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Variation in small mammal food resource niche metrics of Western Barn Owl *(Tyto alba)* at the nesting pair and local population level

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Abstract In the present study, we investigated food resource niche parameters and the degree of specialization of two local Western Barn Owl *(Tyto alba)* populations in two different demographic phases as the crash (2015–2016) and outbreak (2019–2020) of the Common Vole *(Microtus arvalis)*. The study was conducted in two parts of the Transdanubian region of Hungary, namely in Duna-Drava National Park (DDNP) in the south-eastern part, and in Fertő-Hanság National Park (FHNP) in the north-western part. For the analysis, we used food consumption data of 20–20 randomly selected breeding pairs from the DDNP population, while 14 and 17 breeding pairs in FHNP population in the crash and outbreak periods, respectively. Since the small mammal consumption of owls represented 99.3% of the total number of individuals, only data of small mammals as main food resource were taken into account during the analysis. Based on a trait-based framework which taking into account the resemblance between resources, Rao's quadratic entropy metrics was used to estimate the food resource niche breadth at local owl populations and the breeding pair level. The small mammal resource utilization of owls was dependent on populations. The niche breadth of DDNP population was significantly smaller than FHNP population. The estimated niche overlap at the individual level was significantly different between the two populations. The calculated value of specialization of barn owl populations was significantly higher in north-western than south-eastern population. The niche breadth of the owl population living in the DDNP was significantly higher during the crash period. In contrast, the estimated niche breadth of the population living in FHNP did not differ significantly between the two demographic phases. Based on our result, the applied trait-based framework of resource niche pattern analysis demonstrated that the differences of niche breadth were explored in more detail by this method between the local Barn Owl populations of different geographical region.

Keywords: food resource, small mammal traits, estimation of niche parameters, *Tyto alba*

Összefoglalás Jelen tanulmányban két helyi gyöngybagoly *(Tyto alba)* populáció táplálékforrás niche paramétereit és specializálódási fokát vizsgáltuk a mezei pocok *(Microtus arvalis)* különböző demográfiai, mint az összeomlás (2015–2016) és gradáció (2019–2020) fázisban. A vizsgálat a Dunántúl régió két részén, nevezetesen a délkeleti részén a Duna-Dráva Nemzeti Park (DDNP), valamint az északnyugati részén a Fertő-Hanság Nemzeti Park (FHNP) területén valósult meg. Az elemzéshez a DDNP populációból 20–20 véletlenszerűen kiválasztott, míg az FHNP populációból összesen 14, illetve 17 költőpár táplálékfogyasztási adatait használtuk fel az összeomlás, illetve gradáció időszakban. Mivel a baglyok kisemlős fogyasztása az összes meghatározott egyedszám 99,3%-át tette ki, az elemzés során csak a kisemlősök, mint fő táplálékforrás adatait vettük figyelembe. A források közötti hasonlóságot figyelembe vevő tulajdonság alapú keretrendszer alapján Rao kvadratikus entrópia mérőszámát használtuk az táplálékforrás niche szélességének becslésére a lokális bagolypopulációk és az egyes költőpárok szintjén. A baglyok kisemlős forrás hasznosítása populációfüggő volt. A DDNP populációban a niche szélesség szignifikánsan kisebb volt, mint az FHNP populációban. A becsült niche-átfedés az egyedek szintjén szignifikánsan különbözött a két populáció között. A gyöngybagoly populációk specializációjának számított értéke szignifikánsan magasabb volt az északnyugati, mint a délkeleti populációban. A DDNP területén élő bagolypopuláció niche szélessége szignifikánsan nagyobb volt az összeomlás időszakban. Ezzel szemben az FHNP területén élő populáció becsült niche szélessége nem különbözött szignifikánsan a két demográfiai fázis között. Eredményeink alapján az alkalmazott táplálékforrás niche mintázat elemzés jelleg-alapú keretrendszere azt mutatta, hogy ezzel a módszerrel részletesebben feltártuk a niche szélesség különbségeit a különböző földrajzi régiók helyi gyöngybagoly populációi között.

Kulcsszavak: táplálékforrás, kisemlős jellegek, niche paramérek becslése, *Tyto alba*

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Introduction

The Western Barn Owl, *Tyto alba* (Scopoli, 1769) is the most widespread medium-sized nocturnal raptor species on Earth that inhabits mostly open areas, including synanthropic habitats, agricultural lands, natural and semi-natural grasslands in temperate ecosystems (Mikkola 1983, Tylor 1994, Roulin 2020). This owl species is common in semi-arid grasslands, fragmented farmlands, irrigated fields and vineyard agroecosystem in Mediterranean region (Charter *et al*. 2009, 2017, Wendt & Johnson 2017, Huysman & Johnson 2021a, 2021b), while its hunting territories are also include a wide variety of open areas, such as arid and semi-arid plains, palm plantations, rice fields and urban areas in the subtropical and tropical zone (Lenton 1984, Goodman *et al*. 1993, Bonvicino & Bezerra 2003, Hafidzi & Na Im 2003, Delgado-V & Cataño-B 2004, Saufi *et al*. 2020).

Although the Western Barn Owl have a wide food spectrum, especially due to the consumption of many potentially alternative preys in different geographical regions (Herrera 1974, Janžekovič & Klenovšek 2020, Romano *et al*. 2020), this owl species was characterized as a small mammal specialist nocturnal raptor, because it has adapted mainly to the hunting and consumption of nocturnal small mammals (Rodentia and Eulipotyphla) in its range (Taylor 1994, Romano *et al*. 2020). Studies on feeding habits and trophic niche breadth, and overlap variation of the Western Barn Owl at the level of intra- and interspecific feeding ecology are well known from several literature sources along its European (Pezzo & Morimando 1995, Bontzorlos *et al*. 2005, Kitowski 2013, Petrovici *et al*. 2013, Milchev 2016), North American (Marsk & Marti 1984, Marti *et al*. 1993, Jiménez *et al*. 2020), and South American (Trejo *et al*. 2005, Nanni *et al*. 2012) distribution range in temperate ecosystems. It is important to highlight the studies that evaluated the trophic niche pattern of the Western Barn Owl based on geographical variation or trends (Korpimäki & Marti 1995, González-Fischer *et al*. 2011, Milana *et al*. 2016), or along different gradients such as vegetative (Trejo & Lambertucci 2007), longitudinal-latitudinal (Leveau *et al*. 2006), and urban-rural (Teta *et al*. 2012, Hindmarch & Elliott 2015) gradients or in comparison of different landscape structures (Milchev 2015, 2022), focusing on the importance of agricultural intensification in the resource utilization of Barn Owls (Veselovský *et al.* 2017, Horváth *et al*. 2018, Romanowski & Lesiński 2020, Jiménez-Nájar *et al*. 2021). Moreover, the temporal dynamics of food-niche and dietary trends were analysed with trophic niche metrics of Barn Owls (Marti 1988, 2010), while other studies performed the niche metric analysis with regard to the biological control of Hantavirus reservoir (Muñoz-Pedreros *et al.* 2010, 2016).

