ORNIS HUNGARICA

ISSN 1215-1610

JOURNAL OF THE BIRDLIFE HUNGARY

BirdLife INTERNATIONAL

Ornis Hungarica 2020. 28(2): 1–18.
DOI: 10.2478/orhu-2020-0013

Winter diet and roosting site use of urban roosting Long-eared Owls *(Asio otus)*, and the change in the species' population size in Southeast Hungary[×]

László Bozó[1]*, Tamás Rutkai[2], András István Csathó[3] & Erna Bozóné Borbáth[4]

[×] Presented at 2nd Hungarian Owl Research Conference held in Pécs on 11th September 2020.

Received: September 16, 2020 – Revised: October 21, 2020 – Accepted: October 27, 2020

Bozó, L., Rutkai, T., Csathó, A. I. & Bozóné Borbáth, E. 2020. Winter diet and roosting site use of urban roosting Long-eared Owls *(Asio otus)*, and the change in the species' population size in Southeast Hungary. – Ornis Hungarica 28(2): 1–18. DOI: 10.2478/orhu-2020-0013

Abstract The Long-eared Owl *(Asio otus)* was chosen as the bird of the year in Hungary by BirdLife Hungary in 2020 to pay more attention to this species. In the present study, we analysed the data collected on the food, changes in the population and the use of the roosting sites of the owls wintering Southeast-Hungary. A total of 4,683 pellets were collected in four winter seasons between 2016 and 2020, of which 5,265 prey animals were identified. We counted the individuals roosting in the winter roosting sites, and from their maximum number we estimated the local population change of the species as well as the success of the breeding. For this, we also used roadkill data from the nearby town, Battonya.

The diet of Long-eared Owls in the study area was similar to that observed in other parts of the Carpathian Basin. The smaller differences were mainly due to the different geographical distribution of different prey species. We also identified some species previously having no or very few data, thus we confirmed their stable presence in the area. Different weather factors within the season did not effect owls' diet. The most varied diet was found in the warmest, least snowy winter. Comparing the feeding data with the data from the 1960s and 1970s, it can be seen that the proportion of preys changed significantly. The proportion of House/Steppe Mice decreased by an order of magnitude, while that of rats increased by the same amount over time. The most likely reasons for this may be changes in agricultural cultivation or local demographic conditions (depopulation). In the 2018/19 season, the proportion of Common Vole in the pellets was much higher than in any other years, suggesting this year's gradation of the species. The pellets collected in different roosting sites close to each other typically had the same proportions of prey animals.

The maximum number of birds observed at the roosting sites did not correlate with the weather of the given season, but was probably related to the effectiveness of the previous breeding season.

The population of the species decreased compared to the early 2000's based on the number of roosting individuals. This may be due to a decline in crow populations. It should be noted, however, that according to both the roadkills in Battonya and the maximum number of the roosting individuals in Kevermes, this drastic decline came to a halt in 2010s.

Keywords: bird ringing, *Microtus arvalis*, *Mus spicilegus*, owl pellets, roadkills

Összefoglalás Az erdei fülesbaglyot *(Asio otus)* a Magyar Madártani és Természetvédelmi Egyesület 2020-ban az év madarának választotta, hogy nagyobb figyelem irányuljon erre a fajra. Ebben a cikkben a délkelet-magyarországi Kevermesen telelő erdei fülesbaglyok táplálékáról, állományváltozásáról, illetve nappalozóhely-használatáról gyűjtött adatokat dolgoztuk fel. A táplálkozástani vizsgálatokhoz összesen 4683 köpetet gyűjtöttünk négy téli szezonban 2016 és 2020 között, amelyekből 5265 zsákmányállat került elő. Megszámoltuk a nappalozóhelyeken gyülekező egyedeket, amelyeknek a maximális számából következtettünk a faj helyi állományára, illetve a költés sikerességére is. Ehhez felhasználtunk a közeli Battonya településről származó elütési adatokat is.

Az erdei fülesbaglyok tápláléka a vizsgálati területen hasonló a Kárpát-medence más részein tapasztaltakhoz. A kisebb eltérések elsősorban a különböző zsákmányállat-fajok Kárpát-medencén belüli elterjedési viszonyai miatt adódtak. A köpetekben kimutattunk néhány olyan fajt is, amelyeknek eddig nem, vagy csak nagyon kevés adata volt a területen, és ezáltal igazolást nyert kisszámú, de stabil jelenlétük a térségben. A különböző időjárási tényezők a szezonon belül nem voltak hatással a baglyok táplálékára. A legváltozatosabb táplálékspektrum a legmelegebb, legkevésbé havas télen gyűjtött köpetekben volt. A táplálkozástani eredményeket összehasonlítva az 50–60 évvel korábbi adatokkal megállapítható, hogy a zsákmányállatok aránya szignifikánsan változott, így a güzü/házi egér aránya egy nagyságrenddel csökkent, míg a vándorpatkányé ugyanennyivel nőtt az eltelt időben. Ennek legvalószínűbb okai a mezőgazdasági művelésben bekövetkezett változások, illetve a helyi demográfiai viszonyok (elnéptelenedés) lehetnek. A 2018–2019-es szezonban jóval magasabb volt a mezei pockok aránya a táplálékban, ami a faj ez évi gradációjára utal. A különböző, egymáshoz közeli nappalozóhelyeken gyűjtött köpetekben jellemzően ugyanolyan arányban voltak jelen a különböző zsákmányállatok.

A gyülekezőhelyeken észlelt maximális példányszámok nem mutattak összefüggést az adott szezon időjárásával, hanem valószínűleg az előző költési szezon eredményességével voltak kapcsolatban.

A faj állománya a gyülekezőhelyeken összegyűlt egyedek száma alapján csökkent a 2000-es évek elejéhez képest. Ennek hátterében a varjúfélék állományának csökkenése állhat. Megemlítendő ugyanakkor, hogy mind a battonyai elütési adatok, mind a kevermesi gyülekezőhelyen számolt maximális példányszámok alapján a 2010-es években ez a drasztikus csökkenés megállt.

Kulcsszavak: madárgyűrűzés, *Microtus arvalis*, *Mus spicilegus*, bagolyköpet, elütés

[1] *Department of Systematic Zoology and Ecology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/C. Hungary*
[2] *4484 Ibrány, Tisza utca 12. Hungary*
[3] *5830 Battonya, Somogyi Béla utca 42/A. Hungary*
[4] *South Békés Nature Conservation Society, 5744 Kevermes, Jókai utca 61. Hungary*
* *corresponding author, e-mail: bozolaszlo91@gmail.com*

Introduction

The Long-eared Owl *(Asio otus)* occures in most of Eurasia, North and East Africa and also in North America (Birdlife International 2020). Populations breeding at different points in the distribution area have different migratory strategies. Northern poopulations are migratory, while the tendency to migrate decreases from north to south (Glutz von Blotzheim & Bauer 1980). Most of the Hungarian breeding population is resident. In winter, small numbers of individuals nesting in the north also appear in the Carpathian Basin (Laczik & Sebe 2009). In winter, they roost in flocks in parks, cemeteries, gardens and streets of populated areas (Kalotás 1998, Kovács 2015). They prefer evergreens (pines, thujas) but can also roost on amber-covered acacia and other deciduous trees (Kovács 2015). These roosting sites are usually located in wind-protected areas, often next to buildings, but can also change during the season as the weather changes. Their winter site fidelity is surprisingly high (Gyovai 1986). Because the birds that use the resting place typically come from the surrounding areas, traditional roosting places usually do not change over the years (Gyovai 1986, Laczik & Sebe 2009).

The species feeds primarily on small mammals, in Hungary mainly on Common Voles *(Microtus arvalis)*. This is complemented by the local occurrence of the Wood Mouse (*Apodemus* sp.), The Eurasian Harvest Mouse *(Micromys minutus)* and the House/Steppe Mouse *(Mus musculus / spicilegus)* (Schmidt 1973). Other rodents, shrews (*Crocidura* sp.), European Moles *(Talpa europaea)*, rats (*Rattus* sp.), Water Voles *(Arvicola terrestris)*, Least

Weasels *(Mustela nivalis)* and insects are very rarely predated (Kalotás 1998). The proportion of bird preys is associated with snow cover (Schmidt 1965).

Studies on the feeding of the Long-eared Owls have been carried out in the Carpathian Basin in high number. The literature dealing with this was collected and summarized by Kalivoda (1999a), but there are also publications from subsequent years (e.g. Molnár 2010, Szilágyi-Bónizs *et al.* 2016). Such studies also took place in the south-southeastern part of Békés County in the 1960s and 1970s (Schmidt 1973, 1974a, 1980). In contrast, only a few dealt with the wintering and roosting habits of the species (Gyovai 1986, Pótis 1992, Végvári & Konyhás 2003, Kovács 2015, Gyovai 2020).

The species is considered to be a regular breeder in Kevermes, and have a winter roosting site in the center of the village, probably dating back several decades (Bozó 2017). Therefore, we had the opportunity to examine the feeding and population changes of the species. In addition, based on the number of birds appearing annually in the roosting sites and the number of roadkilled individuals found, we estimated the long-term change in the population of the Long-eared Owl in the study area.

Material and methods

Owl pellets were collected in four winter seasons (2016/17, 2017/18, 2018/19 and 2019/20). Pellets were typically collected at intervals of one to a maximum of two weeks, except in the winter of 2016/17, when pellets were collected only once at the end of the season. The first collection of the season covered a wider time interval from the start of roosting. Pellets were collected regularly from two different locations: Kevermes park (hereafter: the park)

Figure 1. The locations of pellet collections in Kevermes
1. ábra A köpetek gyűjtésének helyszínei Kevermesen

and 100 meters away in the garden of the school (hereafter: school) *(Figure 1)*. In both places, approx. 70-year-old common spruce *(Picea abies)* dominate, however, most owls in the park have roosted on a prickly spruce *(Picea pungens)* with a more closed foliage. The birds occasionally migrated to other parts of the village. These roosting sites were always located on common birch trees *(Betula pendula)*, from one of which we managed to collect a larger amount of pellets in 2017/18.

The identification of small mammals in pellets was based on Ujhelyi (1989), while the identification of birds was based on Kessler (2015) and Ujhelyi (2016). In some cases, the bird species found could not be identified on species level, therefore, they were grouped according to their size. Wood Mouse species (*Apodemus* sp.) were handled together with the exception of the Striped Field Mouse *(Apodemus agrarius)*.

Chi-squared test was used to compare the proportion of different preys in pellets collected in different roosting sites and periods. The proportion of prey animals was also compared with the published literature from the Carpathian Basin (Greschik 1911, Lambrecht 1914, Schaefer 1935, Köves & Schmidt 1964, Csizmazia 1966, Papp 1971, Schmidt & Topál 1971, Marián & Marián 1973, Schmidt 1973, 1974a, 1974b, 1978, 1980, 1987, Andrési & Sódor 1981, 1987, Nagy 1982a, 1982b, Bessenyei *et al.* 1983, Molnár 1983, 1994, Varga 1983, 1984, 1987, Ács 1986, Dániel *et al.* 1986, Endes 1986, Kalivoda 1987, 1994, 1999b, Mátics 1990, Ujhelyi 1991, Tóth 1992, Csathó & Csathó 2009, Molnár 2010, Szilágyi-Bónizs *et al.* 2016). These literature sources were collected on the basis of the summary work of Kalivoda (1999a) and on the basis of the papers published after that date. Because owl pellet surveys were also conducted in the area in the 1960s and 1970s (Schmidt 1980), we were able to compare our results with these 50–60-year-old data.

We used Spearmans's rank correlation to relate the number of the most common preys with the different weather variables. The number of prey animals identified in the pellets collected at the given time was compared with the mean minimum, maximum and average temperature values of the period passed from the previous collection, as well as with the maximum snow thickness recorded in the same period. All temperature data were gathered from the website of the National Centers for Environmental Information (https://www.ncei.noaa.gov) and the website of the Hungarian Meteorological Society (https://www.met.hu).

The long-term changes of the local population of the species were studied with two methods. As they come to each roosting sites mainly from the nearby nesting places (Laczik & Sebe 2009), the local population may also be estimated on the basis of the number of birds at winter roosting sites. Therefore, we have been counting roosting owls every year since 2013. A counting during the winter of 2002/03 was carried out by the first author, which was used as a baseline in the present analysis for comparisonswith the more recent seasons. Countings were not made at regular intervals (every one or two weeks), but for the same duration (half an hour). For further analyses, we used the maximum number of individuals for the given season. We examined whether there was a correlation between the maximum annual numbers at the roosting site and the total amount of snow that fell in a given season, the average temperature between November and March, and the number of snowy days.

