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DIFFERENCE IN SMALL MAMMAL ASSEMBLAGES IN THE DIET OF THE COMMON BARN-OWL *TYTO ALBA* BETWEEN TWO LANDSCAPES

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As an opportunistic predator, the Common Barn-owl (*Tyto alba*) proved to be an appropriate model organism to survey the composition of small mammal assemblages. This study analysed barn owls' pellet samples from 14 localities containing 34 animal taxa and 4,088 prey items in two years (2015–2016). Two groups of samples (7–7 localities) were separated based on the dominance of semi-natural habitats and agricultural lands. Rarefaction analysis proved that the species richness and diversity of barn owls' diet were significantly higher in semi-natural landscapes. The multiple regression analysis between PCA scores showed that in the agrarian landscape the abundance of generalist species was influenced by the proportion of forests, while the value of the trophic level index was determined by the size of arable fields. In the case of semi-natural landscapes, the abundance of the synantrop guild and generalist species, especially *S. araneus* and *A. agrarius*, was influenced by the proportion of urban areas, the number of habitats and the size of arable fields. The results of this study suggested that the small mammal consumption of the Common Barn-owl is significantly different in the two landscapes, which reflects the impact of habitat heterogeneity and agricultural activity on prey availability.

Key words: pellet analysis, land use, small mammals, guilds, *Tyto alba*

INTRODUCTION

The intensification of agricultural cultivation leads to biodiversity loss due to homogenisation of the landscape pattern, habitat fragmentation and transformation (Flowerdew 1997, Brooks *et al.* 2002, Lundstrom 2002, Benton *et al.* 2003, Hanski 2005, Groom *et al.* 2006, Fischer & Lindenmayer 2007, Chaudhary *et al.* 2016), and also contributes to the decline of ecosystem services (Tscharntke *et al.* 2005). The main sources of biodiversity in agricultural areas are semi-natural habitats (e.g., hedgerows, forests, grasslands, pastures) (Hietala-Koivu *et al.* 2004, Billeter *et al.* 2008, Moreno-Mateos *et al.* 2011, Gentili *et al.* 2014), which include grazing sites, food resources and shelters for populations living in disturbed habitats, in addition to facilitating the movement and spread of species between adjacent patches (Tscharntke *et al.* 2007, Eycott *et al.* 2012) and the recolonisation of habitats (Hanski 1999).

However, in recent decades, many previously widespread species have become rare or extinct not only due to an increase in agricultural intensity but also due to a decrease in semi-natural landscape features (Krebs *et al.* 1999, Robinson & Sutherland 2002).

The diet composition and trophic niche of the Common Barn-owl have been investigated in the context of landscape structure in different geographical regions (Burel *et al.* 2004, Horváth *et al.* 2005, Hindmarch *et al.* 2012, González Fischer *et al.* 2012, Milchev 2015, Veselovský *et al.* 2017, Szép *et al.* 2017, Horváth *et al.* 2018). This owl species proved to be a suitable and useful model organism to survey the composition of small mammal or rodent assemblages (Avenant 2005, Massa *et al.* 2014, Torre *et al.* 2015). Measuring the consumption of small mammals based on pellet analysis is an appropriate method to investigate the impact of the intensity of human intervention on the changes in community structure and the abundance of small mammal species in farmlands (Love *et al.* 2000, Bontzorlos *et al.* 2005, Marti 2010, Teta *et al.* 2012, Veselovský 2017). These parameters of small mammal communities are particularly affected by different agri-environment schemes (Millán de la Peña *et al.* 2003, Rodríguez & Peris 2007, Charter *et al.* 2009) and seasonal differences in landscape associations (González Fischer *et al.* 2012) in agroecosystems. The Common Barn-owl is very sensitive to the configuration of landscape elements and the changes in landscape composition (Andries *et al.* 1994, Bond *et al.* 2005, Frey *et al.* 2011, Hindmarch *et al.* 2012). Thus, several studies emphasised the impact of change in agricultural practices and intensification on its foraging pattern, which depends on the most frequent prey species, especially different herbivore microtine voles that are considered to be agricultural pests (Taylor 2004, Marti 1998, Bernard *et al.* 2010, Kross *et al.* 2016). On the other hand, several studies examined the hypothesis that variation in habitat features surrounding the nest sites determine the reproductive success of Common Barn-owls (Meek *et al.* 2009, Frey *et al.* 2011, Charter *et al.* 2012). The findings of these studies are contradictory, or there was only insufficient evidence for the correlation between landscape composition and breeding parameters (Bond *et al.* 2005, Meek *et al.* 2009, Frey *et al.* 2011, Charter *et al.* 2012). In other cases, it was demonstrated that the Common Barn-owl's breeding performance was more successful in semi-natural than in arable fields (Leech *et al.* 2009). It occupied undisturbed and structurally complex areas, including some types of semi-natural landscape elements (Martínez & Zuberogoitia 2004), and the temporal instability of agricultural field structure and quality due to crop harvesting negatively influenced the survival of Common Barn-owls (Martin *et al.* 2010). However, it is evident that the diet composition and the food-niche breadth of the Common Barn-owl vary depending on habitat structure in the landscape (Hindmarch & Elliott 2015, Milchev 2015, Kross *et al.* 2016, Horváth *et al.* 2018).

Based on the analysis of barn owls' diet composition, Marti (1988) showed an increased proportion of microtine rodents (*Microtus* spp.) in the uniform landscape. Despite the predominance of the Common Vole, Millán de la Peña *et al.* (2003) demonstrated that agricultural intensification adversely affected rare and habitat specialist species and had a positive impact on habitat generalist species, while agricultural activities did not affect species richness or species composition, however, it influenced the relative frequency of species. Similarly, the increase in the relative abundance of generalist and competitively subordinated species was observed in the temperate region of South America (Massa *et al.* 2014). Frey *et al.* (2011) found significant relationships between the habitat composition of the landscape and the proportion of Common Voles and Eurasian Water Voles (*Arvicola amphibius*), although this study confirmed that the results of the pellet analysis reflect the foraging habitat and the accessibility of prey more than the abundance of small mammals in the given spatial localities of the landscape. In addition, Milchev (2015) demonstrated a significant relationship between habitat and food niche overlaps of barn-owls' and confirmed the positive impact of the proportion of wetlands as highly diverse semi-natural habitats on the consumption rate of wetland species such as water shrews.

Besides the large number of case studies that evaluated the impact of agricultural intensification on the barn owls' diet composition, more detailed investigation is needed to understand how semi-natural elements in a given landscape affect the food habits and dietary shift of barn owls. In this work, we investigate the hypothesis that the attributes of small mammal assemblages are determined by the differences of landscapes, which can be measured by the difference in the abundance of the predominant Common Vole as the Common Barn owl's main prey and by the distribution of the given small mammal guilds in the owl's diet. The objects of the present study are: 1) to compare the diet of barn owls, between landscapes dominated by semi-natural and agricultural patches, with particular attention to small mammal assemblages, 2) to estimate species richness and diversity of food composition in two different landscape types and 3) to analyse the effects of land-use composition on the abundance of small mammal species and guilds.

