száma közötti összefüggés az M2 modell főhatása alapján (B)

Visualization of the Common Vole's main effect demonstrated a significant positive relationship between the proportion of this main prey and the number of fledglings (Table 5, Figure 7b). Regarding the effect of prey diversity, a significant effect of both model parameters and their interaction were confirmed by the Type III test (H^2 : $\chi^2 = 12.63$, $P = 0.0003$; Region: $\chi^2 = 4.37$, $P = 0.0365$; $H^2 \times$ Region: $\chi^2 = 6.11$, $P = 0.0135$). The impact of diversity on the number of fledglings differed in the mesoregions, the significant positive regression

Table 6. Quasi-Akaike's rank parameters of the candidate GLM models in case of the derived percentage values of successes (For the abbreviations of the predictor variables see Material and Methods)

6. táblázat Az alkalmazott GLM modellek Quasi-Akaike rang paraméterei a sikerek származtatott százalékos értékei esetén (A magyarázó változók rövidítését lásd a Materials and Methods fejezetben)

coefficient of the interaction indicated that the MTBHC region positively affected the brood size at fledging in contrast to the other mesoregion (DFP) (Table 5). The effect plots of interaction demonstrated a strong negative relationship between prey diversity and number of fledglings in the DFP region and a weaker positive regression between the two variables in case of MTBHC region (Figure 8a). Visualization of the main effect of Shannon diversity showed a significant negative relationship between diversity and brood size at fledging (Figure 8b). Furthermore, considering the large body mass rodents (LBMR) as potential alternative prey, the significant impact of Phase ($\chi^2 = 14.89$, $P = 0.0006$) and LBMR \times Phase ($\chi^2 = 11.11$, $P = 0.0038$) was demonstrated by the Type III test, while the main effect of the LBMR prey category was not important in the best supported M1 model (Table 4). The significant estimated slope

Y _i /Predictor/Model (ID)	QAICc	Δ_i	w_i
hatching success			
<i>Apodemus</i> spp.			
~ Asp \times Phase (M1)	46.5	0.00	0.766
~ " \times Region (M2)	48.9	2.39	0.232
~ " \times Phase \times Region (M3)	58.4	11.84	0.002
<i>Crocidura leucodon</i>			
~ Cle \times Region (M2)	42.5	0.00	0.947
~ " \times Phase (M1)	48.4	5.96	0.048
~ " \times Phase \times Region (M3)	53.0	10.56	0.005
fledging success			
<i>Microtus arvalis</i>			
~ Mar \times Region (M2)	87.2	0.00	0.895
~ " \times Phase (M1)	92.0	4.78	0.082
~ " \times Phase \times Region (M3)	94.6	7.39	0.023
Muridae			
~ Muridae \times Region (M2)	89.1	0.00	0.773
~ " \times Phase (M1)	91.8	2.75	0.196
~ " \times Phase \times Region (M3)	95.4	6.38	0.032
<i>Apodemus</i> spp.			
~ Asp \times Region (M2)	89.2	0.00	0.616
~ " \times Phase (M1)	90.7	1.54	0.285
~ " \times Phase \times Region (M3)	92.8	3.65	0.099
Shannon diversity (H')			
~ H' \times Region (M2)	86.5	0.00	0.889
~ " \times Phase (M1)	90.9	4.37	0.100
~ " \times Phase \times Region (M3)	95.2	8.68	0.012
LBMR			
~ LBMR \times Phase (M1)	86.6	0.00	0.773
~ " \times Region (M2)	89.4	2.82	0.188
~ " \times Phase \times Region (M3)	92.6	5.97	0.039
reproductive success			
LBMR			
~ LBMR \times Phase (M1)	98.9	0.00	0.990
~ " \times Region (M2)	108.9	9.98	0.007
~ " \times Phase \times Region (M3)	110.3	11.40	0.003

QAICc: Quasi-Akaike Information Criterion corrected for small sample size

Δ_i : QAICc differences

w_i : Akaike weights

Table 7. Results of regression coefficient estimation in case of the derived percentage values of successes (GLM model/explanatory variables and their interaction), showing only the significant results (For the abridgment of the predictor variables see Material and Methods)