The other method used for the estimating possible changes in the species' population was based on roadkilled individuals. We collected detailed data in a town with similar geographical features (Battonya) located 19 km from Kevermes. Between 2012 and 2019, we carried out roadkill surveys in the entire administrative area of Battonya (14,577 hectares). There are four busy roads in the outer area of Battonya: Kovácsházi road (length: 8.4 km), Dombegyházi road (4.3 km), Tornyai road (5.0 km) and Mezőhegyesi road (3.4 km) (Csathó & Csathó 2009). The surveys were carried out in most cases once a month during the whole year. Estimated date of the collision together with its location along the road was noted for each individual. We used Spearmans's rank correlation to relate the number of the roadkilled Long-eared Owls after the months of the fledging (May – September) with the seasonal percentage of the Common Vole found in the pellets, and also to the annual maximum numbers of the roosting Long-eared Owls in Kevermes. Statistical analyses were carried out using Past 3.14 (Hammer *et al.* 2001).

Results

The proportion of prey animals of the Long-eared Owl found in the literature from the Carpathian Basin are summarized in *Table 1*.

A total of 4,683 pellets were analyzed, in which 5,265 individuals of 19 different species of mammals and birds were identified *(Table 2)*. The most common prey animals were the Common Vole (72.4%), Wood Mice (21.9%), Striped Field Mouse (2.4%) and House/Steppe Mouse (1.1%). We also found Hazel Dormouse *(Muscardinus avellanarius)*, European Hamster *(Cricetus cricetus)*, European Pine Vole *(Microtus subterraneus)* and Eurasian Harvest Mouse. The most common bird species found in the pellets was the Eurasian Tree Sparrow *(Passer montanus)* (0.7%). There was no significant difference between the proportion of the preys in our samples and the data collected from the Carpathian Basin (χ^2 = 8.818, p = 0.184). The proportion of different preys from the pellets collected in different roosting sites did not differed significantly either (χ^2 = 0.170, p = 0.982). Comparing the results of the pellet analyses in Békés County in the 1960s and 1970s with the results obtained by us, we found a significant difference (χ^2 = 14.841, p = 0.011). In the case of the House/Steppe Mouse, we detected significantly smaller amount in the present study, while the proportion of rats increased significantly *(Table 3)*.

No correlation was found between the temporal distribution of prey animals and temperature or the thickness of snow cover *(Table 4)*.

The first wintering individuals usually appeared at the roosting sites in October (occasionally in September), and typically stayed until mid-March (occasionally early April) *(Table 5)*. Of the winter seasons examined, the highest number of birds observed at one time was 120 in 2002/03, while the lowest (11 birds) in 2012/13. There was no significant relationship between the maximum number of birds observed and the average temperature (R = -0.31, p = 0.41), the number of snowy days (R = 0.13, p = 0.73) and the total amount of snow during the whole winter season. (R = 0.03, p = 0.96).

There was no significant correlation between the annual distribution of roadkilled individuals in Battonya during the breeding season and the maximum number of owls observed in the following wintering season (R = 0.18, p = 0.67). The proportion of Common Voles

Table 1. The prey animals of the Long-eared Owl in the Carpathian Basin (summarized data based on the literature, see Material and methods)

1. táblázat Az erdei fülesbagoly zsákmányállatai a Kárpát-medencében (irodalmi adatok alapján összesítve, lásd Material and methods)

Rodentia	
Microtus arvalis	62.52%
Apodemus sylvaticus	12.74%
Mus musculus	4.41%
Microtus agrestis	2.52%
Microtus subterraneus	2.17%
Micromys minutus	1.97%
Apodemus agrarius	0.87%
Myodes glareolus	0.47%
unid. Mouse	0.43%
Microtus oeconomus	0.33%
Arvicola amphibius	0.31%
Arvicolinae	0.19%
Rattus sp.	0.08%
Soricidae	
Sorex araneus	0.51%
Crocidura suaveolens	0.28%
Sorex minutus	0.22%
Crocidura leucodon	0.22%
Neomys fodiens	0.14%
Soricidae	0.01%
Chiroptera	
Nyctalus sp.	0.95%
Pipistrellus nathusii	0.95%
Myotis blythii	0.95%
Plecotus austriacus	0.95%
Nyctalus noctula	0.18%
Chiroptera	<0.01%
Other Mammalia	
Talpa europaea	1.92%
Muscardinus avellanarius	<0.01%
Lepus europaeus	<0.01%
unid. Mammalia	<0.01%
Mustela nivalis	<0.01%
Cricetus cricetus	<0.01%
Leporidae	<0.01%
Insecta	
Geotrupidae	<0.01%
Melolonthinae	<0.01%
Carabidae	<0.01%

Aves	
Passer domesticus	0,89%
Unid. Aves	0,56%
Passer montanus	0,43%
Turdus merula	0,11%
Carduelis carduelis	0,11%
Alauda arvensis	0,06%
Linaria cannabina	0,06%
Emberiza citrinella	0,06%
Parus major	0,04%
Coccothraustes coccothraustes	0,04%
Parus sp.	0,03%
Passer sp.	0,03%
Acanthis flammea	0,03%
Emberiza calandra	0,03%
Glareola cristata	0,02%
Sylvia sp.	0,02%
Turdus sp.	0,02%
Fringilla coelebs	0,02%
Chloris chloris	0,02%
Unid. Passeriformes	0,01%
Pica pica	0,01%
Cyanistes caeruleus	0,01%
Hirundo/Delichon sp.	0,01%
Regulus regulus	0,01%
Serinus serinus	0,01%
Coturnix coturnix	<0.01%
Rallus aquaticus	<0.01%
Certhia sp.	<0.01%
Sitta europaea	<0.01%
Troglodytes troglodytes	<0.01%
Turdus pilaris	<0.01%
Erithacus rubecula	<0.01%
Pyrrhula pyrrhula	<0.01%
Emberiza schoeniclus	<0.01%
Amphibia	
Pelobates fuscus	0.95%

Table 2. Time and location of the pellet collections during the research period, and the number of prey animals found in the pellets. The abbreviations of the collection sites are as follows: par: park, sch: school, bat: Battonyai street. The abbreviations of prey animals are as follows: ARV: *Microtus arvalis*, SYL: *Apodemus sylvaticus*, MUS: *Mus musculus*, AGR: *Apodemus agrarius*, MIN: *Micromys minutus*, RAT: *Rattus* sp., LEU: *Crocedura leucodon*, CRI: *Cricetus cricetus*, AVE: *Muscardinus avellanarius*, SUB: *Microtus subterraneus*, DE: *Streptopelia decaocto*, MO: *Passer montanus*, DO: *Passer domesticus*, CA: *Carduelis carduelis*, TU: *Turdus* sp., EM: *Emberiza* sp., AL: *Motacilla alba*, PA: *Parus* sp., SV: *Sylvia* sp., SB: small bird, 21. large bird, 22. unidentified bird

2. táblázat A kutatási időszakban összegyűjtött bagolyköpetek gyűjtési ideje, helye, ill. a köpetekben talált zsákmányállatok száma. A gyűjtés helyének rövidítései a következők: par: park, sch: iskola, bat: Battonyai utca. A zsákmányállatok rövidítései a következők: ARV: *Microtus arvalis*, SYL: *Apodemus sylvaticus*, MUS: *Mus musculus*, AGR: *Apodemus agrarius*, MIN: *Micromys minutus*, RAT: *Rattus* sp., LEU: *Crocedura leucodon*, CRI: *Cricetus cricetus*, AVE: *Muscardinus avellanarius*, SUB: *Microtus subterraneus*, DE: *Streptopelia decaocto*, MO: *Passer montanus*, DO: *Passer domesticus*, CA: *Carduelis carduelis*, TU: *Turdus* sp., EM: *Emberiza* sp., AL: *Motacilla alba*, PA: *Parus* sp., SV: *Sylvia* sp., SB: kistestű madár, 21. nagytestű madár, 22. meghatározatlan madár

Season	**Date**	**Place**	**Pellet no.**	**Prey no.**	***ARV***	***SYL***	***MUS***	***AGR***	***MIN***	***RAT***	***LEU***	***CRI***	***AVE***	***SUB***	***DE***	***MO***	***DO***	***CA***	***TU***	***EM***	***AL***	***PA***	***SV***	**SB**	**LB**	**B**
2016/17	–	sch	505	489	325	121	10	23	0	2	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0
	–	par	40	66	39	24	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
2017/18	8.12.2017	par	40	33	25	4	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	15.12.2017	par	40	37	17	16	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
	24.12.2017	par	40	46	26	16	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	31.12.2017	par	40	44	28	9	0	2	2	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
	07.01.2018	par	40	36	16	13	0	2	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0
	20.01.2018	par	40	39	21	13	0	1	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	03.02.2018	par	53	47	34	8	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	11.02.2018	par	8	8	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	06.03.2018	par	51	44	39	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	06.03.2018	bat	100	114	51	53	2	3	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
2018/19	28.10.2018	par	226	255	242	11	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	18.11.2018	par	200	286	273	8	3	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	09.12.2018	par	130	142	124	12	0	5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	25.12.2018	par	100	112	87	22	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	19.01.2019	par	150	422	333	77	2	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	02.02.2019	par	340	297	201	91	2	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	10.02.2019	par	250	310	216	82	2	6	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
	24.02.2019	par	266	266	199	58	3	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0
	28.10.2018	sch	72	84	80	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	18.11.2018	sch	150	185	163	16	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	09.12.2018	sch	52	72	45	24	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	25.12.2018	sch	100	111	97	13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	19.01.2019	sch	97	103	84	15	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	02.02.2019	sch	45	48	26	20	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	10.02.2019	sch	106	132	105	24	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	24.02.2019	sch	73	85	70	14	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0

Season	**Date**	**Place**	**Pellet no.**	**Prey no.**	***ARV***	***SYL***	***MUS***	***AGR***	***MIN***	***RAT***	***LEU***	***CRI***	***AVE***	***SUB***	***DE***	***MO***	***DO***	***CA***	***TU***	***EM***	***AL***	***PA***	***SV***	**SB**	**LB**	**B**
2019/20	16.11.2019	par	105	123	72	35	7	6	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0
	05.12.2019	par	150	161	117	32	4	4	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0
	21.12.2019	par	100	117	82	27	1	4	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
	29.12.2019	par	90	91	61	24	0	3	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0
	11.01.2020	par	107	95	63	19	3	0	1	0	2	0	0	2	0	4	0	0	0	0	1	0	0	0	0	0
	25.01.2020	par	107	104	60	30	4	3	0	1	0	0	0	4	0	0	0	0	0	0	1	0	0	1	0	0
	16.02.2020	par	190	192	109	63	3	8	0	1	0	0	0	0	0	4	0	0	1	0	0	2	0	0	0	1
	01.03.2020	par	100	79	54	23	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	25.01.2020	sch	150	160	92	42	4	11	0	0	1	0	0	4	1	1	0	0	1	1	1	0	1	0	0	0
	16.02.2020	sch	150	157	83	61	1	7	0	0	0	0	0	3	0	1	0	0	0	0	0	1	0	0	0	0
	01.03.2020	sch	80	73	44	27	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
TOTAL			**4683**	**5265**	**3811**	**1154**	**59**	**128**	**9**	**9**	**4**	**1**	**2**	**22**	**2**	**36**	**5**	**1**	**3**	**2**	**3**	**3**	**1**	**6**	**2**	**2**

Table 3. Comparison of the results of Long-eared Owl pellet analyses in Békés County in the 1960s and 1970s (source: Schmidt 1980) with the results of this study

3. táblázat A Békés megyében az 1960-as és 1970-es években végzett bagolyköpet-elemzések eredményeinek (forrás: Schmidt 1980) összehasonlítása a saját vizsgálatunkban talált kisemlősfajok százalékos arányával

Prey	**Békés**	**Kevermes**				
	1960s and 1970s	**2016/17**	**2017/18**	**2018/19**	**2019/20**	**Total**
Sorex araneus	0.05	0	0	0	0	0
Sorex minutus	0.1	0	0	0	0	0
Neomys sp.	0.01	0	0	0	0	0
Crocidura suaveolens	0.7	0	0	0	0	0
Crocidura leucodon	0.5	0	0.2	0	0.2	0.08
Muscardinus avellanarius	0.03	0	0	0.03	0.07	0.04
Microtus subterraneus	1.5	0	0	0.1	1.41	0.4
Microtus arvalis	56.4	66.9	58.5	80.9	61.9	72.4
Arvicola amphibius	0.02	0	0	0	0	0
Micromys minutus	2.4	0	1.8	0	0.07	0.17
Apodemus sylvaticus	24.6	26.7	34.4	18.8	28.8	21.9
Apodemus agrarius	1.6	4.2	3.3	1.5	3.47	2.4
Mus spicilegus/musculus	12.2	1.8	1.1	0.5	2.1	1.1
Rattus sp.	0.02	0.4	0.7	0.03	0.2	0.17
Cricetus cricetus	0	0	0	0.03	0	0.02