MATERIAL AND METHODS

Study area and sample collection – The study was conducted in the southeastern part of the Transdanubian region in South Hungary, where sampling sites were situated in the area of Baranya County (4429.6 km²) (46°04′N, 18°14′ E). The climate of this region is determined by the Mediterranean effect with a high number of sunny hours, relatively small fluctuations of temperatures and mild winters. On the other hand, the area of the county is characterised by a large number of villages (the number of settlements is 301) and an active and successful artificial nest box installation program (the number of available nest boxes was 158 in 2015 and 161 in 2016). The continuous monitoring of breeding success and the diet analyses of barn owls have been going on since 1994. In the present study, pellets and prey remains were collected from 14 villages (11 nest boxes and 4 church towers as 'natural' environment) at the end of the barn owl breeding season between 2015 and 2016 in Baranya County. The location of sampling sites are presented in Figure 1, indicating two land-use categories.

Pellets were processed by the dry technique. The individual pellets were broken down by hand (Schmidt 1967), and prey items were identified to the lowest possible taxonomical level. Small mammals and bats were identified based on skeletal parameters (features of skull, mandible and teeth), following published literature (Schmidt 1967, März 1972, Niethammer & Krapp 1978, 1982, 1990, 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 categorised commonly as *Apodemus spp*. If the striped field mouse (*A. agrarius*) could not be separated from the Sylvaemus group (*Apodemus* spp.), the individuals were categorised as 'unidentified *Apodemus*'. The sibling species of the genus Mus were determined by Macholán (1996) and Kryštufek and Macholán (1998). In addition, birds were identified by their skulls, bills, feet, pelvises and feathers (Kessler 2015), and frogs (Anura) by their skulls and bones of postcranial skeleton (Schaefer 1932). If major skeletal elements were missing, prey items were identified to the genus (small mammals, birds), the order (frogs) or the class (birds) level.

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 mammals (Klein & Cruz-Uribe 1984, McDowell & Medlin 2009, Torre *et al.* 2015, Tulis *et al.* 2015) and skulls, mandibles and long bones for birds, as well as skulls, remnants of ilium or frontoparietal bones for frogs. The percent frequency of occurrence (MNI%) was calculated for the total number of prey found in all pellets in the two different landscape categories. In addition, the ratio of insectivores to rodents as an environmental (Paspali *et al.* 2013) or trophic level index (TLI) (Prete *et al.* 2012) and the ratio of Microtinae/Murinae (MMR) were calculated. The first index is a suitable indication of possible biotope alteration (Mazzotti & Caramori 1998, Paspali *et al.* 2013), while the MMR is an environmental index suitable for the indication of intensively cultivated landscapes, like the agronomic value, which is a measure of the intensity of agricultural activity (Prete *et al.* 2012).

Different guilds of small mammals were determined by habitat requirements (Torre *et al.* 2015, Veselovský *et al.* 2017) to analyse the difference of small mammal assemblages between the two groups of landscapes. Four guilds were separated: 1) forest guild, composed of *Apodemus spp.* and *Myodes glareolus*; 2) open-land guild, which included *Microtus arvalis*, *M. agrestis*, *M. subterraneus*, *Mus spicilegus*, *Crocidora suaveolens* and *C. leucodon*; 3) urban guild, with *Mus musculus*, *Rattus norvegicus* and *R. rattus* as synanthropic species; 4) wetland guild, which included the water-tolerant species, like *Neomys fodiens*, *N. anomalus*, *Arvicola amphibius* and *Micromys minutus,* which prefer wet habitats. In addition, small mammals that were not included in either guild were considered in our analysis as a group of generalist species (Generalist spp. - *S. araneus*, *S. minutus*, *A. agrarius*).

Determination of land use categories – Landscape composition and agricultural intensity were assessed using Google Earth (2013). Landscape elements were analysed within a 1 km radius around each nest site because this results in an area that approximates the home range (3 km^2) of a Barn Owl in the breeding season (Taylor 2004, Bond *et al.* 2005, Hindmarch *et al.* 2012, Kross *et al.* 2016, Horváth *et al.* 2018). We identified the following land-use types and calculated the percentage of these categories: 1) agricultural field (an-

Table 1. Average value and ranges of the land-use types and the landscape features in the two different landscape types.

Landscape	Agricultural land (D-AL)		Semi-natural habitats (D-SNH)	
Land-use categories	mean±SE	range	mean±SE	range
Agricultural field (%)	69.18±1.85	61.88– 75.19	35.81±4.73	17.36–56.41
Wetland (%)	0.97±0.41	0.00–2.75	1.56±0.86	0.00–6.42
Forest (%)	10.30±2.67	1.67–18.95	36.42±5.00	15.83–58.88
Urban area (%)	11.52±2.03	4.31–21.96	11.57±2.21	2.59–19.44
Arable field (%)	77.22±1.79	69.24–82.80	50.45±5.37	23.99–63.57
Arable field (ha)*	8.04±2.26	0.43–16.99	14.64±2.13	6.63–21.05
Number of habitats	123.43±19.72	30.00–202.00	140.57±21.40	67.00–239.00

* the average size of arable fields

nual and perennial crops, orchards, vineyards); 2) wetland (including river banks, streams, artificial lakes, fishponds), 3) forest (all forest habitats) and 4) urban (all built-up surfaces) areas (Table 1). Using these land cover classifications, three more landscape features were

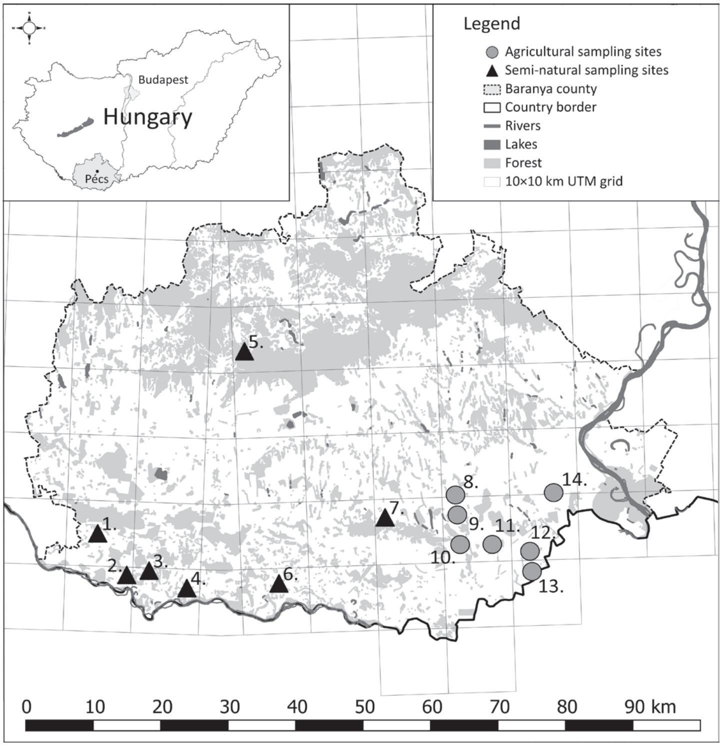

Fig. 1. Study area in the South-Transdanubian region, Hungary, showing the location of sampled nesting sites (settlements) and the two separated landscape types, indicated by different symbols