7. táblázat A regressziós koefficiens becslés eredményei a sikerek származtatott százalékos értékei esetén (GLM modell/magyarázó változók és ezek interakciói), csak szignifikáns eredményeket mutatva (A magyarázó változók rövidítését lásd a Material and Methods fejezetben)

Model (ID)	Variable/Interaction	B	± SE	t	P
hatching success					
~ Asp × Phase (M1)	Asp	0.051	0.025	2.028	< 0.05
	Phase	2.211	0.924	2.393	< 0.05
~ Cle × Region (M2)	Cle × Region-MTBHC	-0.302	0.128	-2.351	< 0.05
fledging success					
~ Mar × Region (M2)	Mar	0.026	0.012	2.096	< 0.05
	Region-MTBHC	1.967	0.845	2.329	< 0.05
~ Muridae × Region (M2)	Muridae × Region-MTBHC	0.046	0.020	2.261	< 0.05
~ Asp × Region (M2)	Asp × Region-MTBHC	0.066	0.029	2.249	< 0.05
~ LBMR × Phase (M1)	Phase	1.612	0.490	3.292	< 0.01
	Phase-Peak	1.013	0.423	2.395	< 0.05
	LBMR × Phase-Increase	-0.231	0.112	-2.069	< 0.05
	LBMR × Phase-Peak	-0.214	0.095	-2.255	< 0.05
~ D × Region (M2)	D	3.974	1.741	2.283	< 0.05
	Region-MTBHC	1.735	0.795	2.182	< 0.05
~ H' × Region (M2)	H'	-0.967	0.462	-2.094	< 0.05
reproductive success					
~ LBMR × Phase (M1)	Phase-Increase	1.428	0.406	3.516	< 0.001
	Phase-Peak	0.835	0.362	2.306	< 0.05
	LBMR × Phase-Peak	-0.174	0.086	-2.024	< 0.05

of the regression line indicated that the proportion of LBMR negatively affected the amount of fledglings in the peak phase compared to the crash phase of the Common Vole (*Table 5*).

The hatching success was affected by the proportion of wood mice (*Apodemus* spp.) and the relative consumption frequency of the Bicolored White-toothed Shrew. In case of the wood mice, M1, while in the case of *Crocidura* species, M2 was the best supported model to explain the relationship between the variables (*Table 6*). The analysis of deviance table showed that the main effect of *Apodemus* spp. ($\chi^2 = 4.51$, $P = 0.0337$) and Phase ($\chi^2 = 7.19$, $P = 0.0274$) was significant, but the interaction of these two variables did not prove to be an important predictor. Conversely, in case of M2 model of shrew species, the effect of the explanatory variables' (Cle × Region) interaction was significant ($\chi^2 = 8.51$, $P = 0.0035$), however, the test did not confirm the importance of these variables as independent effects. The significant regression coefficient indicated a weaker positive relationship between the proportion of the *Apodemus* spp. and hatching success (*Table 7*), while a