Table 4. The relationships between the ratio of prey animals found in the pellets at the time of collection and the temperatures and snow thickness of the current period. The abbreviated variables are as follows: min. temp: minimum temperature, max. temp: maximum temperature, ave temp: average temperature

4. táblázat A köpetekben talált zsákmányállatok gyűjtési időpontonkénti aránya és a hőmérséklet és hóvastagság közti kapcsolat az aktuális időszakban. A rövidített időjárási változók a következők: min. temp: legalacsonyabb hőmérséklet, max. temp: legmagasabb hőmérséklet, ave temp: átlaghőmérséklet

Species	**Place**	**Variable**	**R**	**p**
Microtus arvalis	park	min. temp	-0.02	0.95
Apodemus sylvaticus			-0.12	0.64
Mus musculus/spicilegus			-0.17	0.51
Microtus agrestis			-0.03	0.91
Aves			0.06	0.82
Microtus arvalis		max. temp	0.30	0.22
Apodemus sylvaticus			-0.35	0.15
Mus musculus/spicilegus			-0.14	0.59
Microtus agrestis			-0.11	0.67
Aves			0.05	0.85
Microtus arvalis		ave temp	-0.01	0.97
Apodemus sylvaticus			-0.11	0.67
Mus musculus/spicilegus			-0.19	0.46
Microtus agrestis			0.15	0.55
Aves			0.11	0.66
Microtus arvalis	school	min. temp	0.41	0.33
Apodemus sylvaticus			-0.33	0.39
Mus musculus/spicilegus			0.30	0.49
Microtus agrestis			-0.04	0.94
Microtus arvalis		max. temp	0.55	0.17
Apodemus sylvaticus			-0.43	0.27
Mus musculus/spicilegus			0.41	0.33
Microtus agrestis			-0.33	0.42
Microtus arvalis		ave temp	0.47	0.22
Apodemus sylvaticus			-0.38	0.36
Mus musculus/spicilegus			0.27	0.36
Microtus agrestis			-0.15	0.73
Microtus arvalis	school + park	snow thickness	0.15	0.58
Apodemus sylvaticus			0.01	0.98
Mus musculus/spicilegus			-0.10	0.70
Microtus agrestis			-0.39	0.13
Aves			-0.21	0.45

Table 5. The maximum number of Long-eared Owls observed in different winter seasons, the dates of these observations, and the starting and ending of wintering in each season

5. táblázat A különböző téli szezonokban észlelt maximális erdei fülesbagoly példányszámok, azok időpontjai, ill. a gyülekező madarak megjelenésének és távozásának időpontjai az adott szezonban

Season	Max. number	Date of max. number	Start of wintering	End of wintering
2002/03	120	–	–	–
2012/13	11	02.03.2013	late September	late March
2013/14	30	27.12.2013	late October	mid-February
2014/15	40	01.12.2014	mid-October	early April
2015/16	70	14.11.2015	late October	early March
2016/17	70	08.01.2017	mid-October	early March
2017/18	15	19.11.2017	mid-September	mid-March
2018/19	40	10.12.2018	mid-October	mid-March
2019/20	27	25.01.2020	mid-September	mid-March

found in the pellets was not related to the number of roadkilled owls (R = -0.32, p = 0.95). Within a year, the number of roadkilled birds shows a clear peak in June *(Figure 2)*. Most individuals (7–7) were found in 2014 and 2016, while in 2012, no roadkilled bird was detected *(Figure 3)*.

Discussion

The Long-eared Owl, in contrast to the Barn Owl *(Tyto alba),* is a selective hunter (Mikkola 1983). The diet of the Long-eared Owl includes different animal species in different geographical regions, but voles are dominant in most places (Schmidt 1975). In Northern Europe and the British Isles, the *Microtus* species (Hagen 1969, Glue & Hammond 1974), in Southern Europe the House Mouse (Kontogeorgos *et al.* 2019), while in Central and Eastern Europe, including Hungary, the Common Vole is the dominant prey (Schmidt 1975, Kalotás 1998, Stasiak *et al.* 2018).

Common Voles accounted for more than 60% of the diet of Long-eared Owls nesting and wintering in Hungary (Schmidt 1965). According to Schmidt (1973), the proportion of prey animals, such as Common Vole, also varies within the country. The highest proportion (85.7%) was found in North-Northeast Hungary, while the lowest proportion (53.9%) was found in the Great Hungarian Plain. However, there was no significant difference between the proportion of Common Voles in the collected literature and our results. In our study, at all three collection sites and in all seasons, Common Voles were the dominant species. The proportion of Common Vole varied between 58.5% (2017/18) and 80.9% (2018/19) in our samples. Since the population of Common Voles grows in a gradual manner every 3–4 years and then collapses for natural reasons (Schmidt 1968, Bihari 2007), the differences obtained are due to their population dynamics.

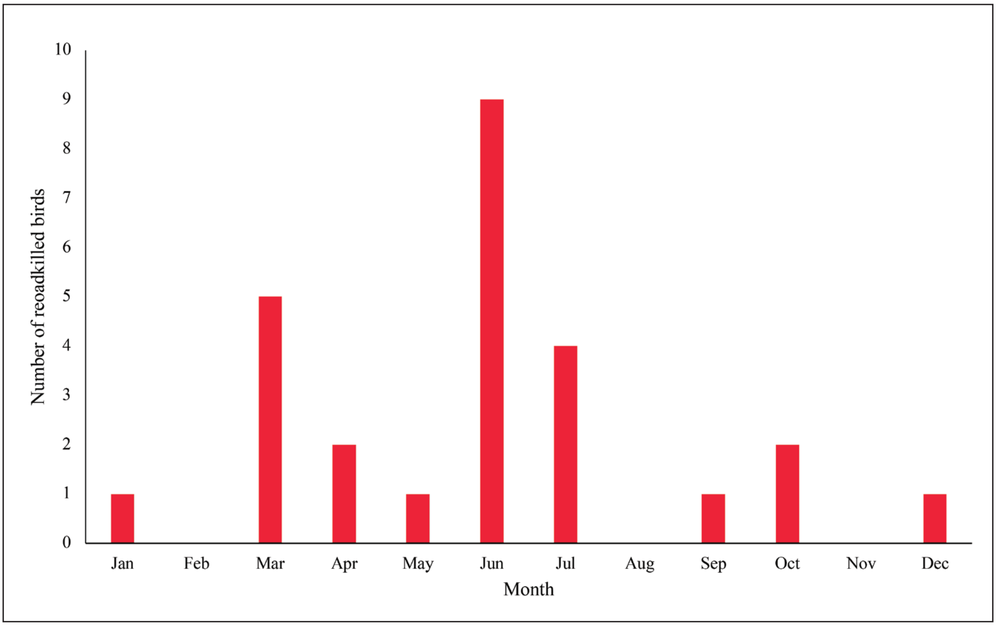


Figure 2. Monthly distribution of roadkilled Long-eared Owls found in Battonya between 2012–2019
2. ábra A Battonyán 2012 és 2019 között talált, elütött erdei fülesbaglyok száma havi bontásban

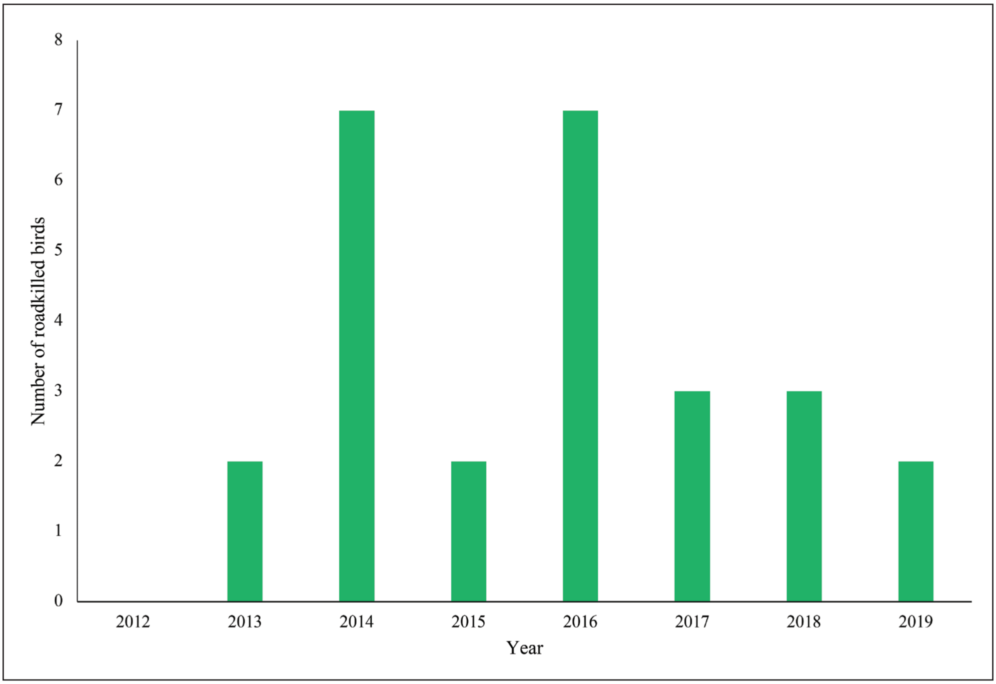


Figure 3. Annual distribution of roadkilled Long-eared Owls found in Battonya between 2012–2019
3. ábra A Battonyán 2012–2019 között talált, elütött erdei fülesbaglyok száma éves bontásban

In the gradation years, Long-eared Owls can breed up to two times (Haraszthy 2019), so the local number of individuals of the species obviously increases, which should also be reflected in the number of individuals roosting in the area and hit on the road. Out of the four winter seasons of the study period, the number of wintering owls was highest in the year of gradation (2018), but no correlation was found between the number of roosting individuals and the proportion of Common Voles in the pellets, neither between the number of roadkilled owls and the number of wintering individuals. However, the fewest Long-eared Owls were in the area when the proportion of Common Voles in the diet was the lowest during the four study years. This is due to the fact that owls may not be able to breed in food-poor years, and in extreme cases may even disappear from the area (Haraszthy 2019). The lack of correlation between the number of wintering birds and winter weather may confirm the assumption that the number of birds is mainly related to the annual breeding success.

Owl pellet analyses, together with roadkill surveys, were carried out in Battonya in 1998 and 1999 (Csathó & Csathó 2009). Based on the number of roadkilled individuals, the last significant gradation of the Common Vole occured in 2014, although the results of pellet analyses show a definite gradation in 2018. This discrepancy indicates that the two methods do not necessarily lead to similar results. Further studies are needed to explore the causes. It is conceivable that, although the geographical distance between the two areas is very small, somewhat different methods are used in agriculture, which may lead to the differences.

In addition to the Common Vole, the proportion of Wood Mouse species was also significant in the prey (on average about 25%). This proportion is much higher than indicated by the collected literature on the Carpathian Basin (about 12%) *(Table 2)* and contradicts the fact that the proportion of Wood Mice is higher in forested areas (Bihari 2007). Csathó and Csathó (2009) found the proportion of roadkilled Wood Mice to be 31.9% in 1998 and 1999, which also indicates that *Apodemus* species are present in high proportions in the area.

The Striped Field Mouse was the third prey animal to be found in the pellets at a rate of over 1% each year. This species, similar to Wood Mouse species, was present in a somewhat higher proportion in the samples we collected than considering the entire area of the Carpathian Basin. This can certainly be explained by the fact that Striped Field Mouse are more common in the eastern parts of the Great Hungarian Plain than elsewhere (Schmidt 1969).

Radiotelemetry studies show that Long-eared Owls typically roam 185–370 hectares per night during the winter season (Wijnandts 1984). According to the studies of Gyovai (1986), the variability of prey in Csongrád County varied depending on the type of soil. Large monoculture arable land, characterized by hard ground, reduces the diversity of small mammals and causes dominance of Common Voles, while alluvial soils are home to a much more diverse vegetation cover with diverse small mammal fauna. In view of these findings, it is not surprising that the percentage distribution of prey animals did not change during the season. In Kevermes, monocultural arable lands are typical, where the diversity of small mammals is low and owls do not have the opportunity to prey in other types of habitats.