calculated according to Tuck *et al.* (2014), namely: (i) the proportion of arable fields; (ii) the number of habitats and (iii) the average size of arable fields in the landscape (ha) (Table 1). The proportion of arable fields is a measure of land-use intensity and the number of habitats represents landscape complexity, while the average size of arable fields reflects the extent of agricultural activity in a given landscape (Tuck *et al.* 2014). After the landscape digitalisation of the 1 km radius hunting area, the settlements were divided into two groups, semi-natural habitats (D-SNH) and agricultural lands (D-AL), depending on the cumulative percent distribution of wetland and forest, as well as agricultural fields. If the proportion of the agrarian patches in a given locality was higher than 50% and the cumulative proportion of wetland and forest habitats was lower than 20%, the hunting areas were classified as agricultural lands (D-AL). In the case of the semi-natural dominated habitats (D-SNH), the proportion of agricultural fields did not exceed 50%, while the cumulative proportion of wetlands and forests was higher than 20%. The two groups differed in the distribution of land use, which was supported by t-tests. The transformed percentage of arable fields ($t = 6.37$, $P < 0.001$) and agricultural areas ($t = 4.82$, $P < 0.001$) was significantly higher in areas dominated by agricultural lands, while the proportion of forest patches ($t = 4.68$, $P < 0.001$) was significantly higher in other landscape type.

Statistical analysis – Species richness, Shannon diversity (H) and Dominance index (D) were calculated by individual-based rarefaction to compare the food diversity of barn owls between the two landscape types. This analysis, as a powerful standardisation technique, is a suitable statistical method for estimating the number of species expected to be present in a random sample of individuals taken from any given collection (Gotelli & Colwell 2001). Rarefaction is a frequently used tool for defining community structure and comparing species richness and different community parameters based on the food composition of owls in space and time (Flikweert *et al.* 2007, Marti *et al.* 2007, Torre *et al.* 2015). Furthermore, it can be used for comparing different top predators (Arim & Jaksic 2005) or sampling methods (Torre *et al.* 2004, Rocha *et al.* 2011, Heisler *et al.* 2016). Rarefaction was performed by using the Ecosim 7.0 software (Gotelli & Entsminger 2001).

In the comparison of the small mammal assemblages, differences in the abundance of species and functional groups, as well as the proportion of identified land-use categories were investigated. All relative frequencies (abundances and land-use types) were arcsine square-root transformed prior to analyses. After the analysis of normality (Shapiro-Wilk test) (Zar 2010), independent *t* test was performed between two sample groups of the given parameter using Statistica 8.0 software (StatSoft, Bedford, UK). The means are presented as arithmetic mean±standard error. The statistical tests were considered significant at the level $P \leq 0.05$ as standard in all analyses (Sokal & Rohlf 1997).

Principal component analysis (PCA) based on the correlation matrix of arcsine square-root transformed variables was conducted to characterise land-use parameters and the abundance of small mammals at the levels of species and guilds among samples, the latter analysis including the two derived indices (trophic level index, ratio of Microtinae/Murinae). In the case of the species level PCA analysis, only the abundance of the Common Vole, as the most dominant prey species, other frequent alternative prey species (*Sorex araneus*, *Neomys fodiens*, *Crocidura leucodon*, *C. suaveolens*, *Apodemus agrarius*), and the abundance of the Sylvaemus group (*Apodemus* spp.) were taken into account. To assess the results of PCA, variable factor maps with a correlation circle were used for graphical interpretation. To analyse the relationship between landscape features and abundance of small mammals and guilds, multiple regression with forward stepwise selection was used based on PCA scores of predictors (land use – LPC) and response variables (abundance of species – SPC; guild level – GPC). We use the R^2 measure to assess the error because the R^2 statistic is commonly interpreted as the proportion of variance explained by the regression. The best candidate model was selected based on the highest significant (F-statistic) coefficient of determination (R^2). The relationships between the PCA scores of the response and predictor variables were evaluated based on standardised partial regression coefficients (β) and their t-tests. All PCA and multiple regression analyses were conducted separately for semi-natural habitats (D-SNH) and agricultural lands (D-AL). PCA analyses were performed in the statistical package R v. 3.3.2 (R Development Core Team 2016) and STATISTICA software version 12.0 (StatSoft 2013) was used for multiple regression.

RESULTS

Based on all samples from 14 localities, 34 animal taxa and 4,088 prey items were identified from the examined pellets (Table 2). Small mammals were the most frequent in the barn owl's diet in both investigated landscape types (D-AL: 99.45±0.24%; D-SNH: 98.66±0.39%). In the other prey categories, the importance of birds was the greatest and bird consumption of barn owls was more determinant in the landscape dominated by semi-natural habitats than in the case of agricultural land dominance (D-SNH: 1.02±0.33%; D-AL: 0.45±0.25%).

Based on rarefaction analysis, the accumulation of species richness was similar in the landscape dominated by semi-natural patches as in agriculture-dominated areas (Fig. 2). However, over 500 individuals, after including all sampled individuals, species richness was significantly higher in the semi-natural (D-SNH) than the agricultural (D-AL) landscape because the confi-

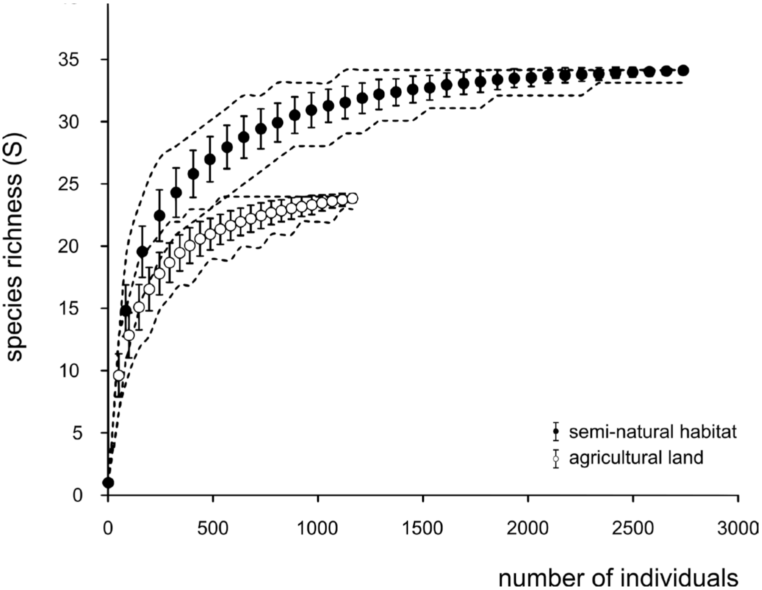

Fig. 2. Difference of estimated species richness of the Common Barn-owl's food composition between two landscape categories, based on individual rarefaction analysis

Table 2. Diet composition of the Common Barn-owl in the two different landscape types (MNI: minimum number of individuals, MNI%: percentage frequency of occurrence).