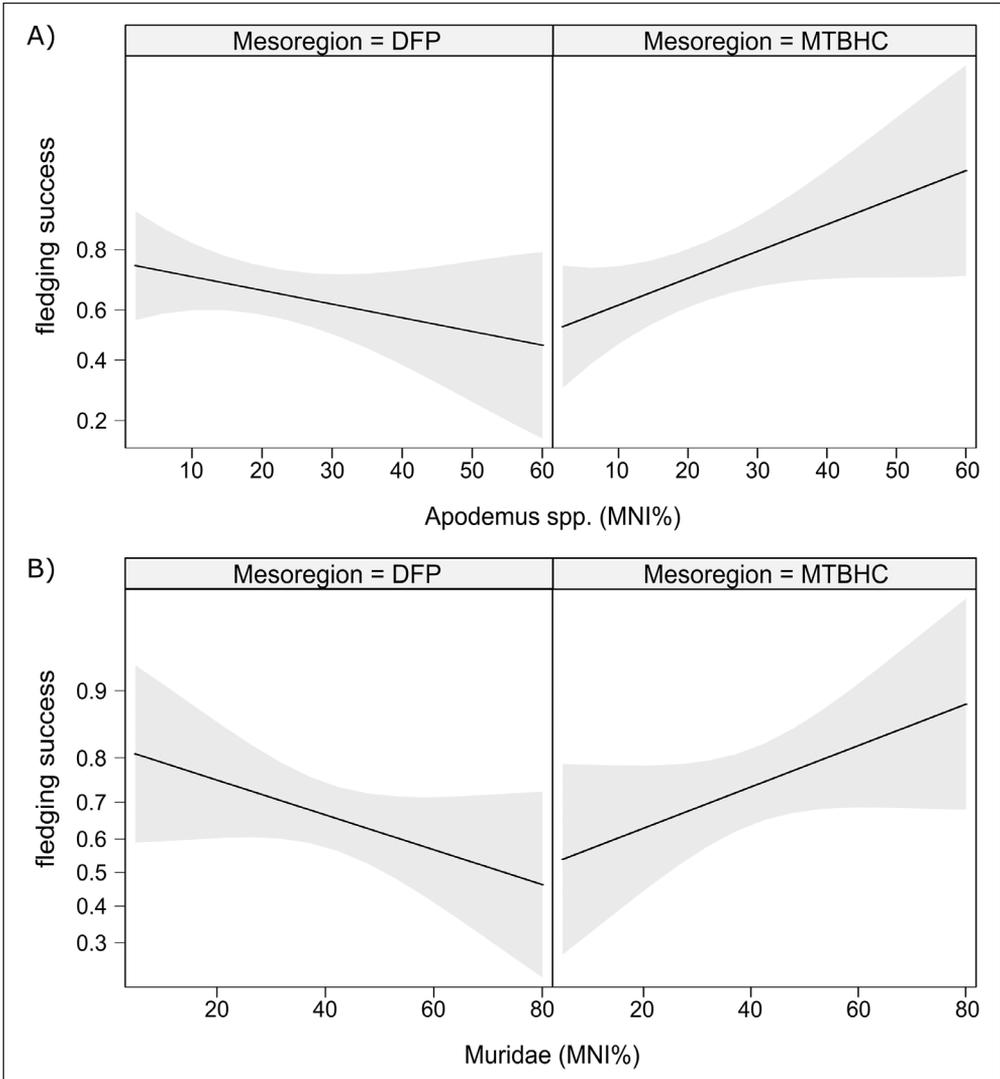


Figure 9. The interaction effect plot of the M2 model in case of *Apodemus* spp. (A) and Muridae (B) as potential alternative prey categories of the Common Barn-owl, showing the different impact of these predictors on the variation of fledging success in the two investigated mesoregions

9. ábra Az M2 modell interakciós hatás ábrái az *Apodemus* spp. (A) és a Muridae (B), mint a gyöngybagoly potenciális alternatív zsákmánykategóriái esetén, melyek a két vizsgált közép-tájban mutatják e prediktorok különböző hatását a kirepülési siker változására

negative relationship was detected by the estimated parameter between relative abundance of the Bicolored White-toothed Shrew and hatching success in the area of MTBHC compared to the other region (Table 7).

The fledging success was affected by the relative consumption rate of the Common Vole and the total proportion of the *Apodemus* spp. and Muridae, based on best supported M2