The most varied food spectrum was found in the 2019/20 season, when least snow fell in the study area. The species typically prey on higher numbers of birds in snowy winters (Schmidt 1965), however, due to the collapse of the Common Vole population, the proportion of other species, such as birds and other small mammals had to be increased regardless of snow thickness. In addition, due to the mild winter, several bird species were present in larger numbers in the area, which normally migrate to the south, thus increasing the likelihood of bird prey. A good example of this is the White Wagtail *(Motacilla alba)*, as this species typically leave the area by the end of October (Bozó 2017). However, in the 2019/2020 season, we still saw two individuals in the area on the 17th of November (Bozó L. pers. obs.).

We have found species that are not considered common in the area. Two data of Hazel Dormouse have been known so far from Kevermes (Bozó 2018) and 12 published data exist from Battonya (Csathó & Csathó 2009, 2014). The two individuals found in the pellets provide further evidence that the Hazel Dormouse may be present in this less-forested area. Furthermore, during the national population survey of the Hazel Dormouse, there were data only from North Békés, the Körös region, not from the southern parts dominated by agricultural areas (Hecker *et al.* 2003, Bihari 2007).

Based on data of owl pellet analyses, the Eurasian Harvest Mouse is widespread in Hungary (Váczi *et al.* 2019). In Kevermes, it occurred in only two seasons during the study period, the cause of which is not obvious, but perhaps due to the fact that the species occurs only on certain, fragmented habitats that are further away from the typical hunting territories of the owls. This is why it was found only in the samples of a season when Long-eared Owls widen the hunting area and visit these small fragmented habitats.

The situation may be similar for European Pine Vole, a widespread species in Hungary mainly in the central and southern parts of Transdanubia, while in the Great Plain it is especially rare (Schmidt 1974c). According to Schmidt (1974c), the species also occurred in Battonya and Mezőhegyes in the early 1970s. Perhaps, we witnessed such a gradation during the 2019/20 season, when far more European Pine Voles were found in the pellets than in the previous season.

Definitely, it is worth mentioning the European Hamster, which is very rarely found in Long-eared Owl pellets. In the literature from the Carpathian Basin *(Table 1)*, only one indiviual was found in a pellet collected in 1984 at the botanical garden in Dunaszentmiklós (Dániel *et al.* 1986). The species is rare prey of Long-eared Owls because of its large body size.

Compared to the 1960s and 1970s, we detected an order of magnitude fewer House/Steppe Mice in the current study. Although the two species differ significantly in their behavior and habitat (Barkasi & Zagorodniuk 2016), they are morphologically very difficult to separate, so usually treated together. The change in the number of House/Steppe Mice in the last decades may certainly be due to changes in agricultural cultivation (increase in parcel size, change in cultivated plant varieties, increased use of chemicals, more modern, less environmentally friendly tillage technologies). In addition, there were significant changes in the storage of crops, which may have caused a significant decline in the number of House Mouse. Until the early 2000s, maize was mainly stored in open granaries, but this method has completely disappeared and the harvested grain is placed in closed granaries. In contrast, the number of rats in the pellets increased, which may be related to the unfavorable human demographic conditions in the area. With the slow depopulation of settlements, more and more abandoned houses are serving as excellent habitats for the rats. Negative demographics also affect the local population of another owl species, the Little Owl *(Athene noctua),* which increased significantly in the area over the last decade thanks to more and more abandoned houses that provide a quiet nesting place and excellent feeding ground for the species (Bozó & Csathó 2017).

Birds also appeared regularly in the pellets. The proportion of bird prey was similar to that obtained in studies in other areas of the Carpathian Basin with a rate of 2.7% *(Table 1)*. The dominant species was the Eurasian Tree Sparrow, which is also the most dominant bird prey in the Carpathian Basin *(Table 1)*.

During the four years of the study, no bats were found in the pellets. This is interesting because the Long-eared Owl regularly prey on small numbers of bats (Schmidt & Topál 1971, Ujhelyi 1991), and many bats can be found in the study area until November.

The first Long-eared Owls typically appeared in the roosting sites in October, but often some birds were already there in September. Since winter roosting sites are first occupied by members of the local population (Wijnandts 1984), it can be assumed that these early individuals may have breed in the park and its immediate vicinity. The species also breeds increasingly in human settlements in Hungary (Kovács 2015, Haraszthy 2019). The roosting sites were typically left until early to mid-March, with later observations likely to apply to members of the local population. This is because the species starts breeding early in the spring, the clutch become complete in early April, but they can breed as early as March, sometimes even in winter (Balogh 2006, Monoki 2010).

According to the roadkill data, the largest number of Long-eared Owls were hit by the traffic in the summer period after the independence of the young birds (June – July). Similar results were obtained by Bozó and Csathó (2017) in case of Little Owl, with the difference that the maximum number of roadkilled individuals were found in the second half of the summer (July – August).

Based on the maximum number of individuals counted in the roosting sites, it is likely that the species was a more common breeder in Kevermes in the early 2000s than in the 2010s. The reason for the decline may be the drastic local population decline of the Common Magpie *(Pica pica)* and the Hooded Crow *(Corvus cornix)* (Bozó 2017), which are the most important host species whose nest are occupied by Long-eared Owls. In addition, cutting of older tree lines and forest patches may contribute to this process, further reducing the likelihood of nesting. The disappearance of corvids and nesting sites cannot be compensated even by the urbanization of the species. However, the period from 2010 to 2020 does not indicate a trend-like decrease in Kevermes and Battonya either. The changes experienced occurred from one year to the next. These changes draw attention to the fact that there may be differences even between close areas with similar geographical features, and it is not possible to draw general, landscape-level conclusions from studies of a narrower region. It should also be noted that although there was no significant correlation between the number of roadkilled birds and the amount of bird observed in the roosting sites, similarities could be detected between the data sets. Between 2012 and 2014, an increasing trend can be observed in both data series, while between 2016 and 2019 the trends were decreasing.

Acknowledgements

We would like to thank to András János Csathó for his help in the survey of roadkilled animals, and to Tibor Csörgő for reviewing the early version of the manuscript and for his useful suggestions.

References

Ács, A. 1986. Néhány adat a Zala megyében telelő erdei fülesbaglyok *(Asio otus)* táplálkozásáról [Some data on the feeding of Long-eared Owls *(Asio otus)* wintering in Zala County]. – Madártani Tájékoztató 10(1): 76–78. (in Hungarian)

Andrési, P. & Sódor, L. 1981. A zsákmányállatok megoszlása fülesbagoly *(Asio otus)* köpetekben talált maradványok alapján [Distribution of prey animals based on residues found in Nortnern Long-eared Owl *(Asio otus)* pellets]. – Madártani Tájékoztató 5(4): 233–234. (in Hungarian)

Andrési, P. & Sódor, M. 1987. Sopron és környékének kisemlős faunája. I. rész [The small mammal fauna of Sopron and its surroundings, Part I.]. – Soproni Szemle 41(3): 211–225. (in Hungarian)

Balogh, Gy. 2006. Városi fülesbaglyok [Urban Long-eared Owls]. – Madártávlat 13(1–2): 30–31. (in Hungarian)

Barkasi, Z. & Zagorodniuk, I. 2016. The taxonomy of rodents of the Eastern Carpathians. – Scientific Notes of the State Museum of Natural History 32: 137–154.

Bessenyei, B., Dudás, M. & Sándor, I. 1983. Adatok az erdőspusztán fészkelő bagolyfajok táplálkozásának ismeretéhez [Data for the knowledge of the feeding of owl species nesting in the forest steppe]. – Madártani Tájékoztató 7(3–4): 112–113. (in Hungarian)

Bihari, Z. 2007. Magyarország emlőseinek atlasza [Atlas of the mammals of Hungary]. – Kossuth Kiadó, Budapest (in Hungarian)

BirdLife International 2020. Species factsheet: *Asio otus*. – http://www.birdlife.org on 03/08/2020.

Bozó, L. 2017. Kevermes madárvilága [Birds of Kevermes]. – Dél-békési Természetvédelmi és Madártani Egyesület, Kevermes (in Hungarian with English Summary)

Bozó, L. & Csathó, A. I. 2017. The status and population changes of the Little Owl *(Athene noctua)* in the south of Békés County (Hungary). – Ornis Hungarica 25(2): 23–33. DOI: 10.1515/orhu-2017-0013

Bozó, L. 2018. Dél-Békés természeti értékei [Nature assets of South-Békés]. – Dél-békési Természetvédelmi és Madártani Egyesület, Kevermes (in Hungarian)

Csathó, A. I. & Csathó, A. J. 2009. Elütött állatok Battonyán [Roadkills and the dynamics of the faunal casualties in Battonya (SE Hungary)]. – CSEMETE Természet- és Környezetvédelmi Egyesület, Battonya–Szeged (in Hungarian with English Summary)

Csathó, A. I. & Csathó, A. J. 2014. Az idén huszadik éves battonyai elütöttállat-felmérés legutóbbi öt évének (2010–2014) adatai [Data of the past five years (2010–2014) of the twentieth year old roadkill surveys in Battonya]. – In: Lengyel, Sz. (ed.) IX. Magyar Természetvédelmi Biológiai Konferencia. – „Tudományoktól a döntéshozatalig". – Absztrakt-kötet. – Magyar Biológiai Társaság – Szegedi Tudományegyetem Ökológiai Tanszék – MTA Ökológiai Kutatóközpont, Szeged, pp. 45–46. http://www.mtbk.hu/mtbk09/doc/IX.MTBK_AbsztraktKotet.pdf (in Hungarian)

Csizmazia, Gy. 1966. Beiträge zur Fledermaus-Fauna des Ungarischen Tisza-Tales [Contributions to the bat fauna of the Hungarian Tisza Valley]. – Tiscia 2: 127–130. (in German)

Dániel, Á., Frank, T. & Pellinger, A. 1986. Erdei fülesbagoly *(Asio otus)* táplálékának vizsgálata [Examination of the diet of the Long-eared Owl *(Asio otus)*]. – Madártani Tájékoztató 10(1): 79. (in Hungarian)

Endes, M. 1986. Bagolytáplálkozási megfigyelések [Observations on feeding of owls]. – Madártani Tájékoztató 10(1): 78. (in Hungarian)

Glue, D. E. & Hammond, G. J. 1974. The feeding ecology of the Long-eared Owl in Britain and Ireland. – British Birds 67: 361–369.

Glutz von Blotzheim, U. N. & Bauer, K. M. 1980. Handbuch der Vögel Mitteleuropas, Band 9. Columbiformes – Piciformes [Handbook of the birds of Central Europe, Vol. 9. Columbiformes – Piciformes]. – Akademische Verlagsgesellschaft, Wiesbaden (in German)

Greschik, J. 1911. Hazai ragadozómadaraink gyomor- és köpettartalom vizsgálata. II. Baglyok [Studies on the stomach and pellet content of the Hungarian birds of prey. II. Owls]. – Aquila 18: 141–177. (in Hungarian and German)

Gyovai, F. 1986. Telelő erdei fülesbaglyok *(Asio otus)* demográfiai vizsgálata Csongrád megyében [Population studies on overwintering Long-eared Owls *(Asio otus)* in Csongrád County, Hungary]. – MME II. Tudományos Ülése, Szeged, pp. 301–311. (in Hungarian with English Summary)

Gyovai, F. 2020. Bagolyleltár. Telelő erdei fülesek demográfiai vizsgálata [Owl control. Demographic study of wintering Long-eared Owls]. – Élet és Tudomány (10): 302–304. (in Hungarian)

Hagen, Y. 1969. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent population fluctuations. – Fauna 22: 73–126.

Hammer, Ø., Harper, D. A. & Ryan, P. D. 2001. PAST: Paleontological statistics software package for education and data analysis. – Palaeontologia Electronica 4(1): 9.

Haraszthy, L. 2019. Magyarország fészkelő madarainak költésbiológiája. 1. kötet. Fácánféléktől a sólyomfélékig [Breeding biology of Hungarian nesting birds, Vol. 1. Non-Passeriformes]. – Pro Vértes Nonprofit Kft., Csákvár, pp. 679–683. (in Hungarian)

Hecker, K., Bakó, B. & Csorba, G. 2003. Distribution ecology of the Hungarian dormouse species, based on the national biodiversity monitoring system. – Acta Zoologica Academiae Scientiarum Hungaricae 49(Suppl.1.): 45–54.