The trophic ecology studies of the Western Barn Owl demonstrated that the food-niche breadth of this owl species depends on habitat structure (de la Peña *et al*. 2003, Milchev 2015, 2022, Horváth *et al*. 2018), and it is influenced by small mammal community composition, the population fluctuation and density of prey species, particularly the availability of agricultural pest rodents (Kross *et al*. 2016), such as microtine vole species (Marti 1988, Taylor 1994, Petrovici *et al*. 2013, Purger 2014, Hindmarch & Elliott 2015). In European grasslands and different agricultural landscapes, the Common Vole *(Microtus arvalis)* is the main prey of the Western Barn Owl, and it is characterized by multiannual fluctuations with 3–5 year-long population cycles in agricultural fields (Tkadlec & Stenseth 2001, Cornulier *et al*. 2013, Jacob *et al*. 2014, 2020). The past availability of rodents significantly determines the food habits and trophic niche pattern of Barn Owls (Bernard *et al*. 2010, Szűcs *et al*. 2010, Milchev 2015, Veselovský *et al*. 2017, Horváth *et al*. 2018). Several studies have shown the relationship between the productivity and breeding success of the Western Barn Owl and the availability and population fluctuation of the Common Vole (Klok & de Roos 2007, Bernard *et al*. 2010, Pavluvčík *et al.* 2015). Earlier study of Horváth *et al*. (2020) demonstrated that the clutch size of the Western Barn Owl was determined ultimately by the availability and consumption rate of the Common Vole as main prey and this study confirmed the alternative prey role in case of the murid rodent prey categories (*Apodemus* spp., Muridae). Furthermore, numerous studies reported negative correlation between the vole (*Microtus* spp.) frequency and food-niche breadth of the Western Barn Owl (Marti 2010, Hindmarch & Elliott 2015, Milchev 2015, 2016, Horváth *et al*. 2018). These studies pointed out that the availability and abundance fluctuation of the microtine vole species, as the main prey for Barn Owls, significantly determined the food resource utilization, and thus, the resource niche parameters and trophic niche pattern of owls.

The present study aims to examine the food resource niche parameters with a trait-based framework of two local Western Barn Owl *(Tyto alba)* populations, taking into account the resemblance between resources (1), to analyse the niche pattern in two different demographic phases, namely the crash and outbreak of the Common Vole as main prey in both owl populations (2) and to evaluated the degree of resource specialization of the Western Barn Owl at the nesting pair and local population level (3).

Material and Methods

Study area and sample collection

In this study, we investigated two local populations of Western Barn Owl in Danube-Drava National Park (DDNP) (494.78 km^2) and Fertő-Hanság National Park (FHNP) (335.87 km^2). The Danube-Drava National Park is located in the southern Transdanubian region (32° 30′

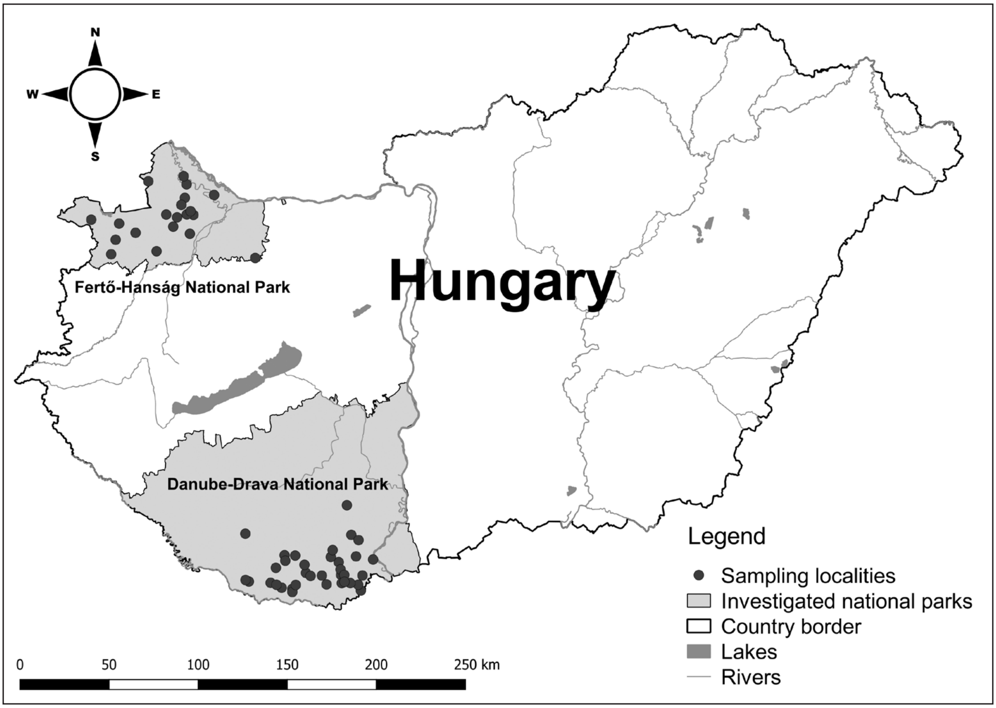

Figure 1. Study area located in the Duna-Drava National Park (DDNP) and Fertő-Hanság National Park (FHNP), Hungary, showing the location of sampled breeding pairs/sites in the two local populations of the Western Barn Owl

1. ábra A Duna-Dráva (DDNP) és a Fertő-Hanság Nemzeti Park (FHNP) területén található vizsgálati terület, feltüntetve a mintavételezett költőpárok/települések elhelyezkedését a gyöngybagoly két lokális populációjában

N, 35° 30′ E), which is part of the Danube-Drava-Sava Euroregion. The meteorological conditions of this area are influenced by the Mediterranean and sub-Mediterranean climates. The pellet samples were collected in two mesoregions: the Drava floodplain and the Mecsek and Tolna-Baranya hill country *(Figure 1)*.

The area of the Drava floodplain includes the erstwhile flood basin of the Drava, and the climate is moderately warm and humid. The average annual temperature is 10.4–10.6 °C, the number of sunny hours is 2,000–2,080, and the annual amount of precipitation is 630–720 mm.

The Mecsek and Tolna-Baranya hill country is located north of the previous mesoregion. The average annual temperature is between 9 °C and 12 °C, the number of sunny hours is 1,400–1,450, and the yearly mean precipitation is 680–720 mm. The Mediterranean climatic impact and the large number of village creates suitable environmental conditions for the survival and stability of Western Barn Owl stock; thus the largest local population of this species in Hungary can be found here (Bank *et al*. 2019).

FHNP is located in the western Transdanubian region (47° 45′ N, 16° 45′ E), covering the northern part of the West Pannonia Euroregion. The sampling sites are situated in four different mesoregion, most of the sampling sites are situated in the Győr basin and in Sopron-Vasi plains, but a few samples also came from the feet of the Alps and Bakony region. A moderately dry and cool climate is typical in the lowland areas of the national park. The average number of hours of sunshine is 1,700–1,900, the annual amount of precipitation is 650–750 mm, and the average annual temperature is 9–10 °C. This region is characterized by a strong westerly-north-westerly air movement. The mountainous mesoregions (feet of the Alps, Bakony region) are cooler and wetter than their surroundings. The density of the Western Barn Owl population is relatively low in this area.

The owl pellet sample collection and diet analyses were carried out within the framework of Hungarian Biodiversity Monitoring System (HBMS) (Horváth *et al*. 2019). Due to lower local density of Barn Owls, in the case of the FHNP, the pellet samples collected from fewer breeding pairs. Considering on the DDNP population, 20–20 breeding pairs were randomly selected for the evaluation, a total of 123 pellet samples and 4,046 owl pellets were processed during the analysis *(Table 1)*.

In total, 2,619 and 1,427 pellets of DDNP and FHNP Western Barn Owl population were analysed, respectively. 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). In case of small mammal prey items, 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 'unidentifed *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 (Kessler 2015), and frogs (Anura) by their skulls and bones of the postcranial skeleton (Schaefer 1932). Prey items were identified to genus (small mammals, birds), to order (frogs), and to class (birds) level if major skeletal elements were missing.