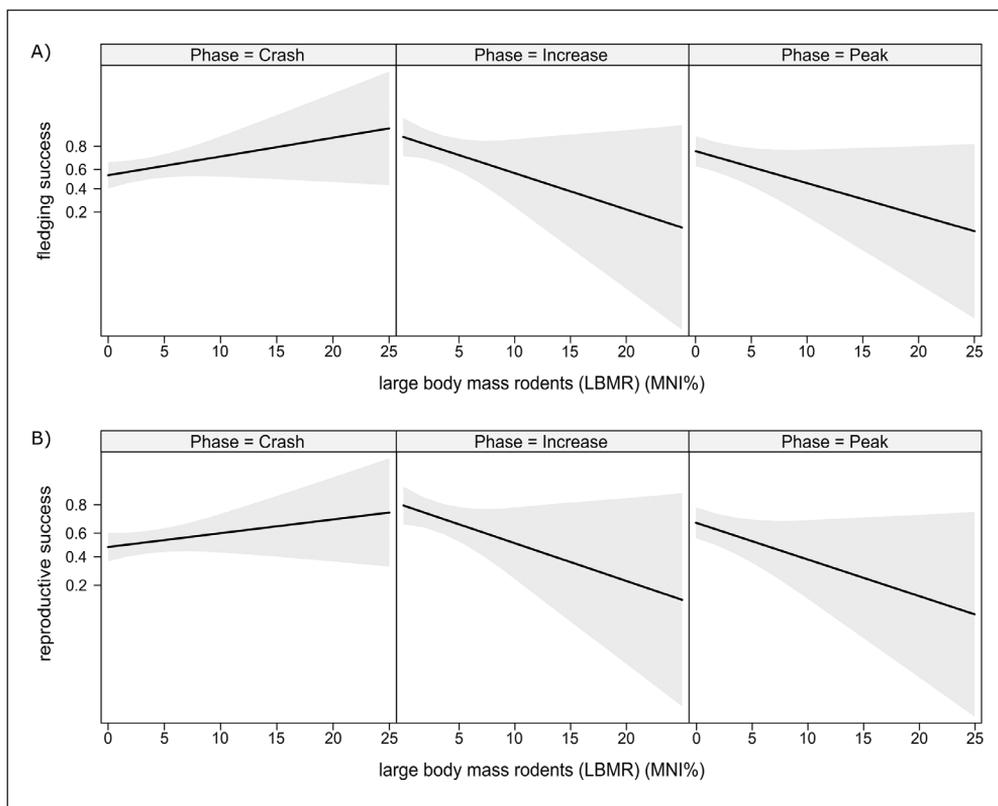


Figure 10. The interaction effect plot of the M1 model in case of fledging success (A) and reproductive success (B), showing the different impact of the abundance of large body mass rodents (LBMR) on the variation of fledging and reproductive success during a given demographic phase of the Common Vole

10. ábra Az M1 modell interakciós hatás ábrái a kirepülési siker (A) és a szaporodási siker (B) esetén, melyek a mezei pocok adott demográfiai fázisában mutatják a nagy testtömegű rágcsálók gyakoriságának hatását a kirepülési és szaporodási siker változására

model (Table 6). In case of the Common Vole, the significant main effect of predictors (Mar: $\chi^2 = 4.82$, $P = 0.0282$; Region: ($\chi^2 = 5.66$, $P = 0.0174$) and their interaction was confirmed by the Type III test. The estimated parameter indicated a weaker but significant positive relationship between the proportion of the Common Vole and fledging success (Table 7). In case of *Apodemus* spp. as a potential alternative prey group, the interaction built into the M2 model had significant explanatory power ($\chi^2 = 5.44$, $P = 0.0197$), however, according to analysis of deviance table, the independent main effect of this predictor was not significant. Based on the positive estimated slope, the proportion of *Apodemus* spp. positively influenced the fledging success in the MTBHC mesoregion compared to the DFP region (Table 7). The opposite relationship in comparing the two landscapes was demonstrated by the effect plot of interaction (Figure 9a). Likewise, in case of Muridae, the Type III test of the best approximating M2 model (Table 6) confirmed the significant effect of the interaction ($\chi^2 = 5.35$, $P = 0.0207$) but rejected the importance of main effects. Compared to the