Kalivoda, B. 1987. Adatok az erdei fülesbagoly *(Asio otus)* táplálkozásához [Data on the feeding of the Long-eared Owl *(Asio otus)*]. – Madártani Tájékoztató 11(3–4): 27. (in Hungarian)

Kalivoda, B. 1994. Adatok az erdei fülesbagoly *(Asio otus)* táplálkozásához [Data on the feeding of the Long-eared Owl *(Asio otus)*]. – Madártani Tájékoztató 18(1): 14. (in Hungarian)

Kalivoda, B. 1999a A magyar bagoly-táplálkozástani irodalom annotált bibliográfiája [The annoted bibliography of the Hungarian literature on owl food]. – Crisicum 2: 221–254. (in Hungarian with English Summary)

Kalivoda, B. 1999b Adatok a Karcagi Arborétumban telelő erdei fülesbaglyok *(Asio otus)* táplálkozásáról [Data on the feeding of Long-eared Owls *(Asio otus)* wintering in the Karcag Arboretum]. – A Puszta 16: 101–102. (in Hungarian)

Kalotás, Zs. 1998. Erdei fülesbagoly [Long-eared Owl]. – In: Haraszthy, L. (ed.) Magyarország madarai [Birds of Hungary]. – Mezőgazda Kiadó, Budapest, pp. 221–222. (in Hungarian)

Kessler, J. 2015. Osteological guide of songbirds from Central Europe. – Ornis Hungarica 23(2): 62–155. DOI: 10.1515/orhu-2015-0016

Kontogeorgos, I., Kiamos, N., Montiel-Ruiz, P., Georgopoulou, E., Mylonas, M. & Xirouchakis, S. M. 2019. Feeding ecology and prey selection by wintering Long-eared Owls *Asio otus* in Mediterranean agrosystems. – Ornithological Science 18(1): 95–110. DOI: 10.2326/osj.18.95

Kovács, Á. 2015. Telelő erdei fülesbaglyok *(Asio otus)* nappalozási szokásaira vonatkozó preferencia vizsgálatok városi gyülekezőhelyeken [Studies on the roosting habits of wintering Long-eared Owls *(Asio otus)* in urban roosting sites]. – A Puszta 25: 185–215. (in Hungarian)

Köves, E. O. & Schmidt, E. 1964. Adatok Tornyosnémeti környéke kisemlősfaunájának ismeretéhez bagolyköpetvizsgálatok alapján [Data for the knowledge of the small mammal fauna of Tornyosnémeti and its surroundings based on owl pellets]. – Vertebrata Hungarica 6(1–2): 97–108. (in Hungarian with German Summary)

Laczik, D. & Sebe, K. 2009. Erdei fülesbagoly [Long-eared Owl]. – In: Csörgő, T., Karcza, Zs., Halmos, G., Magyar, G., Gyurácz, J., Szép, T., Bankovics, A., Schmidt, A. & Schmidt, E. (eds.) Magyar madárvonulási atlasz [Hungarian Bird Migration Atlas]. – Kossuth Kiadó Zrt., Budapest, pp. 366–368. (in Hungarian with English Summary)

Lambrecht, K. 1914. Adatok a karvaly és az erdei fülesbagoly táplálékának ismeretéhez [Data for the knowledge of the feeding of the Eurasian Sparrowhawk and the Long-eared Owl]. – Aquila 21: 275. (in Hungarian and German)

Marián, M. & Marián, O. 1973. Anuren-Knochenreste aus Eulengewöllen [Remnants of anuric bones from owl pellets]. – Vertebrata Hungarica 14: 9–18. (in German with Hungarian and English Summary)

Mátics, R. 1990. Bagolyköpet vizsgálatok [Studies on owl pellets]. – Madártani Tájékoztató 14(3–4): 30–31. (in Hungarian)

Mikkola, H. 1983. Owls of Europe. – T & AD Poyser, Calton

Molnár, I. 1983. Bagolytáplálkozási adatok a Dunántúlról [Data on the feeding of owls from Transdanubia]. – Madártani Tájékoztató 7(3–4): 106–110. (in Hungarian)

Molnár, I. 1994. Erdei fülesbagoly *(Asio otus)* táplálkozási adatai Zircről [Feeding data of the Long-eared Owl *(Asio otus)* from Zirc]. – Madártani Tájékoztató 18(2): 33. (in Hungarian)

Molnár, L. 2010. Adatok az erdei fülesbagoly (*Asio otus* L.) téli táplálkozásához Sepsiszentgyörgyön köpetvizsgálatok alapján [Contributions to the dietary habits in winter of the Long-eared Owl (*Asio otus* L.) in

Sepsiszentgyörgy (Sf. Gheorghe)]. – Acta Siculica 2011–2012: 145–153. (in Hungarian with English and Romanian Summary)

Monoki, Á. 2010. Erdei fülesbaglyok *(Asio otus)* városi és laza telepes fészkelése [Urban and loose colony nesting of Eurasian Long-eared Owls *(Asio otus)*]. – A Puszta 23: 290–291. (in Hungarian)

Nagy, S. 1982a A zsákmányállatok megoszlása fülesbagoly *(Asio otus)* köpetekben talált maradványok alapján [Distribution of prey animals based on residues found in Eurasian Long-eared Owl *(Asio otus)* pellets]. – Madártani Tájékoztató 6(2–3): 113. (in Hungarian)

Nagy, S. 1982b A zsákmányállatok megoszlása fülesbagoly *(Asio otus)* köpetekben talált maradványok alapján [Distribution of prey animals based on residues found in Eurasian Long-eared Owl *(Asio otus)* pellets]. – Madártani Tájékoztató 6(4): 304. (in Hungarian)

Papp, J. L. 1971. Aranyosgadány kisemlősfaunája gyűjtések és bagolyköpet vizsgálatok alapján [The small mammal fauna of Aranyosgadány based on collecting and the examination of regurgitated owl pellets]. – Vertebrata Hungarica 12: 69–78. (in Hungarian with English Summary)

Pótis, L. 1992. Adatok az erdei fülesbagoly *(Asio otus)* teleléséhez Ungváron (Uzgorod) és környékén [Data for the wintering of the Long-eared Owl *(Asio otus)* in and around Ungvár (Uzhhorod)]. – Madártani Tájékoztató 16(2): 26. (in Hungarian)

Schaefer, H. 1935. Inhalte einiger Eulengewölle aus Südungarn [Contents of some owl pellets from southern Hungary]. – Acta Biologica 3(3): 226–229. (in German)

Schmidt, E. 1965. Über die Winternahrung der Waldohreulein der VR Ungarn [About the winter diet of the Long-eared Owl in Hungary]. – Zoologische Abhandlungen MuseumTierkunde Dresden 27: 307–317. (in German)

Schmidt, E. 1968. A Magyarországon telelő erdei fülesbaglyok mezei pocok pusztításának elméleti értékelése köpetvizsgálatok alapján [Studies on the Common Vole predation by Long-eared Owls wintering in Hungary based on pellets]. – Aquila 75–77: 259–271. (in Hungarian and German)

Schmidt, E. 1969. Adatok egyes kisemlősfajok elterjedéséhez Magyarországon, bagolyköpet vizsgálatok alapján (Előzetes jelentés) [Data on the distribution of certain small mammal species in Hungary, based on owl pellets (Preliminary report)]. – Vertebrata Hungarica 9: 137–153. (in Hungarian with German Summary)

Schmidt, E. 1973. A gyöngybagoly *(Tyto alba)* és az erdei fülesbagoly *(Asio otus)* legfontosabb táplálékállatai Magyarországon [The most important preys of Barn Owl *(Tyto alba)* and Long-eared Owl *(Asio otus)*]. – Aquila 76–77: 55–64. (in Hungarian with German Summary)

Schmidt, E. 1974a A magyarországi mezei pocok *(Microtus arvalis)* állomány relatív sűrűsége 1969–71-ben bagolyköpetek vizsgálata alapján [The relative population density of Common Vole *(Microtus arvalis)* between 1969–71 on the basis of owl pellets]. – Aquila 78–79: 189–196. (in Hungarian with German Summary)

Schmidt, E. 1974b Adatok Vas megye kisemlősfaunájához baglyok táplálékvizsgálata alapján [Data for the small mammal fauna of Vas County based on the analysis of owl pellets]. – Savaria (Vas megyei Múzeumok Értesítője) 7–8: 71–77. (in Hungarian with German Summary)

Schmidt, E. 1974c Über die Verbreitung und Wohndichte der Kleinwühlmaus (*Pitymys subterraneus* (De Selys-Longchamps)) in Ungarn [About the distribution and population density of the European Pine Vole (*Pitymys subterraneus* (De Selys-Longchamps)) in Hungary]. – Vertebrata Hungarica 15: 45–52. (in German with English Summary)

Schmidt, E. 1975. Az erdei fülesbagoly táplálkozása Európában [The diet of Long-eared Owls in Europe]. – Aquila 80–81: 221–238. (in Hungarian with German Summary)

Schmidt, E. 1978. Adatok a Szigligeti Arborétum és környékének kisemlősfaunájához erdei fülesbagoly *(Asio otus)* köpetvizsgálatok alapján [Data for the small mammal fauna of the Szigliget Arboretum and its surroundings based on the analyses of pellets of Long-eared Owl *(Asio otus)*]. – Veszprém megyei Múzeumok Közleményei 13: 123–127. (in Hungarian with German Summary)

Schmidt, E. 1980. Adatok Békés megye kisemlősfaunájához baglyok táplálékvizsgálata alapján [Data for the small mammal fauna of Békés County based on the feeding analysis of owls]. – Békés Megyei Múzeumok Közleményei 6: 179–188. (in Hungarian)

Schmidt, E. 1987. Erdei fülesbaglyok *(Asio otus)* a Gellérthegyen [Long-eared Owls *(Asio otus)* on Gellért Hill]. – Madártani Tájékoztató 11(1–2): 43–44. (in Hungarian)

Schmidt, E. & Topál, Gy. 1971. Denevérmaradványok magyarországi bagolyköpetekből [Bat residues from owl pellets in Hungary]. – Vertebrata Hungarica 12: 93–102. (in Hungarian with German Summary)

Szilágyi-Bónizs, M., Cseh, V. & Maák, I. E. 2016. Erdei fülesbagoly *(Asio otus)* téli táplálékpreferenciája antropogén élőhelyeken [The food preference of the Long-eared Owl *(Asio otus)* in anthropogenic habitats]. – Acta Scientiarum Transylvanica – Múzeumi Füzetek 23(1): 43–60. (in Hungarian with English Summary)

Tóth, G. 1992. Újabb adat Csorna környékének kisemlős faunájához [New data on the mammal fauna of the area of Csorna]. – Soproni Szemle 46(2): 179–181.

Ujhelyi, P. 1989. A magyarországi vadonélő emlősállatok határozója (küllemi és csonttani bélyegek alapján) [Key for identification of wild mammals of Hungary (on the base of habitus and features of sceleton)]. − A Magyar Madártani és Természetvédelmi Egyesület (MME) Könyvtára 1. Budapest (in Hungarian)

Ujhelyi, P. 1991. Kisemlős-faunisztikai adatok bagolyköpetekből – denevérek [Small mammal data from owl pellets – bats]. – Madártani Tájékoztató 15(1–2): 23–24. (in Hungarian)

Ujhelyi, P. 2016. Cranial morphology of European passerine bird families (Aves, Passeriformes). – Ornis Hungarica 24(2): 54–77. DOI: 10.1515/orhu-2016-0015

Váczi, O., Varga, I. & Bakó, B. (eds.) 2019. A Nemzeti Biodiverzitás-monitorozó Rendszer Eredményei II. – Gerinces Állatok [Results of the National Biodiversity Monitoring System II. – Vertebrates]. – Körös-Maros Nemzeti Park Igazgatóság, Szarvas

Varga, L. 1983. Bagolyköpet-vizsgálatok eredményei Vas megyéből [Results of studies on owl pellets from Vas County]. – Madártani Tájékoztató 7(3–4): 111–112. (in Hungarian)

Varga, L. 1984. Bagolyköpetvizsgálatok eredményei Szombathely környékéről [Results of studies on owl pellets from Szombathely and its surroundings]. – Madártani Tájékoztató 8(1): 60–62. (in Hungarian)

Varga, L. 1987. Bagolyköpet-vizsgálati eredmények Vas megyéből [Results of studies on owl pellets from Vas County]. – Praenorica Folia Historico-naturalia 2: 171–174. (in Hungarian with English and German Summary)

Végvári, Zs. & Konyhás, S. 2003. Az erdei fülesbaglyok *(Asio otus)* és réti fülesbaglyok *(Asio flammeus)* telelő állományának felmérése néhány Hortobágy környéki településen 1996–1998 között [Survey of the wintering population of Long-eared Owls *(Asio otus)* and Short-eared Owls *(Asio flammeus)* in some settlements around Hortobágy between 1996–1998]. – Aquila 109–110: 103–107. (in Hungarian with English Summary)

Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl *(Asio otus)*. – Ardea 55(1–2): 1–92.

sciendo

Ornis Hungarica 2020. 28(2): 19–23.
DOI: 10.2478/orhu-2020-0014

Town avenues as flight corridors for Long-eared Owls *(Asio otus)*[×]

Thomas Oliver Mérő[1,2*] & Antun Žuljević[2]

[×] Presented at 2nd Hungarian Owl Research Conference held in Pécs on 11th September 2020

Received: September 07, 2020 – Revised: October 15, 2020 – Accepted: October 16, 2020

Mérő, Th. O. & Žuljević, A. 2020. Town avenues as flight corridors for Long-eared Owls *(Asio otus)*. – Ornis Hungarica 28(2): 19–23. DOI: 10.2478/orhu-2020-0014

Abstract During winter, Long-eared Owls *(Asio otus)* usually roost in groups in urban areas, but their nocturnal movement patterns are less known. The aim of our study is to provide insight into the local-scale urban movement habits of Long-eared Owls. Our study was carried out between 2015 and 2019 in the autumn and winter period, by observations in the early evening and by ringing and recapture of owls in the town of Sombor (NE Serbia). We observed owls when leaving the roosting site located in the town centre following the greenery of the larger avenues towards the outskirts. Owls were sporadically observed in densely built areas of the town, narrow streets with less greenery. Ringing and recapture data suggest that owls were closely linked to the green corridors. They probably used these corridors for easier orientation and to prey on birds roosting in trees in the town, such as sparrows *(Passer domesticus, P. montanus)*, Common Blackbirds *(Turdus merula)* or Fieldfares *(T. pilaris)* appearing in harsh winters, and sometimes also pigeons.