The number of prey was estimated as the minimum number of individuals (MNI), which was determined by counting the same anatomical parts of bones in the case of small

Table 1. Distribution of the nesting and sample data in case of the two Western Barn Owl populations in the two different demographic phases of the Common Vole

1. táblázat A fészkelő- és köpetminta adatok megoszlása a két gyöngybagoly populáció esetében a mezei pocok két különböző demográfiai fázisában

Local population (NP) / demographic phase of *M. arvalis*	**Nesting data**		**Sample data**	
	locality	**# of nesting pairs**	**# of pellet samples**	**# of pellets**
DDNP – crash (2015–2016)	20	20	43	1726
DDNP – outbreak (2019–2020)	20	20	43	893
FHNP – crash (2015–2016)	12	14	16	540
FHNP – outbreak (2019–2020)	16	17	21	887

mammals (McDowell & Medlin 2009, Torre *et al*. 2015, Tulis *et al*. 2015, Horváth *et al*. 2022) and skulls, mandibles and long bones for birds, as well as skulls, remnants of ilium or frontoparietal bones for frogs.

Data analysis

Data were expressed as percent relative frequency of occurrence (%MNI) calculated for the total number of prey found in all pellets in case of the two local Western Barn Owl populations, and in two different demographic phase (crash vs. outbreak) of the Common Vole. First, to compare the relative abundance of main and alternative prey between the two owl populations in a given demographic phase and between the two time periods (phases) in a given local population, Chi-square (χ^2) heterogeneity test was applied by using the statistical software R with the command 'prop.test'.

As a next step, to evaluate the similarity of small mammal resource composition in the two Western Barn Owl populations and different demographic phases of the Common Vole, permutational analysis of variance (PERMANOVA) with Bray-Curtis similarity index was performed with the adonis2 function in package 'vegan' (v2.6.2, Oksanen *et al*. 2022), and 9,999 permutations were run to test for statistically measurable overall differences in case of both groupings. Pairwise comparisons between the populations and sampled periods were carried out with the FDR p-value adjustment method (Benjamini & Hochberg 1995). The dissimilarities based on the Bray-Curtis similarity index were presented on a scatter plot generated by principle coordinate analysis (PCoA). The 'betadisper' and 'permutes' functions in package 'vegan' were used to test whether there were any differences in dispersion between the samples.

Second, to describe and estimate the resource niche metrics, a trait-based framework was used which takes into account the resemblance between resources, and its key element is the consideration of the geometric relationships between resources (De Cáceres *et al*. 2011). As a first step in estimating niche metrics, four relevant body parameters (body weight (g), body, tail and mandible length (cm)) were used to create the distance matrix of resource (D) *(Table 3)* in order to determine and assess the resemblance between small mammals as food resources, according to literature data (De Bruijn 1979, Görner-Hackethal 1988, von Knorre 1973, Kraft 1982, Wijnandts 1984, Märcz 1987, Prete *et al.* 2012, Veselovsky *et al.* 2012). Due to units of measurement, these body characteristics were standardized to remove differences and the transformed variables were used to calculate the Euclidean distance between pairs of small mammal prey categories (d_{jk}). For further analysis, the distance values were normalized to the maximum to limit the distance values between 0 and 1, where 0 indicates that the two resources are absolutely equivalent, 1 denotes that the two resources are completely different (De Cáceres *et al*. 2011). Then, a hierarchical cluster analysis for graphic display with 'heatmap.2' function of the 'gplots' package (Warnes *et al*. 2022) and the 'colorRampPalette' function of the 'RColorBrewer' package (Neuwirth 2022) was performed to evaluate the arrangement of small mammal prey as food resource elements based on the distance matrix of resources. This analysis showed that the rat taxa (two *Rattus* species and *Rattu*s spp.) which are considered the largest prey, form a separated group on the cluster heat map. The other small mammal taxa formed a larger cluster, within which the European Water Vole *(Arvicola amphibius)* and the European Mole *(Talpa europaea)* are separated by a larger distance value, which present also larger prey. The large body mass rodent (LBMR) species, such as European Water Vole, Brown Rat *(Rattus norvegicus)* and Black Rat *(R. rattus)* may be a possible alternative prey group for the Western Barn Owl to compensate for the lack and/or lower availability of the main prey species such as the Common Vole (Horváth *et al*. 2020). The other three groups form a cluster, within which shrews with low body parameter values are separated with a larger distance value, as well as the Eurasian Harvest Mouse *(Micromys minutus)*. The vole species and mice separated by the smallest distance value form a separate group primarily based on tail and mandible length *(Figure 2)*.

Third, to estimate the niche breadth difference between the two local populations of Western Barn Owl, and in case of each different demographic phases of Common Vole, Rao's quadratic entropy (De Cáceres *et al*. 2011) as adopted niche breadth metrics was used in the 'indicspecies' package with 'nichevar' function (De Cáceres 2013, 2014):

$$B_{pop} = \left(\frac{1}{2}\right) \sum_{j=1}^{r} \sum_{k=1}^{r} f_j f_k d_{jk}^2$$

where f is the relative abundance of the given prey item in the total resources (r) in the diet of Barn Owls, and d_{jk} is the distance between each pair of the small mammal resource.

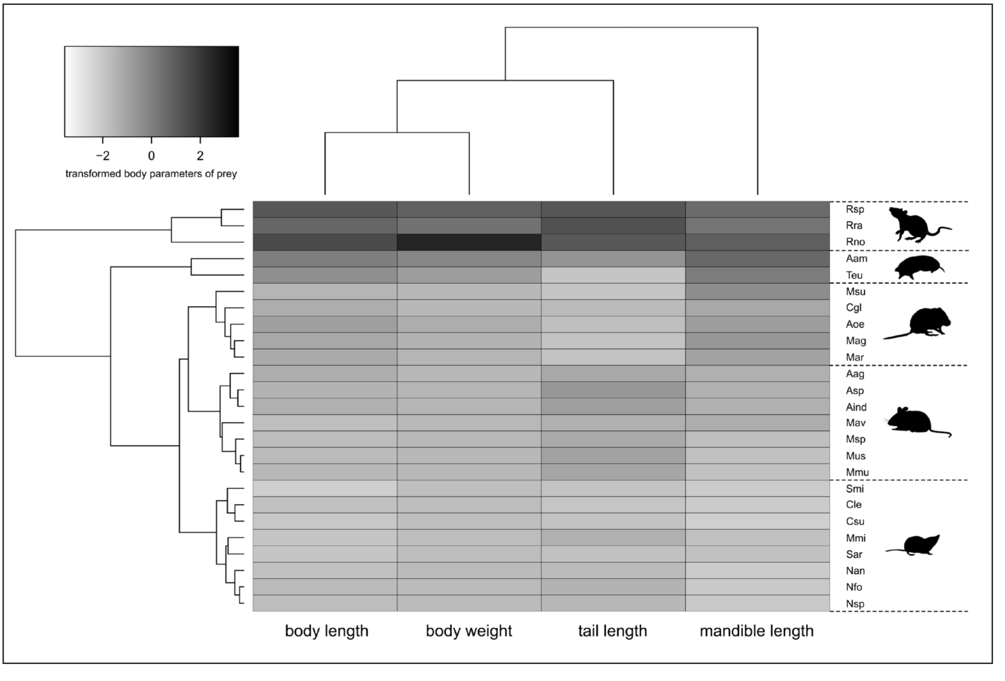

Figure 2. Cluster heat map of the small mammal taxa based on their body parameters
2. ábra A kisemlős taxonok klaszter hőtérképe a testparamétereik alapján