Landscape	agricultural land (D-AL)		semi-natural habitats (D-SNH)	
Taxa	MNI	MNI%	MNI	MNI%
Eulipotyphla	105	8.55	664	23.22
Talpidae	1	0.08	6	0.21
Talpa europaea	1	0.08	6	0.21
Soricidae	104	8.47	658	23.01
Sorex araneus	12	0.98	54	1.89
Sorex minutus	3	0.24	19	0.66
Neomys fodiens	2	0.16	31	1.08
Neomys anomalus	12	0.98	40	1.40
Neomys spp.	4	0.33	6	0.21
Crocidura suaveolens	38	3.09	251	8.78
Crocidura leucodon	33	2.69	257	8.99
Rodentia	1118	91.04	2153	75.28
Cricetidae	739	60.18	1101	38.50
Myodes glareolus	5	0.41	6	0.21
Microtus agrestis	4	0.33	32	1.12
Microtus arvalis	709	57.74	1018	35.59
Microtus subterraneus	8	0.65	12	0.42
Arvicola amphibius	13	1.06	33	1.15
Muridae	379	30.86	1040	36.36
Rattus norvegicus	1	0.08	10	0.35
Rattus rattus	0	0.00	4	0.14
Rattus spp.	7	0.57	12	0.42
Apodemus agrarius	69	5.62	335	11.71
Apodemus spp.	173	14.09	443	15.49
Apodemus indet.	69	5.62	104	3.64
Micromys minutus	9	0.73	41	1.43
Mus spicilegus	14	1.14	19	0.66
Mus musculus	6	0.49	35	1.22
Mus spp.	31	2.52	37	1.29
Gliridae	0	0.00	12	0.42
Muscardinus avellanarius	0	0.00	12	0.42
Other prey	5	0.41	43	1.50
Mammals	0	0.00	3	0.10
Birds	4	0.33	27	0.94
Amphibians	1	0.08	10	0.35
Insects	0	0.00	3	0.10

Table 3. Average value and ranges of the prey taxa, guilds and indices in the two different landscape types.

Landscape	agricultural land (D-AL)		semi-natural habitats (D-SNH)	
Variables	mean (%)±SE	range (%)	mean (%)±SE	range (%)
		Species level		
S. araneus	0.70±0.37	0.00 – 2.13	1.61±0.55	0.00 – 4.00
C. suaveolens	2.48±0.63	0.74 – 5.07	7.21±1.48	1.33 – 12.88
C. leucodon	2.62±0.79	0.00 – 6.57	7.66±1.65	1.33 – 12.47
N. fodiens	0.23±0.15	0.00 – 0.81	1.33±0.70	0.00 – 5.34
M. arvalis	55.27±5.59	35.43 – 76.42	31.76±4.61	13.11 – 48.77
A. agrarius	5.34±1.25	0.81 – 9.15	11.50±1.76	6.24 – 20.05
Apodemus spp.	15.59±2.98	7.32 – 25.42	20.56±4.46	10.18 – 38.67
		Higher taxa		
Soricidae	8.01±1.69	4.24 – 15.75	20.13±3.48	2.67 – 33.15
Arvicolinae	58.21±5.12	36.22 – 77.24	34.95±4.01	20.00 – 50.25
Murinae	33.23±4.60	17.89 – 47.24	43.03±6.87	27.09 – 77.33
		Guild level		
Forest guild	23.06±3.72	12.04 – 36.43	27.31±6.62	14.14 – 58.11
Open-land guild	64.53±6.03	44.92 – 84.75	49.84±7.15	22.97 – 71.72
Urban guild	1.47±0.93	0.00 – 6.78	2.08±0.84	0.00 – 5.56
Wetland guild	4.32±1.62	0.00 – 10.17	6.71±1.69	1.55 – 16.00
Generalist sp.	6.62±1.62	0.85 – 11.89	14.06±1.95	7.93 – 23.54
		Indices		
Trophic level index	0.09±0.02	0.04 – 0.19	0.27±0.06	0.03 – 0.52
Microtinae/Murinae	2.15±0.49	0.77 – 4.32	0.99±0.21	0.26 – 1.85

dence intervals of estimated values did not overlap in this range of rarefaction curves. The increase of species richness showed that it was stabilised much earlier in semi-natural habitats than in the other landscape type where species richness continued to increase until the end of the rarefaction curve (Fig. 2). According to the generated values and the lack of overlap of the 95% confidence intervals, the average diversity of the barn owl's diet was significantly higher in the landscape dominated by semi-natural habitats (D-SNH: H = 2.21 95% *CI* = 2.20 to 2.22; D-AL: H = 1.65 95% *CI* = 1.63 to 1.67), while the estimation of dominance by the rarefaction analysis yielded the opposite result. The average value of the Dominance index was higher in the landscape of D-AL (D = 0.58 95% *CI* = 0.57 to 0.58) than in D-SNH (D = 0.36 95% *CI* = 0.35 to 0.36).

The Common Vole was the most numerous prey in both landscape types (Table 3), however, the abundance of this predominant species was significantly higher in the case of agricultural lands ($t = 3.2$, $P < 0.01$). In addition, the *Apodemus* spp., as alternative prey taxa, was represented in the pellet samples with high frequencies in both land-use types, but the abundance of this prey group was not significantly different ($t = 0.93$, *n. s.*). At the species level, among the other five priority species, the striped field mouse had greater frequency in the samples of two landscapes and its abundance in the diet of barn owl was significantly higher in D-SNH ($t = 2.88$, $P < 0.05$). Differences in abundance were detected in the case of the two *Crocidura* species: *C. suaveolens* and *C. leucodon*. The frequency of these species was significantly higher in D-SNH (*C. suaveolens*: $t = 2.96$, $P < 0.05$; *C. leucodon*: $t = 2.65$, $P < 0.05$). In contrast, the distribution of the two red-toothed shrews' abundance was not significantly different between the two investigated landscape groups: *S. araneus* ($t = 1.55$, *n. s.*) and *N. fodiens* ($t = 2.14$, *n. s.*). In the case of the three main small mammal taxa (shrews, voles, mice), the abundance of shrews was significantly higher in the landscape dominated by semi-natural habitats ($t = 2.85$, $P < 0.05$), while the abundance of voles was significantly higher in the other landscape type ($t = 3.53$, $P < 0.01$). In contrast, the frequency of mice was not significantly different between the two landscapes ($t = 1.21$, *n. s.*). At the guild level, the frequency of generalist species was significantly higher in landscapes dominated by semi-natural habitats ($t = 2.90$, $P < 0.05$), while the abundance distribution of the other guilds was not significantly different ($t = 0.51 – 1.61$, *n. s.*). In addition, the trophic level index was significantly higher in D-SNH ($t = 3.09$, $P < 0.01$), however, the ratio of Microtinae/Murinae was not significantly different between the two groups of investigated sampling sites ($t = 2.14$, *n. s.*).

In case of agricultural land dominance, the PCA analysis of land use categories showed that the first three axes explained 86.91% of the total variance, from which PC1, PC2 and PC3 accounted for 46.85%, 22.49% and 17.57%, respectively (eigenvalue of PC1 = 3.28, PC2 = 1.57 and PC3 = 1.23) at the landscape level. The first component was related positively to forest patches and the size of arable fields while negatively to the number of habitats. The second component was associated negatively with the proportion of arable fields and the amount of habitats but positively with the proportion of the wetland habitats. The third PCA score correlated negatively with the urban areas and positively with agricultural fields (Table 4). According to the variables factor map, the discrimination of sampling sites along PC1 was determined by a decrease in forest proportion and an increase in the quantity of arable fields (Fig. 3).