Keywords: green corridors, urban area, roosting site, *Asio otus*

Összefoglalás Az erdei fülesbagoly *(Asio otus)* télen csapatokba verődve, többnyire városi környezetben nappalozik, azonban éjszakai mozgásmintázata kevésbé ismert. Vizsgálatunk célja az volt, hogy betekintést nyerjünk a baglyok lokális léptékű, városi mozgási szokásaiba. Kutatásunkat 2015 és 2019 között, az őszi és téli időszakban, főként a kora esti órákban végeztük megfigyeléssel, az egyedek gyűrűzésével és visszafogásával Zombor városában (ÉNY Szerbia). Megfigyeltük, hogy a baglyok, miután elhagyták a nappalozó helyet, követték a fákban gazdag sugárutakat (zöld folyosók), melyek a város külterületeire vezetnek. Kevésbé használták viszont a sűrűn beépített területeket, melyeket szűk utcák és gyér vegetáció jellemez. A gyűrűzési és visszafogási adatok arra utalnak, hogy a baglyok szorosan kötődnek a zöld folyosókhoz. Feltételezhető, hogy ezek a folyosók megkönnyítik a tájékozódásukat, és lehetőséget adnak a városban, fákon éjszakázó madarak – pl. verebek *(Passer domesticus, P. montanus)*, fekete rigók *(Turdus merula)*, vagy a zord teleken megjelenő fenyőrigók *(T. pilaris)*, időnként galambok – zsákmányolására is.

Kulcsszavak: zöld folyosók, városi élőhely, nappalozó hely, erdei fülesbagoly

[1] *Department of Tisza Research, Danube Research Institute, Centre for Ecological Research; 4026 Debrecen, Bem tér 18/c, Hungary*
[2] *Nature Protection and Study Society – NATURA, Milana Rakića 20, 25000 Sombor, Serbia*
**corresponding author; e-mail: thomas.oliver.mero@gmail.com*

Introduction

Movement patterns of birds has been the subject of many studies (e.g. Mérő & Žuljević 2014, Rechetelo *et al.* 2016). Birds may use natural or human made formations for orientation in their flight. Migrating birds take advance of valleys, canyons, meanders of rivers, forest-belts and/or tree rows that function as corridors taking them to their feeding, wintering or breeding ranges (e.g. Bentley & Catterall 1997, Calm 1997). However, at a local scale, short bird movements (e.g. within urban habitat, forest) remain understudied and often unclear (Gillies & St. Clair 2008). For example, some authors suggest that Sparrowhawks *(Accipiter nisus)* use the same foraging routes daily in the breeding period (Newton 1986). This might be related to the fact that birds of prey and owls may have hunting territories, even in the non-breeding period (Dawson & Mannan 1991, Martinez *et al.* 1998). Ardia and Bildstein (1997) found that individuals of American Kestrel *(Falco sparverius)* were strongly linked to their hunting ranges in winter, occupying the same ranges during two or more consecutive winter seasons.

Long-eared Owls are nocturnal predatory birds that feed mostly on small mammals and sporadically on small- and medium-sized birds (Bertolino *et al.* 2001, Sándor & Kiss 2008, Bozó *et al.* 2020). In the autumn and winter, Long-eared Owls roost, often in large numbers, in the canopies of deciduous and coniferous trees in urban or semi-urban areas in the nearest vicinity of humans (Makarova & Sharikov 2015). They probably recognize that roosting sites in settlements have advantages such as higher temperatures and/or tend to be safer in winter than rural sites (Clergeau & Simonnet 1996). In harsh winters with hard frosts and snowy periods, urban areas can provide additional feeding resources, such as roosting birds (Glue 1972). Unlike other owl species, Long-eared Owls have no territorial hunting ranges (Hume 1991), and therefore hunting traces are more difficult to explore. The aim of this study was to describe movement habits of Long-eared Owls between their roosting site and their supposed hunting sites.

Material and methods

The town of Sombor is located in north-western Serbia (N 45.79°, E 19.09°). It is a typical lowland settlement (89 m a.s.l.) with a population of around 50,000 inhabitants. The climate is temperate continental with an average annual precipitation of ca. 590 mm and average annual temperature of 10.7 °C (Tomić 1996). From the town centre, five main avenues run toward the outskirts containing at least two or more tree rows *(Figure 1)*. Trees are planted along avenues (total length 121 km, ca. 18,000 trees), in parks and in gardens of private houses (Vojnović 2001). The most frequent tree of the avenues is the common hackberry *(Celtis occidentalis)*, some avenues are planted with London plane *(Platanus × acerifolia)*, horse chestnut *(Aesculus hippocastanum)* and Japanese pagoda-tree *(Sophora japonica)*. In gardens, usually coniferous trees, walnut *(Juglans regia)* and orchard trees occur. For more details, see Mérő and Žuljević (2010, 2014).

The fieldwork was conducted by observing and ringing of Long-eared Owls in the town during the autumn and winter from 2015 until 2019. Long-eared Owls roosted in the centre

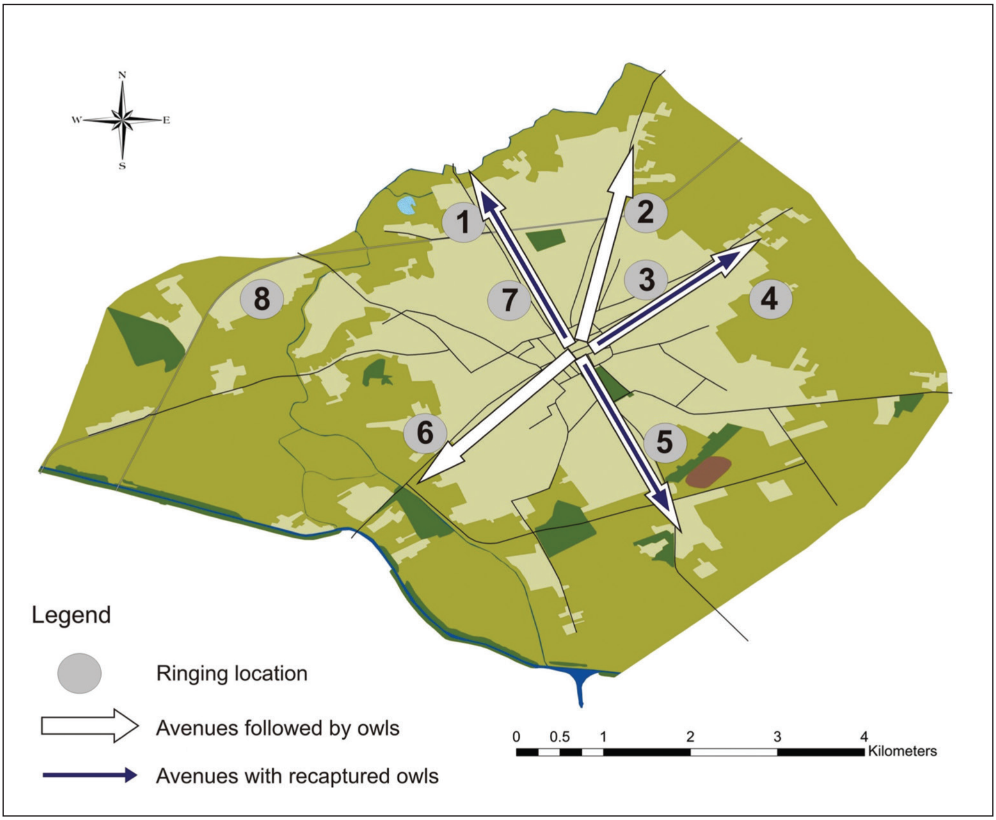


Figure 1. The schematic map of town Sombor. White arrows show the avenues followed by the Long-eared Owls, while blue arrows represent the avenues with recaptures. Grey dots represent ringing locations

1. ábra Zombor város sematikus térképe. A fehér nyilak ábrázolják az erdei fülesbagoly által követett sugárutakat, a kék nyilak pedig a visszafogásokat. A szürke pöttyök a gyűrűzési helyszíneket jelölik

of the town near the courthouse *(Figure 1)*. They often used deciduous trees for roosting, e.g. common hackberry trees, but later, during late autumn and winter, they occupied the surrounding coniferous trees. We have conducted observations of Long-eared Owls on the periphery of the town after sunset. Owls were captured by mist netting (mesh size 60×60 mm) in the early evening hours from 16:30 until 21:30. We used several play-back sounds of field mice calls played from mobile device. The luring voice was mounted near to low, dense shrubs, or dense herbal vegetation, or near heaps of twigs. If the area was relatively open without shrubs, we surrounded the source of the sound by mist nets from two sides, i. e. mist nets were mounted V-shaped. In the case when the sampling location was grown by shrubs, we installed one or two nets (the first followed immediately by the second), the luring call was put in the middle below the nets. We marked owls with aluminium rings at eight locations in the town. We took basic biometric data and determined sex and age using the Euring codes (EURING 2010, Baker 2016).

Results and discussion

We captured altogether 101 Long-eared Owls: 50 males, 49 females and two whose sex could not be determined. Thirty-nine were determined as young individuals (age category 3 or 5, respectively), 53 as adults (age category 4 or 6, respectively), and nine individuals could not be aged (Baker 2016). Besides Long-eared Owls, we ringed four Little Owls *(Athene noctua)* and two European Barn-owls *(Tyto alba)*. Altogether seven individuals were recaptured, four were ringed as adults, and three as young birds. Three owls were recaptured during the same winter and four in the subsequent winter after ringing. All but one of the owls were recaptured in the same corridor they were ringed.

According to our observations, after leaving their roosting site, owls mainly follow the greenery of the main avenues that lead out of the town *(Figure 1)*. We observed up to ten owls flying above the canopy of the trees in the avenues near the outskirts of the town. In the densely built parts of the town and in the outskirts with less greenery, we observed only one or two individuals. Our observations were supported by our ringing activities. Most owls were captured near green corridors.

Despite of the relatively few recaptures, there are implications that owls always use the same corridor (blue arrows in *Figure 1*), apart from one exception. The recapture of the owls is difficult at the location of ringing since they become more alert. We often observed individuals that did not even stop to listen for the mice call (despite we varied calls), suggesting that they already had the "bad" experience of being ringed. In March 2018, we had an opportunity to ring owls in a larger garden (location 7) in corridor 1 that is located halfway between ringing location 1 and the roosting site in the town centre *(Figure 1)*. During three evenings, we have recaptured two owls that were ringed about two weeks earlier at location 1. Our observation contradicts the suggestion of Hume (1991) that Long-eared Owls do not have individual specific hunting territories. Our results suggest that fidelity towards each corridor may possibly be related to hunting areas in the rural areas outside the town.

The explanation for why owls follow the green avenues may be that birds use corridors for better orientation. The town avenues may lead them fast and directly to their possible hunting places in the outskirts and rural habitats. This may be related to the architectural concept of the town, i.e. all main avenues are radially positioned, leaving the centre towards the outskirts. Moreover, the dense canopy of the common hackberry trees and shrubs in the lower layer is an excellent roosting site for sparrows, thrushes and pigeons. Based on pellet analysis Laursen *et al.* (2004) reported that in the neighbouring villages of Sombor Long-eared Owls fed mostly on Common Vole *(Microtus arvalis)* and *Apodemus* mice. However, we assume that owls hunt on birds that roost in the green avenues. In the harsh and snowy winter of March 2018, we observed Long-eared Owls hunting Fieldfare *(Turdus pilaris)* roosting en masse in the canopy of the trees near corridor 1. Earlier, European Barn-owls were observed to hunt roosting House Sparrows *(Passer domesticus)* on London plane trees in Sombor (Mérő & Žuljević 2010).