The minimum niche breadth is 0, which is resulted when all resources used are equal or when a single resource is used. In this equation, f_j value is the species relative preference, however, resource availability data are not available in this study, thus the relative species preference is equal to the relative resource use, that is $f_j = p_j$ for all resources (De Cáceres *et al*. 2011). Rao's quadratic entropy (Rao 1982) is a general diversity measure (De Cáceres *et al*. 2011), it was proposed and applied in several studies to evaluate both taxonomic (Pavoina *et al*. 2005, Ricotta & Szeidl 2009) and functional diversity (Botta-Dukát 2005, Laliberté & Legendre 2010, Ricotta & Moretti 2011, Botta-Dukát & Czúcz 2016, Balestrieri *et al*. 2019). In addition, niche overlap between the two local owl populations and in different time periods was calculated with modified and generalized Pianka's symmetrical niche overlap index to take into account the resemblance between resources (De Cáceres *et al*. 2011):

$$O_{pop} = \frac{\sum_{j=1}^{r}\sum_{k=1}^{r} f_{1j} f_{2k}(1 - d_{jk}^2)}{\sqrt{\sum_{j=1}^{r}\sum_{k=1}^{r} f_{1j} f_{1k}(1 - d_{jk}^2)\sum_{j=1}^{r}\sum_{k=1}^{r} f_{2j} f_{2k}(1 - d_{jk}^2)}}$$

This index of overlap is bounded between 0 (no overlap) to 1 (complete overlap). The confidence interval calculation for niche metrics was also performed in 'indicspecies' package with bootstrap estimation. To evaluate the statistical difference of the niche metrics (niche breadth and overlap) between the population/time periods, Wilcoxon's rank test was used from the 'indicspecies' package.

Next, a Principal Coordinates Analysis (PCoA) of matrix D with the 'pcoa' function in 'ape' package was performed to graphical display the resource space ('biplot' function, 'stats' package) which demonstrated the niche centre of the two Western Barn Owl populations and in the given time periods of these populations with the 95% confidence intervals in each resource dimension. Further, the arrows that represent effect vectors of small mammal traits were added, indicating the correlation between resource axes (PCoA) and small mammals' body characteristics (De Cáceres *et al*. 2011).

Finally, the resource niche analysis was performed at the breeding pair level to measure and evaluate the degree of Barn Owls' individual specialization. Due to absent of the sampling replicates at the individual level, the confidence interval bootstrap estimation of different niche parameters was not possible. However, the statistical analysis between individual niche metrics was performed with Wilcoxon's rank test. The basic of the individual specialisation analyses is the ratio between the within individual component (average niche width) and the total niche width of the population (WIC/TNW), which was suggested and defined by the study of Bolnick *et al*. (2002). This method was applied in numerous foraging niche variation analysis of birds (e.g. Rooney & Montgomery 2013, Catry *et al*. 2014, Maldonado *et al*. 2017). Similarly to this, the following proposed specialization measure was used, which takes into account the resemblance between resources (De Cáceres *et al*. 2020, Sol *et al*. 2021):

$$S_{pop} = \frac{\sum_{i=n}^{n} B_i / n}{B_{pop}}$$

where B_i is the niche breadth of each individual, and B_{pop} is the niche breadth of the population. In order to assess the statistical difference between the specialization of two population and time periods, the degree of specialization of each individual was calculated ($S_i = B_i/B_{pop}$) and Wilcoxon's rank test was also implemented for this analysis (De Cáceres *et al*. 2020).

All statistical analyses were conducted in R v4.2.3 (R Core Team 2023). Statistical tests were considered significant at the level $P \leq 0.05$ in all analyses (Sokal & Rohlf 1995).

Results

A total of 7,550 prey specimens were determined from the collected pellets in the two geographical region and investigated periods, of which 7,497 individuals were small mammals. Based on this, other prey accounted for less than 1% of the food composition, so only data of small mammals as main food resource were taken into account during the statistical analysis and evaluation. Within the order Eulipotyphla, we identified 1 species of Talpidae and 6 species of Soricidae. Furthermore, within the order of rodents, 6 species of Cricetidae, 6 species of Muridae, and 1 species of Gliridae were found in the diet of Barn Owls *(Table 2)*.

Based on the abundance data for the Danube-Drava National Park, the Common Vole proved to be the most common prey species in both periods, however, compared to its population crash (37.74%) this main prey was detected with higher proportion (62.80%) during the outbreak period (prop.test: $\chi^2 = 250.050$, $P < 0.001$) in the food composition *(Table 2)*. At the same time, the relative proportion of the wood mice prey group was the second highest in both the crash (19.73%) and outbreak (16.06%) periods ($\chi^2 = 8.910$, $P = 0.003$) *(Table 2)*. The Striped Field Mouse had a percent relative frequency of nearly 8% during the crash, and more than 6% during the period of the outbreak, the consumption of this species showed homogeneous distribution in the diet of the Barn Owls ($\chi^2 = 1.116$, $P = 0.291$) *(Table 2)*. Among the shrews, during the crash phase the Bicolored White-toothed Shrew *(Crocidura leucodon)* appeared with the highest relative abundance value ($\chi^2 = 75.992$, $P < 0.001$), in the outbreak period the Lesser White-toothed Shrew's *(C. suaveolens)* abundance was around 5% (DDNP crash vs outbreak: $\chi^2 = 7.881$, $P = 0.005$), while the relative frequency of the bigger *Crocidura* species was below 1% *(Table 2)*.

Based on the relative abundance data of FHNP population, the Common Vole was the most frequent prey during the crash phase, and it was present with an abundance of nearly 50% in the food composition. However, during the outbreak, contrary to the expected result, it reached a lower percent relative frequency of occurrence (27.38%) ($\chi^2 = 143.490$, $P < 0.001$) *(Table 2)*. The wood mice (*Apodemu*s spp.) appeared in the food composition with a relative abundance of around 9% during the crash phase and around 5% during the outbreak ($\chi^2 = 13.569$, $P < 0.001$) *(Table 2)*. Among the Soricidae species, the Common Shrew *(Sorex araneus)* was the most frequent prey in both demographic phases; during the crash, it was present in an abundance approaching 14% while in the outbreak it exceeded 34%, so this small mammal was the most frequent prey in this latter period ($\chi^2 = 163.550$, $P < 0.001$) *(Table 2)*.

Table 2. Diet composition of the Western Barn Owl in the two investigated populations (MNI: minimum number of individuals, %MNI: percentage frequency of occurrence)

2. táblázat A gyöngybagoly táplálék-összetétele a két vizsgált populációban (MNI: minimum ismert egyedszám, %MNI: minimum ismert egyedszám százalékos értéke)