At the species level in agricultural lands, PC1, PC2 and PC3 accounted for 38.43%, 26.44% and 16.20% (eigenvalue of PC1 = 2.69, PC2 = 1.85 and PC3 = 1.13), thus, the first three axes explained 81.06% of the total variance. The first axis was positively related to the abundance of *C. suaveolens* and *M. arvalis* while negatively correlated with the abundance of *Apodemus* species. There was a positive relationship between the second component and the propor-

Table 4. The principal component values of predictor (land use) and two response variables (species and guild level) based on the three PCA axes in case of the agricultural lands (D-AL).

Variables	Axis 1	Axis 2	Axis 3
Landscape features			
Agricultural field	0.2853	**–0.4839**	**0.5015**
Wetland	0.2208	**0.4566**	0.3563
Forest	**–0.4817**	0.3353	0.1900
Urban	0.3043	-0.2522	**–0.6554**
Arable fields	0.3746	0.3517	–0.0079
Arable fields (ha)	**0.4920**	–0.1135	0.3275
Number of habitats	**–0.4920**	**–0.4947**	0.2205
Species			
S. araneus	0.0004	**0.5863**	0.0354
N. fodiens	0.1696	–0.3083	**–0.6875**
C. suaveolens	**0.4061**	0.3255	0.1784
C. leucodon	0.3412	0.2397	**–0.5887**
M. arvalis	**0.5279**	–0.1124	0.3330
A. agrarius	–0.2665	**0.6119**	–0.1889
Apodemus spp.	**–0.5832**	–0.1039	–0.0324
Guilds/indices			
Forest guild	**0.4639**	–0.3252	-0.0705
Open-land guild	**–0.5145**	0.0823	0.0407
Urban guild	0.184	**0.5952**	0.0643
Wetland guild	0.355	–0.2359	**0.6339**
Generalist species	0.2973	0.3678	**–0.5660**
TLI	0.1314	**0.5839**	**0.4921**
MMR	**–0.5046**	0.0369	0.1578

Values above 0.4 in bold.

tion of *S. araneus* and *A. agrarius*. The third PCA axis was negatively associated with the abundance of *N. fodiens* and *C. leucodon* (Table 4). The sampling sites were also discriminated by PC1 and PC2 axis. In case of the first axis, the discrimination was determined by the increase of the abundance of the *Crocidura* species and Common vole (*M. arvalis*) and the decrease of the proportion of *Apodemus* spp., while the discrimination along the second axis was determined by the *A. agrarius*, *S. araneus* – *N. fodiens* gradient (Fig. 3). The multiple regression analysis did not result in a significant relationship between the PCA scores of the land use and of the prey species.

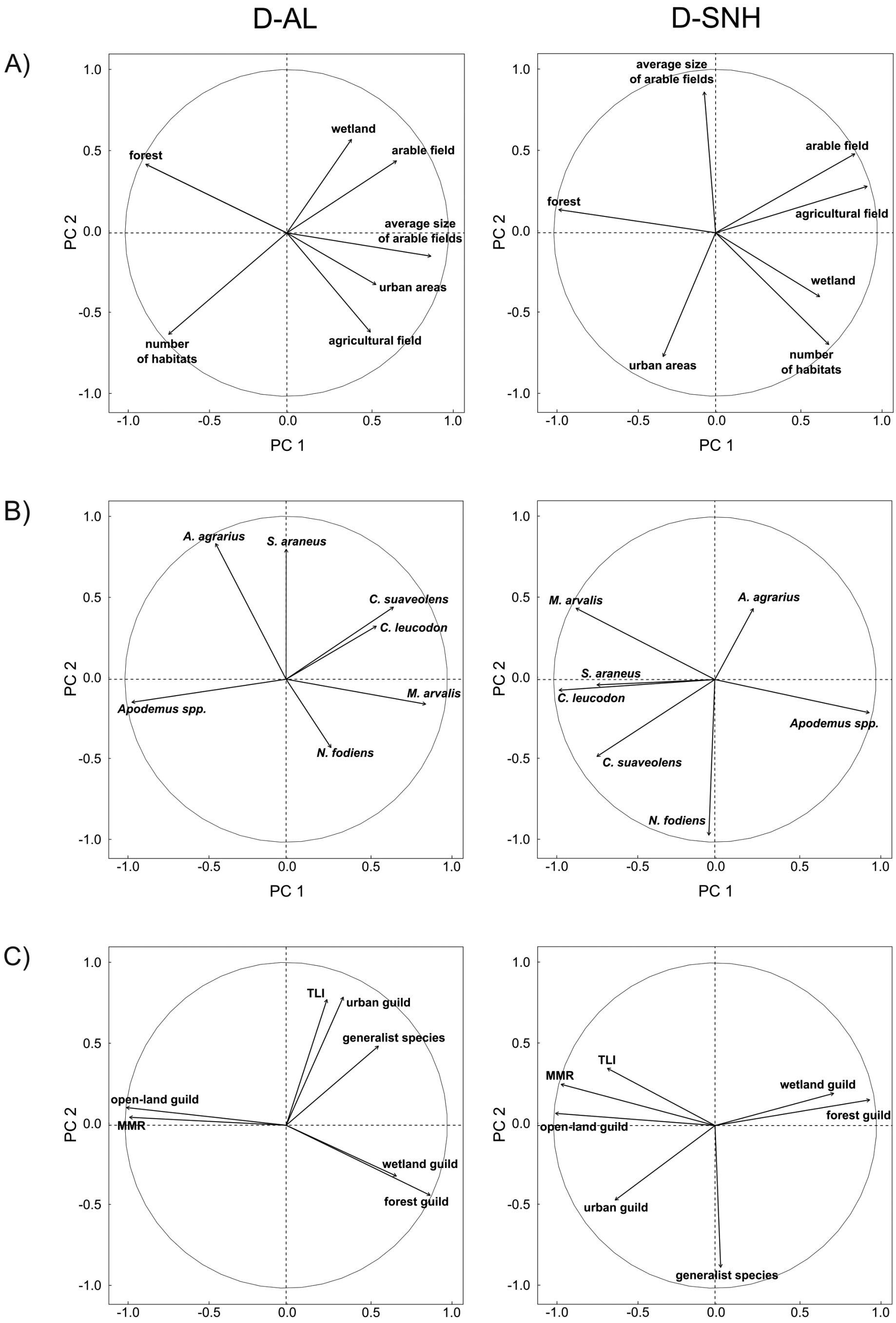

Fig. 3. Variables factor maps at land-use level (A), species level (B) and guild level (C) in case of the agricultural lands (D-AL) and the semi-natural habitats (D-SNH)