For stronger evidences and conclusions on the movements of Long-eared Owls between roosting sites and hunting areas further research is needed with larger number of marked individuals on two or more ringing sites per corridor, as well as radio tagging.

Acknowledgements

The ringing permission was issued by the Centre for Animal Marking, Natural-history Museum in Belgrade and by the Ministry of Environmental Protection. The map was drawn by Katalin Varga. T.O.M was supported by the grant from the National Research, Development and Innovation Office of Hungary (NKFIH-OTKA PD 128002). The authors declare no competing interests.

References

Ardia, D. R. & Bildstein, K. L. 1997. Sex-related differences in habitat selection in wintering American Kestrels, *Falco sparverius*. – Animal Behavior 53(6): 1305–1311. DOI: 10.1006/anbe.1996.0364

Baker, J. 2016. Identification of European Non-Passerines. – British Trust for Ornithology, Norfolk

Bentley, J. M. & Catterall, C. P. 1997. The use of bushland, corridors, and linear remnants by birds in southeastern Queensland, Australia. – Conservation Biology 11(5): 1173–1189. DOI: 10.2307/2387400

Bertolino, S., Ghiberti, E. & Perrone, A. 2001. Feeding ecology of the Long-eared Owl *(Asio otus)* in northern Italy: is it a dietary specialist? – Canadian Journal of Zoology 79: 2192–2198. DOI: 10.1139/CJZ-79-12-2192

Bozó, L., Rutkai, T., Csathó, A. I. & Bozóné Borbáth, E. 2020. Winter diet and roosting site fidelity of urban roosting Long-eared Owls *(Asio otus)*, and the change in the species' population size in Southeast Hungary. – Ornis Hungarica 28(2): 1–18. DOI: 10.2478/orhu-2020-0013

Calm, J. B. 1997. Stream corridors for bird movement. – Wildlife Notes 2: 2–5.

Clergeau, P. & Simonnet, E. 1996. Microclimate in communal roost sites of Starlings *Sturnus vulgaris*. – Journal of Ornithology 137: 358–361. DOI: 10.1007/BF01651076

Dawson, J. W. & Mannan, W. R. 1991. The role of territoriality in the social organization of Harris Hawks. – The Auk 108: 661–672. DOI: 10.2307/4088106

EURING 2010. The EURING exchange-code 2000 Plus v112. – Thetford

Gillies, C. S. & St. Clair, C. C. 2008. Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. – Proceedings of the National Academy of Sciences of the USA 105: 19774–19779. DOI: 10.1073/pnas.0803530105

Glue, D. E. 1972. Bird prey taken by British owls. – Bird Study 19(2): 91–96. DOI: 10.1080/00063657209476330

Hume, R. 1991. Owls of the world. – Running Press, Philadelphia

Laursen, T. J., Fritze, E. & Žuljević, A. 2004. Prey composition in the Long-eared Owl *Asio otus* winter diet at three localities in Bačka. – Ciconia 13: 194–196.

Martinez, D. R., Figueroa, R. A., Ocampo, C. L. & Jaksic, F. 1998. Food habits and hunting ranges of Short-eared Owls *(Asio flammeus)* in agricultural landscapes of southern Chile. – Journal of Raptor Research 32(2): 111–115.

Makarova, T. & Sharikov, A. 2015. Winter roost place selection of Long-eared Owls in European Russia. – Journal of Raptor Research 49(3): 333–336. DOI: 10.3356/JRR-13-65.1

Mérő, T. O. & Žuljević, A. 2010. Birds of Sombor. – Nature Protection and Study Society – NATURA, Sombor

Mérő, T. O. & Žuljević, A. 2014. Does the weather influence the autumn and winter movements of tits in urban areas? – Acta Zoologica Bulgarica 66(4): 505–510.

Newton, I. 1986. The Sparrowhawk. – T & AD Poyser, Calton, Staffordshire

Rechetelo, J., Grice, A., Reside, A. E., Hardesty, B. D. & Moloney, J. 2016. Movement Patterns, Home Range Size and Habitat Selection of an Endangered Resource Tracking Species, the Black-Throated Finch *(Poephila cincta cincta)*. – PLoS ONE 11: e0167254. DOI: 10.1371/journal.pone.0167254

Sándor, A. D. & Kiss, B. J. 2008. Birds in the diet of wintering Long-eared Owls *(Asio otus)* in the Danube Delta, Romania. – Journal of Raptor Research 42(4): 292–295. DOI: 10.3356/JRR-08-02.1

Tomić, P. 1996. Klima. – In: Đuričić, J. (ed.) Opština Sombor. – Prirodno-matematički fakultet, Institut za geografiju, Prosveta, Novi Sad, pp. 16–21. (in Serbian)

Vojnović, M. 2001. Sombor. – Publikum, Sombor

Ornis Hungarica 2020. 28(2): 24–36.
DOI: 10.2478/orhu-2020-0015

Analysis of landscape structure, habitat selection and urbanisation in edge populations of Scops Owls *Otus scops* in Central Europe[×]

Ákos Klein[1*], István Szentirmai[2], Zsófia Dobos[1] & Miklós Laczi[1,3]

[×]Presented at 2nd Hungarian Owl Research Conference held in Pécs on 11th September 2020.

Received: October 14, 2020 – October 23, 2020 – Accepted: October 30, 2020

Klein, Á., Szentirmai, I., Dobos, Zs. & Laczi, M. 2020. Analysis of landscape structure, habitat selection and urbanisation in edge populations of Scops Owls *Otus scops* in Central Europe. – Ornis Hungarica 28(2): 24–36. DOI: 10.2478/orhu-2020-0015

Abstract The habitat selection of Scops Owl *Otus scops* has not been studied in Hungary so far. The population in the Carpathian Basin can be considered as a range edge population. Yet, studying and conserving breeding population at the edge of the species' range is important for the evolutionary potential of the species. In the present study, we examined Scops Owl populations situated on both sides of the Hungarian-Slovenian border. Although breeding density is significantly higher in Slovenia than in Hungary, we found no difference in the ecological diversity of the Goričko Nature Park (GNP), Slovenia and Vas County, Hungary. We found that both the proportion and total edge length of dry grasslands and intensively managed mesic grasslands were lower in Hungary. Similarly, market gardens were present in a larger proportion in GNP. These landscape features all indicate that the complex cultivation is still pronounced in GNP, favouring the Sops Owl as less intensive cultivation modes, like rural market gardens and grasslands play a key role in its habitat selection. Points with Scops Owl observations appeared to be closer to settlements than randomly generated points. They also were observed farther from primary roads than from secondary roads. This is in accordance with other studies revealing that these nocturnal birds avoid noisy roads. We briefly discuss why conserving range edge populations is important, and how time and effort optimised species conservation measures should accompany landscape protection at the political level.

Keywords: range edge population, farmland bird, common agriculture policy, predation, Tawny Owl

Összefoglalás A füleskuvik *Otus scops* a Kárpát-medencében perempopulációnak tekinthető az európai állomány zömét alkotó mediterrán népességhez képest. Mégis, az elterjedési terület szélén elhelyezkedő költőállomány vizsgálata és védelme evolúciós szempontból fontos. A jelen tanulmányban a magyar-szlovén határ két oldalán megtalálható, denzitásában jelentősen eltérő füleskuvik állományt vizsgáltuk. Nem találtunk eltérést a Goričko Tájpark és Vas megye ökológiai diverzitásában. Kimutatható volt, hogy a szlovén mintaterületen magasabb arányban vannak jelen a komplex művelésre utaló mezőgazdasági kultúrák (száraz gyepek, közepesen intenzíven kezelt gyepek, település közeli zöldségeskertek). E művelési ágak egymás melletti sokfélesége kedvez a füleskuvikok megtelepedésének. Kimutattuk, hogy a füleskuvikok a véletlenszerűhöz képest közelebb helyezkednek el a településekhez és a településekhez kötődő utakhoz, de az elsőrendű, forgalmasabb úttípusoktól távolabb fordulnak elő. Eredményeink erősítik a korábban már leírtakat, miszerint az utak elsősorban zajterhelésükkel taszítják a gyakran vokalizáló madarakat. A hazai viszonyokra javasoljuk a tájban kialakítani a veterán fák és állandósult cserjesorok hálózatát, illetve hosszútávon elkerülhetetlen a tájszerkezet további leromlásának megfékezése erőteljes szakpolitikai döntések segítségével.

Kulcsszavak: perempopuláció, Közös Agrárpolitika, urbanizáció, zajterhelés, predáció, macskabagoly

[1] *The Barn Owl Foundation, 8744 Orosztony Temesvári utca 8.*
[2] *Őrség National Park Directorate, 9941 Őriszentpéter, Városszer 57.*
[3] *Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University, 1117 Budapest Pázmány Péter sétány 1/C*
**corresponding author, e-mail: barnowlfoundation@gmail.com*

Introduction

The Scops Owl *Otus scops* is the only long-distance migrant European owl species. Its largest population can be found in the Mediterranean. Its spatial distribution in Europe is constrained by the chains of Alps and Carpathians, and this species reaches north in Asia as far as the 16 °C isotherm line (Gill & Donsker 2019). The total European population is cca. 232,000–393,000 pairs that constitutes approximately 60% of the world population (BirdLife International 2020).

Both the large geographic range and population size justify that its IUCN (International Union for Conservation of Nature) status is „least concern". Contrastingly, it is regarded as one of the most rapidly declining owl species in Europe (Sergio *et al.* 2009). Several recent publications intended to reveal the most important factors that can explain this decrease (Denac *et al.* 2019, Ivajnšič *et al.* 2020).

In many species, populations close to the edge of their range are especially important for their preservation as breeding individuals may often occupy suboptimal habitats, hence evolutionary forces can act differently to the central populations. Highly variable recruitment, lower fecundity, increased population fragmentation and increased adult dispersal are only some of the factors that can contribute to the vulnerability of edge populations (Gaston 2009).

Hungary, Slovakia and Ukraine constitute the Northern brim of Scops Owl's European range. A moderate expansion of this species was detectable in the 1950s in the Carpathian Basin, similarly to Syrian Woodpeckers *(Dendrocopos syriacus)* and Eurasian Collared Doves *(Streptopelia decaocto)* (Randik 1959). Ornithologists, almost seven decades ago, had already explained this expansion with the increase of the average temperature in Europe (Barthos 1957, Randik 1959).

The distribution of the Scops Owl in Hungary is not exhaustedly mapped yet. The breeding population in Hungary is about 300–600 pairs (Hadarics & Zalai 2008, MME 2020). The highest population density can be found in Central Hungary (Duna-Tisza Interfluvial), whereas in the Western part of Hungary, only very sporadic breeding records are known. At the same time, in Northeast Slovenia (Goričko Region), 210 calling males were recorded in the investigated area covering 442 km^2 in 1997 (Štumberger 2000), and even after a severe 70% population decline, there are still 60-70 breeding pairs in this region (Denac *et al.* 2019). Northeast Slovenia and West Hungary are adjacent areas in Central Europe, and they share many similarities in terms of landscape characteristics, climate and geography.

In this study, we endeavoured to reveal why geographically similar areas carry Scops Owl populations of very different sizes. We also tried to find explanations about landscape features that may be accountable for Scops Owl distribution in West Hungary (Vas County). In order to answer these questions, we carried out systematic Scops Owl surveys in 2019.

Landscape structure was compared between the Slovenian and the Hungarian study areas. We investigated the relationship between road network, settlements and water courses and the spatial distribution of the Scops Owl.

Material and methods

Study area and data collection

Data were collected in Vas County (Hungary, 3,336 km^2, 47°05'13"N, 16°42'17"E) and in Goričko Nature Park (Slovenia, 463.5 km^2, mentioned as GNP hereafter, 46°46'32"N, 16°11'46"E) *(Figure 1)*. A representative Scops Owl survey was carried out in 2019 in 79 out of the total of 632 UTM quadrates (2.5 × 2.5 km each) that covers 14.8% of the territories of Vas County. The 79 quadrates were systematically selected: 50% of them within the area of the National Ecological Network (http://web.okir.hu/map), the other half outside of this network. Data arising from 2019 and previously recorded observations from national databases (www.birding.hu 2006.06.30-2019.04.02., www.map.mme.hu 2008.05.03-2018.10.09., Őrség National Park database 2012.03.17-2018.10.18.) were pooled. Prior to 2019, a total of 43 Scops Owl observations were extracted from the database. In 2019, a total of 10 calling males were observed from the 79 UTM quadrates. Data from Goričko were kindly provided by K. Denac (DOPPS, BirdLife Slovenia). For the analyses, we used a total of 12 Hungarian and 18 Slovenian independent observations. The rest of the data points were multiple observations from the same locations that were excluded from the analyses.