National Park	**Danube-Drava NP**				**Fertő-Hanság NP**			
	crash		**outbreak**		**crash**		**outbreak**	
Taxa [abbrevation]	**MNI**	**%MNI**	**MNI**	**%MNI**	**MNI**	**%MNI**	**MNI**	**%MNI**
Eulipotyphla	496	18.85	131	8.22	348	28.83	1027	48.49
Talpidae	2	0.08	3	0.19	0	0.00	0	0.00
Talpa europaea [Teu]	2	0.08	3	0.19	0	0.00	0	0.00
Soricidae	494	18.78	128	8.03	348	28.83	1027	48.49
Sorex araneus [Sar]	32	1.22	7	0.44	167	13.84	726	34.28
Sorex minutus [Smi]	10	0.38	12	0.75	53	4.39	107	5.05
Neomys fodiens [Nfo]	29	1.10	1	0.06	1	0.08	66	3.12
Neomys anomalus [Nan]	40	1.52	7	0.44	1	0.08	57	2.69
Neomys spp. [Nsp]	8	0.30	1	0.06	0	0.00	10	0.47
Crocidura suaveolens [Csu]	199	7.56	85	5.33	52	4.31	46	2.17
Crocidura leucodon [Cle]	176	6.69	15	0.94	74	6.13	15	0.71
Rodentia	2111	80.24	1447	90.78	855	70.84	1082	51.09
Cricetidae	1070	40.67	1036	64.99	622	51.53	852	40.23
Clethrionomys glareolus [Cgl]	9	0.34	7	0.44	11	0.91	20	0.94
Microtus agrestis [Mag]	9	0.34	5	0.31	0	0.00	1	0.05
Microtus arvalis [Mar]	993	37.74	1001	62.80	579	47.97	580	27.38
Microtus subterraneus [Msu]	17	0.65	9	0.56	7	0.58	13	0.61
Alexandromys oeconomus [Aoe]	0	0.00	0	0.00	21	1.74	229	10.81
Arvicola amphibious [Aam]	42	1.60	14	0.88	4	0.33	9	0.42
Muridae	1028	39.07	409	25.66	233	19.30	230	10.86
Rattus norvegicus [Rno]	16	0.61	0	0.00	2	0.17	0	0.00
Rattus rattus [Rra]	2	0.08	0	0.00	0	0.00	0	0.00
Rattus spp. [Rsp]	27	1.03	14	0.88	1	0.08	7	0.33
Apodemus agrarius [Aag]	196	7.45	105	6.59	53	4.39	50	2.36
Apodemus spp. [Asp]	519	19.73	256	16.06	104	8.62	113	5.34
Apodemus indet. [Aind]	128	4.87	1	0.06	14	1.16	0	0.00
Micromys minutus [Mmi]	23	0.87	4	0.25	20	1.66	33	1.56
Mus spicilegus [Msp]	34	1.29	7	0.44	12	0.99	3	0.14
Mus musculus [Mmu]	41	1.56	7	0.44	15	1.24	9	0.42
Mus spp. [Msp]	42	1.60	15	0.94	12	0.99	15	0.71
Gliridae	13	0.49	2	0.13	0	0.00	0	0.00

National Park	Danube-Drava NP				Fertő-Hanság NP			
	crash		outbreak		crash		outbreak	
Taxa [abbrevation]	MNI	%MNI	MNI	%MNI	MNI	%MNI	MNI	%MNI
Muscardinus avellanarius [Mav]	13	0.49	2	0.13	0	0.00	0	0.00
Other prey	24	0.91	16	1.00	4	0.33	9	0.42
Mammals	1	0.04	0	0.00	0	0.00	0	0.00
Birds	14	0.53	16	1.00	4	0.33	9	0.42
Frogs	8	0.30	0	0.00	0	0.00	0.00	0.00
Insects	1	0.04	0	0.00	0	0.00	0	0.00
Total:	**2631**		**1594**		**1207**		**2118**	

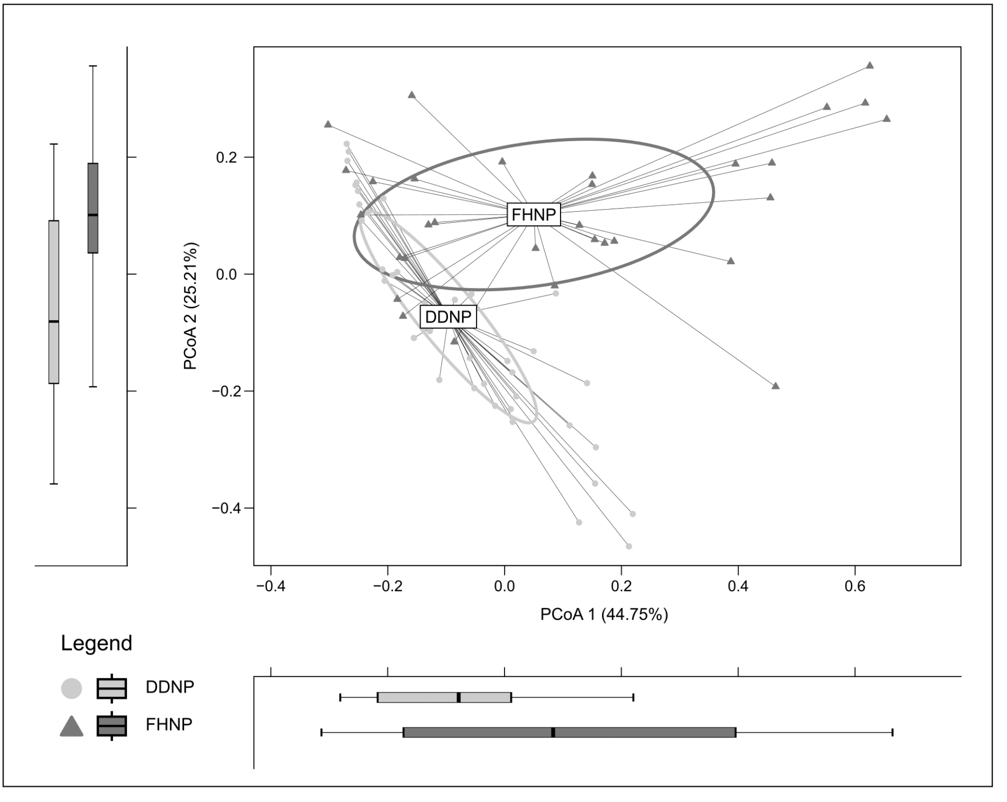

Figure 3. Principle Coordinate Analysis (PCoA) of distance (Bray-Curtis) matrix of small mammal consumption in case of the two examined local Barn Owl populations (ellipses represent a 95% confidence interval around the cluster centroid; box-and-whisker plots shown along each PCoA axis indicate the distribution of samples along the given axis)

3. ábra A kisemlős fogyasztás távolsági (Bray-Curtis) mátrixának főkoordináta-analízise (PCoA) a gyöngybagoly két vizsgált lokális populációja esetén (az ellipszisek 95%-os konfidencia intervallumot képviselnek a klaszter súlypontja körül; az egyes PCoA tengelyek mentén látható doboz diagramok a minták eloszlását jelzik az adott tengely mentén)

Based on summarised data of two examined Western Barn Owl populations, the PERMANOVA analysis confirmed that the small mammal resource utilization of owls was statistically dependent on populations ($F = 11.177$, $P < 0.001$), explaining 13.94% of variance in data. The comparison using PERMANOVA between the two populations yielded a significant result (FDR-$P < 0.001$). Based on the visualization of the PERMANOVA result, the Principal Coordinate Analysis detected significantly different resource dispersion between the populations ($F = 7.915$, $P = 0.005$). The cumulative variance explained by the first two axes was 69.96%. The PCoA scatter plot indicated that the Barn Owls' consumption of small mammal resources was distinct at the population level *(Figure 3)*, which was confirmed by Tukey's Honest Significant Difference test ($DDNP_{pop}$ vs $FHNP_{pop}$: $P = 0.006$).