DFL region, the relative proportion of this prey group positively affected the fledging success in the MTBHC region, thus the different effects of the two regions was expressed, which was visualized by the interaction effect plot (*Figure 9b*). Based on the effect test of the supported M2 model, the main effect of Shannon diversity was significant ($\chi^2 = 4.85$, $P = 0.0277$), contrary to the impact of Region and the interaction. According to the estimated slopes, a slight relationship was detected between prey diversity and fledging success (*Table 7*). In addition, the fledging success was affected by the cumulative proportion of large body mass rodents (LBMR) based on the most supported M1 model. Type III analysis showed that the main effect of Phase ($\chi^2 = 13.01$, $P = 0.0015$) and the impact of LBMR \times Phase interaction ($\chi^2 = 9.37$, $P = 0.0092$) were significant. The estimated parameters indicated that the relative abundance of LBMR significantly and negatively affected fledging success in the increase and peak phase of the Common Vole compared to the crash phase (*Table 7*). The effect plot of the interaction demonstrated a weaker positive relationship between the aforementioned variables, indicating the importance of this prey group in the Barn Owl's diet during the low abundance phase of the Common Vole (*Figure 10a*).

Concerning reproductive success, we found significant effect in case of only one predictor variable. Similar to fledging success, we detected a significant relationship between the proportion of LBMR and reproductive success. Based on the best approximating M1 model, the significant main effect of Phase ($\chi^2 = 13.85$, $P = 0.0009$) and the interaction ($\chi^2 = 7.74$, $P = 0.0209$) were confirmed by the Type III test. The significant estimated slope demonstrated that LBMR abundance negatively affected the reproductive success during the peak phase compared to the crash phase (*Table 7*). The interaction effect plot showed a weaker positive regression between this prey group and the response variable, similar to the results of fledging success (*Figure 10b*).

Considering the remaining investigated alternative prey categories, in case of the *Sorex* genus and the Striped Field Mouse we did not find evidence of significant relationship between the proportions of these prey items and any of the response variables reflecting the breeding performance of the Common Barn-owl.

Discussion

In the present study, we analysed the variation of breeding parameters and the diet composition of the Common Barn-owl in three different demographic phases of the Common Vole in a complete population cycle between two outbreaks. According to the results, we found that the Common Vole was the most abundant and thus, the main prey species in the barn owl's food composition based on our 5-year dataset from the two mesoregions. A similar predominance has been demonstrated by other studies in Central Europe (Horváth *et al.* 2005, 2018, Kitowski 2013, Petrovici *et al.* 2013, Purger 2014, Szép *et al.* 2017, 2019, Veselovský *et al.* 2017).

The mean value of the Common Vole's proportion derived from 81 randomly selected nesting pairs was lower in the peak phase than that reported in some earlier studies of the Common Barn-owl's trophic ecology. However, according to our result, the consumption

rate of this main prey reflected significant difference between the crash (= 37.22%) and the outbreak (= 56.08%) phase. Bohnsack (1966) reported that the proportion of the Common Vole changed in a range between 63% and 95% during the outbreak and similarly high proportion (over 60%) was published by Caboń-Raczyńska and Ruprecht (1977) in Poland, while a higher relative proportion (above 70%) was determined in the food composition analysis of Common Barn-owls in gradation periods (De Bruijn 1979). Conversely, during the vole-poor and non-outbreak years, the Common Vole's consumption rate varied in a lower range (15–46%) as characterized by authors cited above, which interval includes the minimum value (13.12%) of vole consumption also shown in the present study. The examined period between the two outbreaks was characterized by a wider range (13–94%) of Common Vole relative abundance than what was detected (17–81%) in an earlier long-term analysis of the annual fluctuation of the Common Vole in the Common Barn-owl's diet in our study area (unpublished data).

We found significant difference in case of brood size, number of fledglings and reproductive success among the Common Vole demographic phases. Contrary to the expected result, all these three parameters were significantly higher in the increase than the crash phase. From the aspect of the importance of vole increase phase, our results are similar to those of other studies which detected that brood size was maximal during the increase phase as opposed to the peak phase (Korpimäki & Hakkarainen 1991). In contrast with breeding performance values, we found more differences of small mammal prey categories among the vole demographic phases, and the differences were typical only in the crash phase in comparison of the investigated mesoregions. The proportion of more than one shrew categories were significantly higher in crash phase than during the peak phase (the importance of which is evaluated).