The PCA analysis of guilds in agrarian lands showed that the first three axes explained 92.97% of the total variance, from which PC1, PC2 and PC3 accounted for 52.99%, 24.98% and 15.00% (eigenvalue of PC1 = 3.71, PC2 = 1.75 and PC3 = 1.05). The first component was associated positively with the forest guild while negatively with the open-land guild and the Microtinae/Murinae ratio. The second component was positively related to the urban guild and the trophic level index. The third PCA axis correlated negatively with the generalist species and positively with the wetland guild and the trophic level index (Table 4). According to the variables factor map, the discrimination of sampling sites along PC1 was determined by a decrease in the proportion of the open-land guild and the Microtinae/Murinae ratio and an increase in the abundance of the wetland and forest guild (Fig. 3). The multiple regression analysis using PCA scores resulted in a significant regression model for only GPC3 ($R^2 = 0.91$; F = 10.57, $P = 0.042$). The final model included all three PCA scores from the analysis of land use, however, only LPC1 had a significant effect, indicating a positive relationship between GPC3 and LPC1 ($\beta = 0.74 \pm 0.17$, $t = 4.33$, $P = 0.023$). According to the results of PCA, there is a negative relationship between the forest areas and the first axis of the landscape features PCA, and likewise, the abundance of the generalist guild and the third axis of the guild level PCA. The obtained positive slope (standardised partial regression coefficient) between GPC3 and LPC1 scores proves that the proportion of forests in the hunting area had a positive effect on the abundance of the generalist species. The positive regression between GPC3 and LPC1 can also be interpreted as a relationship between the change in the size of arable fields and the values of the Insectivora / Rodentia ratio (TLI), so our results suggest that the size of the cultivated area had a positive effect on the trophic level index.

Considering the landscapes with semi-natural habitat dominance, the PCA analysis of land use categories showed that the first three axes explained 95.42% of the total variance, from which PC1, PC2 and PC3 accounted for 51.02%, 32.46% and 11.94%, respectively (eigenvalue of PC1 = 0.00, PC2 = 0.00 and PC3 = 0.00). According to the results of PCA, the first component was positively related to arable field and agricultural land while negatively related to forest patches. The second component was associated negatively with the proportion of urban area and the number of habitats but positively with the size of arable fields. The third PCA score positively correlated with the proportion of wetlands, urban areas and the size of arable field (Table 5). As shown on the variables factor map, the discrimination of sampling sites along PC1 was determined by the decrease in forest area and the increase in arable and agricultural fields (Fig. 3).

At the species level, PC1, PC2 and PC3 accounted for 53.12%, 22.44% and 15.25% (eigenvalue of PC1 = 3.72, PC2 = 1.57 and PC3 = 1.07), thus, the first three axes explained 90.82% of the total variance. The first axis was positively

Table 5. The principal component values of the variables based on the two PCA axes of predictor (land use) and two response variable (species and guild level) in case of the semi-natural habitats (D-SNH).

Variables	Axis 1	Axis 2	Axis 3
Landscape features			
Agricultural field	**0.4957**	0.1885	–0.2054
Wetland	0.3404	–0.2597	**0.5954**
Forest	**–0.5130**	0.0938	–0.0547
Urban	–0.1717	**–0.5027**	**0.4954**
Arable fields	**0.4554**	0.3206	0.1243
Arable fields (ha)	–0.0371	**0.5716**	**0.5406**
Number of habitats	0.3701	**–0.4539**	–0.2173
Species			
S. araneus	–0.3792	–0.0263	**–0.4216**
N. fodiens	–0.0194	**–0.7640**	–0.1911
C. suaveolens	–0.3792	–0.3774	–0.2249
C. leucodon	**–0.5010**	–0.0524	0.1691
M. arvalis	**–0.4465**	0.3501	0.1645
A. agrarius	0.1236	0.3484	**–0.8240**
Apodemus spp.	**0.4965**	-0.1629	0.0225
Guilds/indices			
Forest guild	**0.4690**	0.1423	–0.2117
Open-land guild	**–0.4838**	0.0673	0.0467
Urban guild	–0.3028	**–0.4136**	–0.2637
Wetland guild	0.3599	0.1786	**0.5324**
Generalist species	0.0171	**–0.7869**	0.4479
TLI	–0.3264	0.3173	**0.6241**
MMR	**–0.4668**	0.2286	–0.0995

Values above 0.4 in bold.

related to the abundance of *Apodemus spp.* while negatively correlated with the abundance of *C. leucodon* and *M. arvalis*. There was a negative relationship between the second component and the proportion of *N. fodiens*. The third PCA axis was negatively associated with the abundance of *S. araneus* and *A. agrarius* (Table 5). In the case of the first axis, the discrimination of sample sites was determined by the increase of the abundance of *Apodemus spp.* and the decrease of the proportion of *S. araneus* and *C. leucodon* (Fig. 3). Based on the multiple regression analysis, there was a significant result only for SPC3, where the best model included LPC2 and LPC3 ($R^2 = 0.90$; F = 18.03, $P = 0.009$). In case of LPC2, the model demonstrated a negative impact on SPC3 ($\beta = -0.74 \pm 0.16$, t = –4.67, $P = 0.009$), in contrast, there was a positive relationship between LPC3 and SPC3 ($\beta = 0.60 \pm 0.16$, t = 3.77, $P = 0.019$). The negative standardised partial regression coefficient for LPC2 demonstrates that the lower proportion of urban area in the hunting territory positively influenced the quantity of *S. araneus* and *A. agrarius* in the diet of owls. Based on this negative regression, the number of habitats had a positive impact on the proportion of both species. In addition, we also found a positive relationship between the size of the arable fields and the abundance of these two species. In the case of LPC3, however, as the proportion of urban areas and size of arable fields increases, the abundance of these two generalist species decreases within the small mammal assemblage.

The principal component analysis of guilds in the semi-natural habitat dominated land showed that the first three axes explained 91.11% of the total variance, from which PC1, PC2 and PC3 accounted for 59.53%, 17.54% and 14.04% (eigenvalue of PC1 = 4.17, PC2 = 1.23 and PC3 = 0.98). The first component was positively related to the forest guild while negatively related to the open-land guild and the Microtinae/Murinae ratio. The second component was negatively associated with the abundance of urban guild and generalist species. There was a positive relationship between the third PCA axis and the proportion of wetland guild and generalist species, as well as the value of the trophic level index (Table 5). Based on the variables factor map, the discrimination of sampling localities along PC1 was determined by a decrease in the abundance of the open-land guild as well as the values of the Microtinae/Murinae ratio and trophic level index, and an increase in the proportion of the wetland and the forest guild (Fig. 3). The multiple regression analysis revealed a significant relationship between the PCA scores, but only in the case of GPC2 ($R^2 = 0.91$; F = 7.89, $P = 0.041$). The best model included LPC2 and LPC3 from the PCA of land use, however, only LPC2 score had a significant effect, which had a negative impact on GPC2 ($\beta = -0.86 \pm 0.23$, t = –3.83, $P < 0.05$). Based on the obtained negative slope, there is a negative relationship between the proportion of urban areas and the abundance of generalist species and the synantrop guild. Similarly, the number of habitats also had a negative impact on these response variables. In the case of the size of the arable fields, we proved the opposite effect.

DISCUSSION

In this study, we analysed small mammal assemblages with Common Barn-owl pellet analysis, comparing landscapes dominated by semi-natural and agricultural habitat.