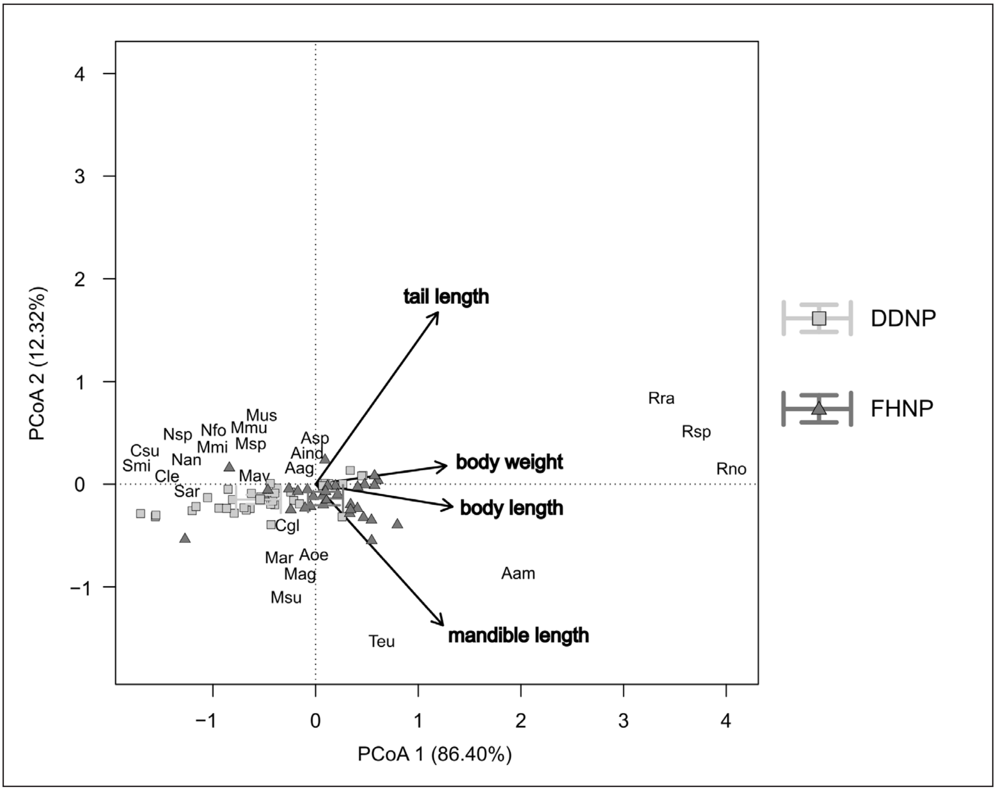

Figure 4. Food resource space displayed by Principal Coordinates Analysis (PCoA) of small mammal trait matrix (D) where the arrows indicating the correlation between resource axes and small mammal body parameters (the niche centres of the two Western Barn Owl populations displayed by square and triangle symbol with the 95% confidence intervals along the two PCoA resource axis)

4. ábra A kisemlős tulajdonságmátrix (D) főkoordináta-analízise (PCoA) által megjelenített táplálékforrás tér, ahol a nyilak a forrástengelyek és a kisemlősök test paraméterei közötti összefüggést jelzik (a két gyöngybagoly populáció demográfiai fázisok szerint elkülönült niche centrumait négy különböző szimbólummal és a két PCoA forrástengely menti 95%-os konfidencia intervallumokkal jelenítettük meg)

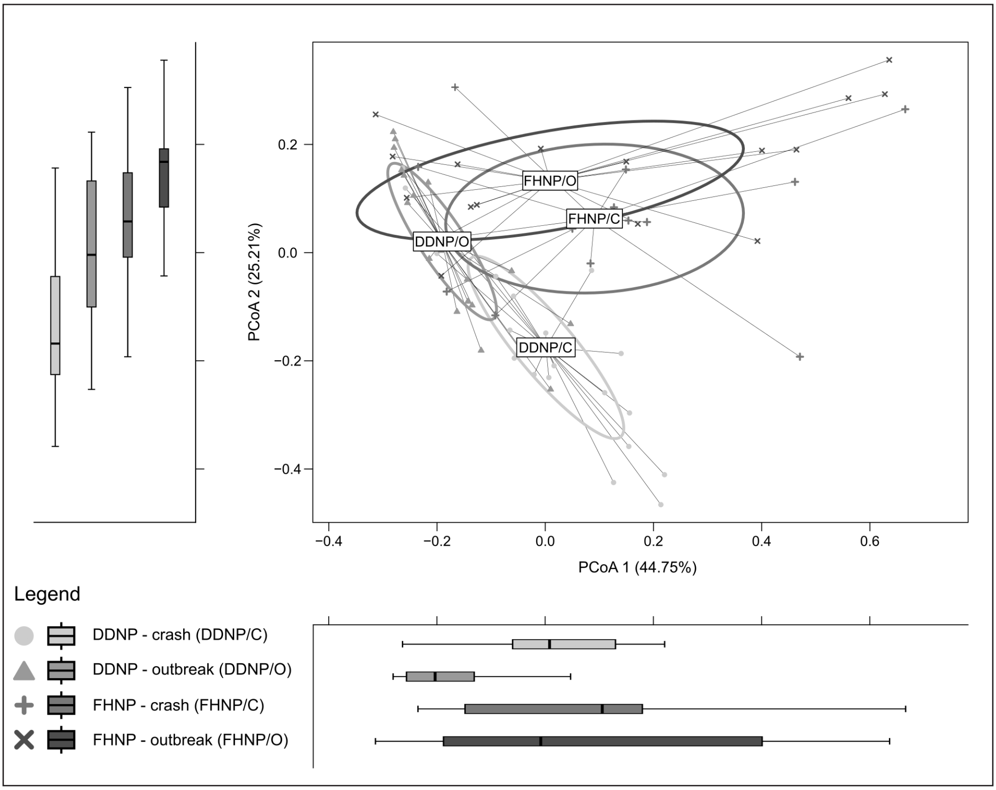

Figure 5. Principle Coordinate Analysis (PCoA) of distance (Bray-Curtis) matrix of small mammal consumption in case in the two Barn Owl populations/two demographic phases of the Common Vole (ellipses represent a 95% confidence interval around the cluster centroid; box-and-whisker plots shown along each PCoA axis indicate the distribution of samples along the given axis)

5. ábra A kisemlős tulajdonságmátrix (D) főkoordináta-analízise (PCoA) által megjelenített táplálékforrás tér, ahol a nyilak a forrástengelyek és a kisemlősök test paraméterei közötti összefüggést jelzik (az ellipszisek 95%-os konfidencia intervallumot képviselnek a klaszter súlypontja körül; az egyes PCoA tengelyek mentén látható doboz diagramok a minták eloszlását jelzik az adott tengely mentén)

According to results of the niche breadth estimation at the level of the two investigated Western Barn Owl populations, which analysis taking into account the resemblance between resources, the niche breadth of DDNP population (B_{pop} = 0.164, 0.145–0.180, 95% CI) was significantly smaller than FHNP population (B_{pop} = 0.103, 0.085 – 0.121, 95% CI) (W = 980, P < 0.001). Regarding the niche overlap between the two owl populations, the estimated niche overlap was very high ($O_{DDNP\ vs\ FHNP}$ = 0.974, 0.947 – 0.988, 95% CI). Based on results of niche overlap among breeding pairs, the niche overlap at the individual level ($\bar{O}_{DDNP}$= 0.936, $\bar{O}_{FHNP}$= 0.966) was significantly different between the two populations (W = 193, P < 0.001). Regarding the visualization of resource space with niche centres of the two examined Barn Owl populations, the PCoA biplot demonstrated that the two niche centres significantly separated in the resource space, the confidence intervals of resource centres

Table 3. Mean value of the body parameters (traits) of small mammal prey ($\bar{x}$) based on the literature data taken into account

3. táblázat A kisemlős zsákmányok átlagos testparaméter értékei ($\bar{x}$) a figyelembevett irodalmi adatok alapján