Clutch size is one of the most important life history traits of birds (Lack 1947, Price & Liou 1989), which has been studied and discussed in the Common Barn-owl's breeding biology literature from different aspects, such as the comparison of first and second clutches (Marti 1994, Martínez & López 1999, Frey *et al.* 2011, Bank *et al.* 2019), seasonal and annual variations of clutch size (Marti 1994, Martínez & López 1999, Toms *et al.* 2001, Roulin 2002), and its relation to main prey abundance (Taylor 1994, Charter *et al.* 2015, Pavlůvčık *et al.* 2015). In our regression analysis and modelling, we found that primarily the proportion of the Common Vole as main prey affected the variation of clutch size, where the independent main effect of this rodent was the most prevailing. These results presented that the increase of the Common Vole's consumption rate in the diet of owls resulted in an increase in clutch size, which is in accordance with results of some earlier studies (Schönfeld & Girbig 1975, Braaksma & de Bruijn 1976, De Jong 1983, De Bruijn 1994). Similar results were found in a study by Pavlůvčık *et al.* (2015) in which a positive relationship between the mean number of eggs and the vole abundance was shown. The positive relationship between clutch size and the vole consumption rate was described as a numerical response also in case of some vole-eating raptors (Korpimäki & Norrdahl 1991, Jędrzejewski *et al.* 1994, Salamolard *et al.* 2000, Reif *et al.* 2004). Salamolard *et al.* (2000) demonstrated that mean clutch size of the Montagu's Harrier (*Circus pygargus*) was strongly correlated with spring vole abundance, while the average number of fledglings was correlated positively

with summer vole abundance. In case of the Tawny Owl (*Strix aluco*), Solonen *et al.* (2015) pointed out that the mean clutch size of this owl species may be used to forecast abundance of voles typical in a given environment.

From the aspect of the potential indicator role of vole-eating owls' and raptors' breeding parameters, especially clutch size, these results are in accordance with those relationships obtained in the present study, namely that the clutch size of the Common Barn-owls is determined ultimately by the availability and consumption rate of the Common Vole as main prey. Moreover, the other investigated prey species or groups as predictors did not influence the annual variation of clutch size. These results supported the relevance of the 'vole specialist' character of the Common Barn-owl, similar to other vole-eating birds of prey (Salamolard *et al.* 2000, Romanowski & Żmihorski 2008, Terraube *et al.* 2011, Tulis *et al.* 2015).

In addition, our results showed that the main effect of the Common Vole positively influenced the variation of the brood size, the number of fledglings and fledging success, but the vole consumption rate was not an important predictor in case of hatching and reproductive success as response variables. In contrast to our results, Frey *et al.* (2010) did not find relationship between the proportion of the Common Vole and breeding parameters, such as clutch and brood size and number of fledglings. Similar to our results, the dominant role of the *Microtus* prey items and the significant impact of its higher consumption rate on the breeding performance of the Common Barn-owl was reported in the Mediterranean region. Charter *et al.* (2015) found a positive correlation between abundance of social voles (*Microtus socialis guentheri*) and the number of fledglings despite the high cumulative proportion of the Murid rodents in the owls' diet, which was typical in the dry environments of the Middle East (Tores & Yom-Tov 2003, Tores *et al.* 2005, Shehab & Charabi 2006, Charter *et al.* 2009).

Considering the potential alternative prey of Common Barn-owl, we did not find significant relationship between the proportion of red-toothed shrews (*Sorex* genus) and reproductive parameters, which could be caused by this group of shrews being a subordinate prey category in the diet of owls in our study area and the examined period. Conversely, other studies found higher consumption rate of *Sorex* species (at the species or genus level) (Benedek *et al.* 2007, Bernard *et al.* 2010, Szűcs *et al.* 2014, Baudrot *et al.* 2016). Benedek *et al.* (2007) reported a higher consumption frequency of Soricidae, which increased the diversity of diet and reflected a low abundance of rodents, particularly that of the Common Vole, although it was characteristic of only one of the two studied areas. Contrary to our results, this study demonstrated a selective predation in the direction of larger body mass shrews (*S. araneus*, *C. leucodon*). However, Common Barn-owls were characterized by non-breeding status in this locality, that is, the higher-diversity diet did not play a dominant role in the reproductive performance of owls (Benedek *et al.* 2007). Bernard *et al.* (2010) demonstrated that the proportions of *Sorex* genus in the diet did not correlate with their abundance in the field, while a negative correlation was observed between the consumption of *Sorex* spp. in the Barn Owl's diet and the abundance of the Common Vole. According to the results, this study pointed out that the frequency of a given prey in the diet depends also on the population density or availability of other species (Bernard *et al.* 2010), which has contributed to our understanding of the prey preference and switching mechanisms in a multi-prey context (Baudrot *et al.* 2016).