Despite that the food habits of barn owls are very diverse in different geographical regions due to the consumption of many potential alternative preys (HERRERA 1974, ROMANO *et al.* 2020, JANŽEKOVIČ & KLENOVŠEK 2020), we found that small mammals were the primary, eudominant (98%<) prey group in the two investigated landscapes. This result confirmed that the Common Barn-owl can be characterised as an opportunistic and small mammal specialist owl (MARTI 1988, DURANT *et al.* 2013, ROMANO *et al.* 2020) and is consistent with similar studies which evaluate the food consumption considering different landscapes and land use (CHARTER *et al.* 2009, MILCHEV *et al.* 2015, HINDMARCH & ELLIOT 2015, HORVÁTH *et al.* 2018). Different bird species constitute a negligible part of the Common Barn-owls' diet (MILCHEV 2015, ROULIN 2015, SZÉP *et al.* 2017, MOYSI *et al.* 2018), which we also supported in our study because this prey group accounted for less than 2% of the food composition of owls. Bird consumption was lower in agriculture-dominated habitats, which may be related to the significant decline in farmland bird populations across Europe in recent years (VÄISÄNEN *et al.* 2007, ROULIN 2015).

The rarefaction analysis showed that species richness and average diversity of the barn owl's diet was significantly higher in semi-natural (D-SNH) than agricultural (D-AL) landscapes. These results are in accordance with other studies which demonstrated that the loss of semi-natural habitats and rapid agricultural intensification caused a dietary shift of barn owls, measured by the reduction in small mammal diversity and changes in species dominance (MILLÁN de la Pena *et al.* 2003, HODORA & POGGIO 2016, BATTISTI *et al.* 2020). In contrast to our results, some studies did not find a significant negative effect between agricultural intensification and species richness (MILLÁN DE LA PENA *et al.* 2003, MICHEL *et al.* 2006). Similar to other pellet analyses (BALESTRIERI *et al.* 2019, BATTISTI *et al.* 2020), our results also confirmed the general relationship, namely that habitat loss and landscape transformation with agricultural intensification and anthropisation lead to a decline in species diversity (KREBS *et al.* 1999, ROBINSON & SUTHERLAND 2002, TSCHARNTKE *et al.* 2005, FAHRIG *et al.* 2011). The result of diversity and dominance estimation between the two considered landscapes are consistent with the study of BATTISTI *et al.* (2020), which reported a simplified community structure with low diversity and high dominance depending on human-induced landscape changes.

Considering the small mammals' abundance distribution at the species level and their association to landscape features, the Common Vole was the most hunted prey, which was also described in several studies (e.g. BERNARD *et al.* 2010, FREY *et al.* 2011, VESELOVSKY *et al.* 2017, HORVÁTH *et al.* 2018). In both landscape types, this species accounted as the main predominant prey in the barn owl's food composition and appeared in a higher proportion in the landscape dominated by agricultural areas, reflecting that the Common Vole is a typical species of open lowlands and farmlands (DELATTRE *et al.* 1996, Heroldová *et al.* 2007, Arlettaz *et al.* 2010, Fischer *et al.* 2011). Although this rodent was the main prey of barn owls in both areas, the significant difference in its abundance showed that this species was a suitable indicator to demonstrate the assumed difference in landscape-dependent food consumption of the barn owls between two landscapes. Similar results were reported in other studies as a demonstration that the abundance of the Common Vole increases depending on the agricultural intensification (Millán de la Pena *et al.* 2003), others pointed out the relationship between the proportion of intensive land use and the consumption rate of the Common Vole by Barn-owls (Veselovsky *et al.* 2017). This result was partially confirmed by the PCA variables factor map in the case of the agricultural landscape (D-AL), the vectors of the Common vole and the average size of arable field point in the same direction, which suggests that there is a positive relationship between the two variables. However, this relationship is not supported by the multiple regression analysis because the abundance of the Common Vole correlates with the PC1 axis, but the final model includes the SPC2 scores.

Among murid rodents, *Apodemus* spp. were the most significant and their importance as an alternative prey was already described in several studies (Pezzo & Morimando 1995, Bontzorolos *et al.* 2005, Rodrígez & Peris 2007, Horváth *et al.* 2020). However, their relative frequency did not differ significantly between the two landscape types because the Wood Mouse and the Yellow-Necked Wood Mouse are not only associated with forests and forest edges but also occur in grasslands, hedgerows, field margins and agricultural areas (Fischer *et al.* 2011, Torre *et al.* 2015, Balestrieri *et al.* 2017). Some previous studies demonstrated that *Apodemus* species also inhabit agricultural landscapes (Millán de la Pena *et al.* 2003, Heroldová *et al.* 2007, Fischer & Schröder 2014) because they can successfully colonise crop fields (Bryja & Zukal 2000, Tattersall *et al.* 2001), especially during summer and autumn (Ouin *et al.* 2000, Janova & Heroldová 2016), and these granivorous mouse species can become agricultural pests (Heroldová *et al.* 2004). Based on the multiple regression, in the case of this prey group, we could not detect similar results in any of the landscape types. However, the land use and species variables factor map showed that *Apodemus* spp. and arable fields were determined by the PC1 axis, and the length and direction of these two PCA vectors in the semi-natural dominated landscape indicate a weak association between the two variables. The Striped Field Mouse is a constant but non-dominant prey species (Horváth *et al.* 2005, Purger 2014, Szép *et al.* 2017), which, as a generalist small mammal, occurs in almost all habitat types such as forests, meadows and urban areas (e.g. Kozakiewicz *et al.* 1999, Łopucki *et al.* 2013, Pieniążek *et al.* 2017, Benedek & Sîrbu 2018), however, in agricultural landscapes, it prefers mainly the margins and hedgerows (Fischer & Schröder 2014). In these habitats, due to the higher vegetation cover, it is less accessible to predators (Arlettaz *et al.* 2010), so the Striped Field Mouse is not as common as other *Apodemus* species in the Common Barn-owls' food composition. In the Slovakian Danube Lowland, this rodent did not occur in the diet of barn owls in an intensively used farmland (Veselovský *et al.* 2017), despite being a widespread species in this country. Because it avoids intensively cultivated areas and inhabits only field margins and hedgerows, we showed a higher proportion in the case of semi-natural habitats despite its lower accessibility, which is in accordance with other studies (Amori *et al.* 2008, Gentili *et al.* 2014). In the case of agrarian landscapes, the multiple regression analysis confirmed a positive relationship between the proportion of forest habitats and the relative abundance of generalist species. The Striped Field Mouse (*A. agrarius*) plays an important role in this, which, as a generalist species, inhabits the forest strips and edges with high density, from which it occupies the inner areas of the forests with density-dependent dispersion (Horváth *et al.* 1996). The result of multiple regression analysis in the case of semi-natural dominated landscapes supported the fact that the Striped Field Mouse avoids intensively cultivated agrarian lands because the size of arable fields had a negative impact on the abundance of this species. Although it has been reported in several studies that the Striped Field Mouse also appears in settlements, the multiple regression is not consistent with this because its frequency decreases as urban areas increase. These relationships were also supported by the guild-level analysis.