Small mammal prey	**weight (g)**	**body length (cm)**	**tail length (cm)**	**mandible length (cm)**
T. europaea	83.50	13.75	3.25	2.17
S. araneus	9.93	6.88	4.25	0.96
S. minutus	4.45	5.15	3.70	0.74
N. fodiens	14.45	8.41	6.20	0.80
N. anomalus	13.25	7.62	5.10	0.75
Neomys spp.	14.52	8.06	5.65	0.78
C. suaveolens	5.06	6.52	3.57	0.65
C. leucodon	9.36	7.55	3.43	0.75
C. glareolus	23.98	10.01	5.23	1.38
M. agrestis	31.78	10.97	3.63	1.66
M. arvalis	26.13	10.58	3.62	1.49
M. subterraneus	19.22	9.00	3.18	1.84
A. oeconomus	45.50	11.90	4.48	1.56
A. amphibius	135.56	16.17	10.27	2.49
R. norvegicus	358.00	23.33	19.50	2.68
R. rattus	186.88	19.67	20.93	2.28
Rattus spp.	227.08	21.50	20.22	2.48
A. agrarius	22.33	10.30	7.82	1.27
Apodemus spp.	26.61	9.64	9.87	1.29
Apodemus indet.	25.88	9.90	8.96	1.28
M. minutus	6.91	6.73	6.82	0.97
M. spicilegus	21.50	8.03	7.32	1.02
M. musculus	20.60	8.63	8.12	0.94
Mus spp.	19.90	8.50	8.50	0.98
M. avellanarius	23.71	7.64	6.72	1.30

Table 4. The estimated value of the niche breadth and its 95% confidence interval at the level of Western Barn Owl population/demographic phases and results of the statistical analysis between the sampling pairs

4. táblázat A niche szélesség és 95%-os konfidencia intervallumának becsült értéke a két gyöngybagoly populáció/demográfiai fázisok szintjén és a mintapárok közötti statisztikai elemzés eredményei

Local population (NP) / phase of *M. arvalis* cycle	**Niche breadth values (Rao's quadratic entropy)**		**Statistical test between niche breadth**	
	Niche breadth (B_{pop})	**95% CI**	**Sample pairs / phase**	**Wilcoxon test (B_{pop})**
DDNP – crash	0.186	0.167 – 0.134	DDNP/C vs DDNP/O	W = 312, $P < 0.01$
DDNP – outbreak	0.134	0.107 – 0.142	DDNP/C vs FHNP/C	W = 238, $P < 0.001$
FHNP – crash	0.119	0.090 – 0.121	DDNP/O vs FHNP/O	W = 253, $P < 0.05$
FHNP – outbreak	0.089	0.069 – 0.168	FHNP/C vs FHNP/O	W = 149, $P = 0.246$

Table 5. The estimated value of the niche overlap and its 95% confidence interval at the level of Western Barn Owl population/demographic phases and results of the statistical analysis between the sampling pairs

5. táblázat A niche átfedés és 95%-os konfidencia intervallumának becsült értéke a két gyöngybagoly populáció/demográfiai fázisok szintjén és a mintavételi párok közötti statisztikai elemzés eredményei

Sample pairs / phase of *M. arvalis* cycle	**Niche overlap values**		**Wilcoxon test ($\bar{O}_{12}$) between niche overlap**
	Niche overlap ($\bar{O}_{12}$)	**95% CI**	
DDNP/C vs DDNP/O	0.978	0.935 – 0.996	W = 57, $P < 0.001$
DDNP/C vs FHNP/C	0.960	0.907 – 0.990	W = 60, $P < 0.01$
DDNP/O vs FHNP/O	0.982	0.961 – 0.995	W = 95, $P < 0.05$
FHNP/C vs FHNP/O	0.997	0.987 – 0.999	W = 41, $P < 0.01$

does not overlap for the two resource dimensions. The cumulative variance explained by the first two axes was 98.72% *(Figure 4)*. This results confirmed the significantly different niche breadth of the two Barn Owl populations. Despite the average value of individual niche breadth being larger than the estimated niche breadth at the population level in the case of both Barn Owl populations, the difference of these two niche breadth value was larger in the case of FHNP (S_{pop} = 2.786) than DDNP (S_{pop} = 1.750) population. Therefore, the calculated value of specialization of these Barn Owl populations was significantly higher in the FHNP than the DDNP population (W = 217, P < 0.001).

Based on small mammal consumption data of the two Barn Owl populations in two demographic phase of the Common Vole, the PERMANOVA analysis showed that the distribution of the small mammal resource utilization was statistically determined by the typically different consumption of populations in the given demographic phases (F = 6.939, P < 0.001), explaining 23.70% of variance in data. The comparison using PERMANOVA between the four sampling groups was significant in case of five sampling pairs (FDR-P = 0.0003 – 0.0007), except between FHNP/C and FHNP/O (FDR-P = 0.314). The Principal Coordinate Analysis which display the PERMANOVA result, detected significantly different resource dispersion between the populations/demographic phases (F = 4.619, P = 0.007). The cumulative variance explained by the first two axes was 69.96%. Although the PCoA scatter plot indicated that the Barn Owls' consumption of small mammal resources was distinct between crash and outbreak phase in DDNP population (with minimal overlap of ellipses which represent 95% CI around the centroid of the given sampling points of breeding pairs) *(Figure 5)*, which was not confirmed by Tukey's Honest Significant Difference test

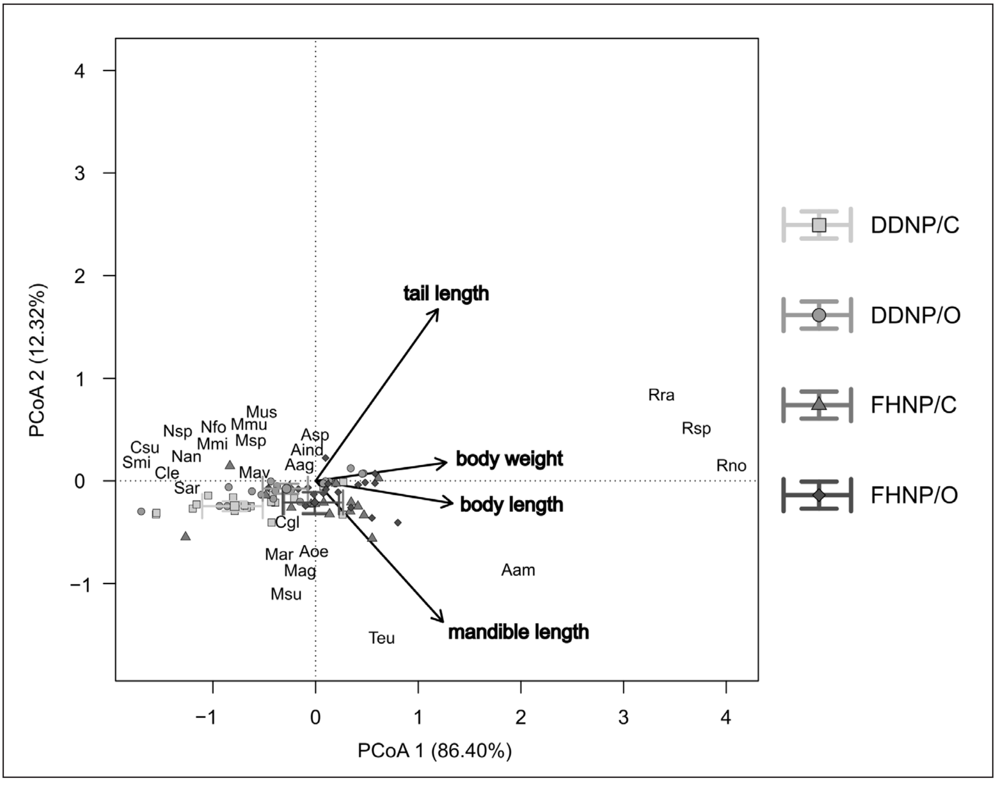

Figure 6. Food resource space displayed by Principal Coordinates Analysis (PCoA) of small mammal trait matrix (D) where the arrows indicating the correlation between resource axes and small mammal body parameters (the niche centres of the two Western Barn Owl populations separated according to demographic phases, displayed by four different symbols with the 95% confidence intervals along the two PCoA resource axis)

6. ábra A kisemlős tulajdonságmátrix (D) főkoordináta-analízise (PCoA) által megjelenített táplálékforrás tér, ahol a nyilak a forrástengelyek és a kisemlősök test paraméterei közötti összefüggést jelzik (a két gyöngybagoly populáció demográfiai fázisok szerint elkülönült niche centrumait négy különböző szimbólummal és a két PCoA forrástengely menti 95%-os konfidencia intervallumokkal jelenítettük meg)

(DDNP/C vs DDNP/O: P = 0.334). Based of larger overlap of confidence ellipses, the statistical test confirmed similar results between crash and outbreak phase in case of FHNP population (FHNP/C vs FHNP/O: P = 0.979) *(Figure 5)*.