We found that the consumption rate of the *Crocidura* prey groups (at the species and genus level) was higher than that of red-toothed shrews (*Sorex* genus), however, our result did not confirm that the total proportion of the shrews (Soricidae) and relative abundance at species or genus level (*Sorex*, *Crocidura*) would positively affect the reproductive parameters of the Barn Owl. Thus, our results do not support their role as alternative prey in the studied region. Moreover, the present study has shown a significant negative relationship between the prey diversity and the breeding performance (brood size, number of fledglings), which indicates that the diet composition of the Common Barn-owl is very diverse when the availability of Common Vole is very low, thus, our results are in accordance with other studies demonstrating that the shrew consumption increases in low abundance phases of the voles (Benedek *et al.* 2007, Bernard *et al.* 2010, Baudrot *et al.* 2016). This change of food composition was explained by optimal diet theory according to which the width of diet spectrum increases when the relative abundance of the main prey species decreases (Schoener 1971, Pyke *et al.* 1977, Salamolard *et al.* 2000).

Despite the fact that mice (Muridae), particularly the *Apodemus* species, representing a profitable prey group similar to *Microtus* voles, often occur as more abundant prey than voles in Mediterranean regions (Pezzo & Morimando 1995, Varuzza *et al.* 2001, Bontzorolos *et al.* 2005, Tores *et al.* 2005, Charter *et al.* 2009), Charter *et al.* (2015) found a negative relationship between the consumption rate of mice and the number of fledglings. Our results are partly consistent with this observation, however, the negative relationship between the proportion of wood mice (*Apodemus* spp.) and the reproductive parameters (brood size, fledging success) was typical in the increase and during peak phase of the Common Vole. On the contrary, a positive regression was observed between the proportion of mice (*Apodemus* spp., Muridae) and the variation of the number of fledglings in the crash phase. In addition, we observed opposing effects of the Murid prey proportion between the two mesoregions, which reflected the different importance of mice in the food of Common Barn-owl. These results suggested that the wood mice (*Apodemus* spp.) and total Muridae can be characterized as important alternative prey groups with higher consumption rate in the diet of Barn Owls to compensate for the lack or lower availability of the main prey.

We found similar results in case of large body mass rodents as potential alternative prey group of owls. A positive regression with weaker slope was detected between their cumulative proportion in the diet and the reproductive parameters (number of fledglings, reproductive success). Some studies discussed the size-dependent predation of the Common Barn-owl (Kotler *et al.* 1988, Bellocq 1998, Roulin 2004b), which may significantly determine the composition of its diet, influencing the applicability of pellet analysis as an indirect method in surveys of small mammal assemblages (Yom-Tov & Wool 1997, Leonardi & Dell'Arte 2006, Zagoršek 2018). Our result suggested that the large body mass rodents may have an alternative prey role to compensate for the lack of the main prey in the low abundance phase of the Common Vole, however, the obtained results are not considered sufficient evidence to accept the alternative prey hypothesis in case of this prey category.

In summary, our results demonstrated that the clutch size of the Common Barn-owl is determined ultimately by the availability and consumption rate of the Common Vole as main prey, while other small mammal prey categories did not affect the clutch size. These results

support the finding that the clutch size of vole-eating raptors and owls, which begin breeding in early spring, reflects the vole abundance of this early spring period. Considering the other investigated small mammal prey groups, only in case of the Murid rodent prey categories (*Apodemus* spp., Muridae) were alternative prey roles confirmed.

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