Considering the Microtinae/Murinae ratio (MMR) as an environmental index with an agronomic value (Contoli 1980), we did not find a significant difference between the two landscape types. Compared to other studies, the range of this index (0.77 – 4.32) was similar in the present study to what was reported earlier in central Italy (see Prete *et al.* 2012). However, the minimum value of MMR was higher than what was calculated (0.61) by Prete *et al.* (2012).

In the case of insectivorous species, the abundance of the Bicoloured White-toothed Shrew (*Crocidura leucodon*) and the Lesser White-toothed Shrew (*C. suaveolens*) was significantly higher in semi-natural habitats. These species occur mainly in open areas and cultivated landscapes (Varuzza *et al.* 2001) but also inhabit drier semi-natural habitats such as abandoned areas, hedges, meadows, shrubs, and forest edges (Anděra & Horáček 2005, Suchomel & Heroldová 2007, Heroldová *et al.* 2007, Poláčiková 2010). Our result is in accordance with the findings of a study in Croatia (Baranja), which also showed that *C. leucodon* was associated to dry semi-natural habitats (Szép *et al.* 2018). In contrast, the abundance of the two red-toothed shrews was not significantly different between the two investigated landscape types. The Common shrew (*Sorex araneus*), as a generalist species, occurs in various habitats (Tattersall *et al.* 2002, Wang & Grimm 2007, Sundell *et al.* 2012, Schlinkert *et al.* 2016) and generally inhabits different forests as well (Rychlik 2000, Baláž & Ambros 2005, Zbytovský & Anděra 2011). Our results are not consistent with these studies, which may be because we showed a very low frequency of the Common Shrew in both landscape types, therefore, we did not detect a difference between the agricultural and semi-natural habitat types. The relative abundance of *S. araneus* was lower than the expected value. This result suggests that the availability of this shrew species is lower for barn owls than what was reported in previous studies (Love *et al.* 2000, Torre *et al.* 2015, Milana *et al.* 2018, Balestrieri *et al.* 2019, Battisti *et al.* 2020). The decline of this insectivorous species can be explained by the human-induced landscape modification (Love *et al.* 2000, Balestrieri *et al.* 2019) and the determinant role of climate change (Szpunar *et al.* 2008, Torre *et al.* 2015). The Water Shrew (*Neomys fodiens*) is present in landscapes only where wetlands are also present; it lives along banks of rivers, streams and ditches and also occurs in swamps and marshlands (Greenwood *et al.* 2002, Burel *et al.* 2004). Furthermore, Milchev (2015) showed a positive relationship between the localities with wetland habitats and the proportion of the Miller's Water Shrew (*Neomys anomalus*) in the barn owls' food composition. However, similarly to the Common Shrew, water shrews were also detected at a very low frequency in the pellet samples, so we could not confirm that it occurs at a significantly higher frequency in semi-natural habitats than in agricultural areas. Mechanical agriculture and the application of chemical products resulted in the simplification of the landscape matrix and the degradation of habitat quality, which negatively affects trophic levels (TL) (Contoli 1980, Balestrieri *et al.* 2019, Battisti *et al.* 2020). Thus, the value of TL is an appropriate indicator of the negative impact of agricultural intensification and landscape homogenisation. Our result is in accordance with these studies because, in the case of semi-natural habitats, the trophic level index was significantly higher than in the agricultural landscapes. Paspali *et al.* (2013) obtained a similar result, as they found that the value of the TL index was higher in a mosaic landscape than in intensively cultivated agricultural fields. Due to anthropisation, the decrease in the number of habitats, as a measure of landscape heterogeneity, causes a decline in the abundance of shrews (Harris *et al.* 1995, Battersby 2005, Michel *et al.* 2006, Balestrieri *et al.* 2019). This was partially confirmed by the multiple regression analysis because the number of habitats had a positive impact on the proportion of *S. araneus* in semi-natural dominated landscapes. In the case of agricultural lands, the multiple regression analysis showed that the increase in the size of the arable fields had a positive effect on the change in the values of the trophic level index. This can be explained by the fact that the drought-tolerant *Crocidura* species associated with agricultural areas are rather predominant in the diet of the Common Barn-owl in the investigated area. Thus, due to the higher occurrence of *Crocidura* species, the value of the trophic level index is also higher in these areas.

At the guild level, the frequency of generalist species was significantly higher in semi-natural habitats. These results are not in accordance with previous studies which described that the occurrence of these species is not affected by habitat type because semi-natural habitats are occupied in the same way as agrarian areas. Using a trapping method, SCHLINKERT *et al.* (2016) showed that the abundance of the habitat generalist Common Shrew was not affected by either the habitat type or the isolation of the hedges. Based on pellet analysis, TORRE *et al.* (2015) demonstrated that habitat generalist species were detected at very low frequency or were not present at all in the area, so they could not show whether habitat type and its change affected the amount of these species. According to the multiple regression analysis, as described above, we showed a positive relationship between the proportion of generalist species and forest habitats. This is in accordance with what was described in several studies, namely that generalist species, such as the Striped Field Mouse and the Common Shrew, occur in almost all types of habitats, but they generally live in different forests, forest patches and hedgerows (KOZAKIEWICZ *et al.* 1999, TATTERSALL *et al.* 2002, FISCHER & SCHRÖDER 2014). In contrast, the abundance of other guilds was not significantly different. In the case of the wetland guild and synantropic species, a similarly low frequency was observed in the food composition of Barn-owls in both landscape types. In the case of typical wetland inhabitants, MILCHEV (2015) has shown that more wetlands in owls' hunting areas lead to higher consumption of these species. The proportion of wetlands in our investigated area was very low, which explains the negligible consumption of the wetland species. The examined localities in this study are smaller villages, so the proportion of urban areas is also low. For this reason, synanthropic species accounted for only a small percentage of the barn owls' food composition. HINDMARCH and ELLIOT (2015) demonstrated that the consumption of rats increased significantly with urbanisation, however, due to the negligible consumption of house mice, this relationship was not detected in the case of this species. The Common Barn-owl does not hunt in forests (MILLÁN DE LA PEÑA *et al.* 2003), only in their edges, so it hunts only a low quantity of typical forest species such as the bank vole and dormice. As mentioned above, the Wood Mouse and the Yellow-necked Wood Mouse, which the owl consumes in higher proportion as alternative prey, are not only associated with woodlands but also occur in open areas. Thus, in the case of the forest guild, we could not detect a significant difference between the two landscape types because this guild is mainly represented by these two species.

We did not prove our hypothesis that due to the larger open areas in the agriculture-dominated landscape, open-guild species are consumed in a significantly higher proportion by the Barn-owls, despite that Common Barn-owls hunt mostly in open areas (SNOW *et al.* 1998, MILLÁN DE LA PEÑA *et al.*

2003) and the food composition is generally dominated by these species such as *Crocidura*, *Microtus* and *Mus* spp. (Miltschev *et al.* 2004) due to their optimal abundance, detectability and accessibility.

In conclusion, we need to focus more on the importance of decreasing semi-natural habitats and on using robust sampling design and statistical methods testing the usefulness of the Common barn-owl pellet analysis in the assessment of changes in small mammal assemblages to understand the impact of anthropogenic interventions and land-use modification, as well as the compensatory role of the semi-natural habitats.

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