Considering the niche breadth estimation of the two owl populations in different demographic phases of the Common Vole, the niche breadth of the owl population living in the DDNP was significantly higher during the crash period. In contrast, the estimated niche breadth of the population living in FHNP did not differ significantly between the two demographic phases *(Table 3)*. In both the crash and outbreak periods, the niche breadth of the Barn Owl population breeding in the DDNP was significantly higher compared to the population living in the region of FHNP *(Table 3)*.

Regarding the niche overlap, the highest niche overlap value was calculated for the population living in FHNP between the two demographic periods, while the lowest overlap was observed between the two investigated populations during the crash period *(Table 4)*. In the case of the investigated populations, there were significant differences between the average niche overlap of the breeding pairs in the comparison of the two periods, while comparing the populations in the two different demographic phases of the Common Vole resulted in a significant difference between the niche overlaps *(Table 4)*.

According to the visualization of resource space with niche centres of the two examined populations in the different demographic phases of the Common Vole, the PCoA biplot demonstrated that DDNP/C niche centres significantly separated from the two FHNP sampling groups, but were not significantly different from DDNP/O due to CI overlap. No significant difference between the niche centres was found in the case of FHNP populations, either *(Figure 6)*. The first two axes explained 98.72% of the cumulative variance.

Finally, in the case of population specialization in the two different demographic phases of the Common Vole, the population living in the FHNP during the crash period was the least specialized (S_{pop} = 1.356), while in the other three cases, we calculated a similar degree of specialization (DDNP/C: S_{pop} = 0.867, DDNP/P: S_{pop} = 0.889, FHNP/O: S_{pop} = 0.882), and these populations were more specialized. Nonetheless, based on the Wilcoxon test, there were no significant differences between the nesting populations in the investigated national parks and between the two periods (DDNP/C vs DDNP/O: W = 164, P = 0.341; DDNP/C vs FHNP/C: W = 135, P = 0.877; DDNP/O vs FHNP/O: W = 171, P = 0.988; FHNP/C vs FHNP/O: W = 112, P = 0.799).

Discussion

In this paper, we investigated the food resource niche parameters of two Western Barn Owl populations in two different demographic phases of the Common Vole. Research on the Barn Owl's diet has described that a significant part of the food composition of this owl species is made up of nocturnal, terrestrial small mammal species (e.g. Bosé & Guidali 2001, Trejo & Lambertucci 2007, Purger 2010, Milchev 2015, Torre *et al.* 2015, Horváth *et al.* 2018, 2020, Szép *et al*. 2021), which is supported by our results since, based on the remains found in the pellets, 99% of the prey in the periods we examined were different small mammals. In the case of the Danube-Drava National Park, the Common Vole was the most common prey in both periods, which corresponds to the results of research conducted in the temperate region of Europe (Frey *et al.* 2011, Veselovsky *et al.* 2017, Horváth *et al.* 2022, 2023), while wood mice (*Apodemus* spp.) proved to be an alternative prey. Several studies have described the higher consumption of different Murid species (*Apodemus* and *Mus* mice) during periods of low availability of the Common Vole in the European and Mediterranean regions (Pezzo & Morimando 1995, Bontzorolos *et al.* 2005, Rodrígez & Peris 2007, Horváth *et al*. 2020). Based on the evaluation of British Barn Owls' food change, the study of Love *et al*. (2000) reported that *Apodemus* mice were an important alternative prey, particularly in summer and autumn, when the relative percent frequency of the given *Microtus* vole species (in this case the Field Vole *(M. agrestis)*) was the lowest.

In the samples from Fertő-Hanság National Park, the Common Vole had the highest relative abundance in the crash period, while the Common Shrew was the most common prey during the outbreak. This was similar with our earlier results (Szűcs *et al*. 2014), thus the result of the previous and current analysis clearly illustrates that shrews, especially the Common Shrew, can be present as significant alternative prey in the Barn Owl's diet in this north-western region. The primary alternative prey character of the Common Shrew was highlighted by more studies in the aspect of the seasonal and multiannual change of the Barn Owls' prey consumption (Taylor 1994, Love *et al*. 2000, Bernard *et al*. 2010, Kitowski 2013). A similarly higher relative frequency of the Common Shrew was shown by the study of Benedek *et al.* (2007). The increased relative frequency of shrews such as the Common Shrew in the food composition of owls was evaluated as being the result of a functional response with prey switching to the decline of the Field Vole population.

Based on the above, Barn Owls can compensate for the lack of Common Voles as their main prey with different alternative prey taxa depending on geographical distribution, landscape structure, and land use, as well as climatic conditions (Love *et al.* 2000, Janžekovič & Klenovšek 2020, Romano *et al.* 2020).

The niche breadth of the Barn Owl's food composition depends on the amount and availability of prey species, so the niche breadth of this species may differ in disparate areas and periods (Marti *et al.* 1988, Pezzo & Morimondo 1995, Love *et al.* 2000, Milana *et al.* 2016). Our results are in accordance with this result, because the niche breadth within Barn Owl populations differed significantly between the populations and also between the two demographic phases.

Several studies described a very high niche overlap between Barn Owl populations in a comparison of nesting localities (Marti 1988, Bosè & Guidali 2001), seasons (Pezzo & Morimando 1995), and subsequent years at a given area (Marti 1988, 2010). In the case of our result, the high niche overlap values at the population level indicated that there is no significant difference in terms of small mammal fauna between the two geographical regions. However, the relative abundance of the prey species may differ significantly locally in the given periods depending on climatic and environmental features, which affects the niche parameters of breeding pairs. In a previously conducted niche analysis in relation to the two investigated regions, Szűcs *et al.* (2014) described that the availability of prey was determined by different geographical conditions and landscape patterns and it has a specific role in the different feeding niche patterns of owls, which is also supported by our results, as we showed a significant difference between the average niche overlap of the breeding pairs in the comparison of the two populations and the two periods.

Individual specialization is one of the many factors that contribute to the variability of niche breadth within a population (Rooney & Montgomery 2013, Sol *et al.* 2021), and it also has important ecological, evolutionary, and conservation implications. Specialization and the resulting niche variability support frequency-dependent interactions that influence population stability, the degree of intraspecific competition, fitness, and the rapid diversification and speciation ability of the population (Bolnick *et al.* 2002). According to our results, the degree of specialization differed between the populations but was not distinct within the populations or between demographic phases. The results of specialization analysis at the population level confirmed the results of significant niche breadth difference between the two populations. In light of the results, the applied trait-based framework of resource niche pattern analysis demonstrated that the differences of niche breadth were explored in more detail by this method between local Barn Owl populations of different geographical regions.

Acknowledgments

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