Environmental variables

The home range of the Scops Owl was defined as a 30 ha circular plot (309 m radius) around the nest site (Martínez *et al.* 2007). We investigated environmental (habitat) variables within a larger, 500 m radius circle drawn around the observation points. A land cover map with a resolution of 10 m/pixel was used to analyse ecological diversity (map created by University of Vienna, M. Pöchtrager in 2019, unpublished). This map was created with the interpretation of Sentinel-2 satellite images (Copernicus Sentinel data 2017 & 2018) in which each pixel was assigned to one of the EUNIS level-2 habitat types (Davies *et al.* 2004). 12 out of the total of 22 habitat types were used for the analyses, after we excluded those that were only represented in small proportion of the 500 m large sample circles *(Table 1)*.

Data and GIS analysis

We performed Mann-Whitney U-tests on the individual habitat variables to compare the Hungarian and the Slovenian observation points of Scops Owls. We adjusted the significance levels by Benjamini-Hochberg FDR correction (Benjamini *&* Hochberg 1995). Then, we explored whether there was any difference between the countries if we treated the habitat variables as composite indices. In order to do this, we performed principal component

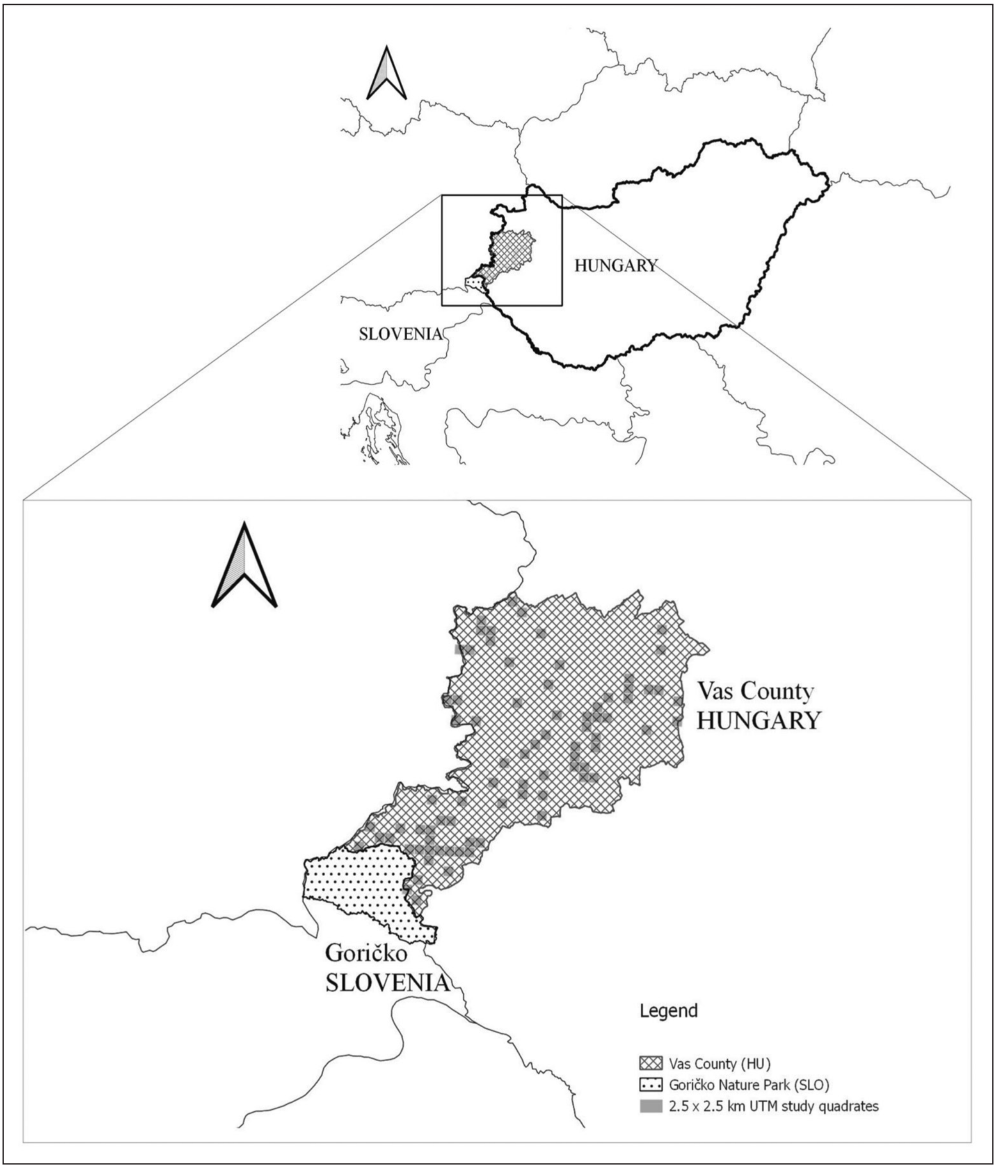


Figure 1. Map of the study area in Hungary (Vas County ▩) and in Slovenia (Goričko Nature Park ⁙)

1. ábra A vizsgálati terület áttekintő térképe (Vas megye ▩, Goričko Tájpark ⁙)

analysis (PCA) on these variables with varimax rotation, and then we compared the principal components (PCs) between countries using Mann-Whitney U-tests. We used in the analyses only PCs of which eigenvalues was larger than one.

In addition, we also applied a Geographic Information System (GIS) approach to generate Ecological Diversity Indices. We used Landscape Ecology Statistics (LecoS v. 3.0.0)

Table 1. Habitat categories generated by remote sensing and used (1) in the landscape analysis
1. táblázat Távérzékelés során kialakított élőhelykategóriák. Az 1 jelű élőhelytípusok kerültek felhasználásra az elemzésben

Habitat type	Used for analysis
Inland surface waters – standing	0
Inland surface waters – watercourses	0
Wetlands with reed, tall herbs	0
Wetlands with pioneer vegetation	0
Mires, bogs and fens	0
Dry grasslands	1
Mesic grassland, intensively managed	1
Mesic grassland, medium intensive	1
Seasonally wet and wet grasslands	1
Temperate thickets and scrub	1
Dry heaths	0
Riverine and fen scrubs	0
Broadleaved deciduous woodland	1
Broadleaved evergreen woodland	0
Coniferous woodland	1
Lines of trees or hedgerows	0
Recently felled areas	0
Arable land and market gardens – intensive	1
Arable land and market gardens – low intensity	1
Cultivated areas of gardens and parks	1
Constructed, industrial and other artificial habitats – with significant green spaces	1
Constructed, industrial and other artificial habitats – high imperviousness	1

module in Quantum GIS (QGIS, 3.10.0-A Coruña). LecoS contains several analytical functions for land cover analysis. It can calculate Shannon diversity, evenness, Simpson diversity, perimeter, area and proportion of habitat patches within a polygon. We compared these metrics between countries using Mann-Whitney U-tests.

We applied square-root transformation on the distance variables in order to achieve normality according to Lilliefors tests and QQ-plots. As the data set of Scops Owl observations with regard to distance from paved roads was only partly overlapping with the data set connected to distances from water bodies and settlements, we investigated these variables separately.

We examined the distance from roads using general linear model (GLM). Distance from roads was the dependent variable, country and road were discrete fixed effects, and we investigated the interaction of these too. As tertiary roads and motorways were absent in the Hungarian areas where Scops Owls were detected, we excluded these two categories from the analyses.

Table 2. Differences of individual habitat variables in Scops Owl observation points between Hungary (N=12) and Slovenia (N=18)

2. táblázat A magyarországi (N=12) és szlovéniai (N=18) füleskuvik megfigyelési pontok körüli élőhelyfoltok fedettségének, arányának és szegélyhosszának összehasonlítása

Variable	**Mean rank**				
	Hungary	**Slovenia**	**U**	**Z**	
LP-Dry grasslands	12.05	20.67	46.00	-2.62	**†
EL-Dry grasslands	11.72	21.17	40.00	-2.88	**†
MPA-Dry grasslands	13.56	18.42	73.00	-1.48	
LP-Mesic grassland, intensively managed	19.96	12.53	54.00	-2.26	*
EL-Mesic grassland, intensively managed	20.00	12.50	54.00	-2.27	*
MPA-Mesic grassland, intensively managed	12.11	20.58	47.00	2.58	**†
LP-Mesic grassland, medium intensive	15.17	16,00	102.00	0.25	
EL-Mesic grassland, medium intensive	14.22	17.42	85.00	0.97	
MPA-Mesic grassland, medium intensive	16,00	14.75	99.00	-0.38	
LP-Seasonally wet and wet grasslands	16.17	14.50	96.00	-0.51	
EL-Seasonally wet and wet grasslands	15.97	14.79	99.50	-0.36	
MPA-Seasonally wet and wet grasslands	17.56	12.42	71.00	-1.57	
LP-Temperate thickets and scrub	16.31	14.29	93.50	-0.61	
EL-Temperate thickets and scrub	16.31	14.29	93.50	-0.61	
MPA-Temperate thickets and scrub	16.05	14.67	98.00	-0.42	
LP-Broadleaved deciduous woodland	15.89	14.92	101.00	-0.30	
EL-Broadleaved deciduous woodland	17.33	12.75	75.00	-1.40	
MPA-Broadleaved deciduous woodland	14.28	17.33	86.00	0.93	
LP-Coniferous woodland	17.75	12.12	67.50	-1.71	
EL-Coniferous woodland	17.97	11.79	63.50	-1.88	
MPA-Coniferous woodland	17.50	12.50	72.00	-1.52	
LP-Arable land and market gardens – intensive	11.72	21.17	40.00	2.88	**†
EL-Arable land and market gardens – intensive	10.50	23,00	18.00	3.81	***†
MPA-Arable land and market gardens – intensive	12.56	19.92	55.00	2.24	*
LP-Arable land and market gardens – low intensity	10.94	22.33	26.00	3.47	***†
EL-Arable land and market gardens – low intensity	9.83	24,00	6.00	4.32	***†
MPA-Arable land and market gardens – low intensity	12.83	19.50	60.00	2.03	*
LP-Cultivated areas of gardens and parks	17.75	12.13	67.50	-1.71	
EL-Cultivated areas of gardens and parks	17.17	13,00	78.00	-1.27	
MPA-Cultivated areas of gardens and parks	18.53	10.96	53.50	-2.31	*
LP-Constructed habitats – significant green spaces	15.56	15.42	107.00	-0.04	
EL-Constructed habitats – significant green spaces	14.33	17.25	87.00	0.89	
MPA-Constructed habitats – significant green spaces	18.33	11.25	57.00	-2.16	*
LP-Constructed habitats – high imperviousness	14.08	17.63	82.50	1.08	
EL-Constructed habitats – high imperviousness	13.53	18.46	72.50	1.50	
MPA-Constructed habitats – high imperviousness	16.36	14.21	92.50	-0.66	

LP – landscape proportion, EL – edge length, MPA – mean patch area

* P<0.05, ** P<0.01, *** P<0.001, † P values remained significant after Benjamini-Hochberg FDR correction were marked with bold)

Table 3. Loadings of the principal components (PCs) performed on habitat variables
3. táblázat A főkomponens (PC) elemzés során az élőhelyjellemzőkre számított származtatott változók

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
LP-Dry grasslands	0.03	-0.11	0.01	0.14	-0.12	**0.96**	-0.10	0.01	-0.02
EL-Dry grasslands	0.11	-0.18	0.04	0.37	-0.17	**0.85**	-0.11	0.00	-0.06
MPA-Dry grasslands	-0.08	-0.14	0.07	-0.14	-0.17	**0.91**	-0.11	0.06	-0.05
LP-Mesic grassland, intensively managed	0.13	-0.06	-0.05	**0.93**	-0.10	0.08	-0.01	0.00	-0.01
EL-Mesic grassland, intensively managed	0.07	-0.10	-0.02	**0.94**	-0.13	0.12	0.01	0.05	-0.01
MPA-Mesic grassland, intensively managed	0.20	-0.17	0.00	**0.85**	-0.25	0.05	-0.07	0.02	-0.10
LP-Mesic grassland, medium intensive	-0.34	-0.34	0.36	0.43	-0.24	0.42	-0.04	0.05	-0.18
EL-Mesic grassland, medium intensive	-0.11	-0.33	0.25	**0.62**	-0.02	0.53	0.01	0.13	-0.15
MPA-Mesic grassland, medium intensive	-0.46	-0.38	0.42	0.14	-0.29	0.19	-0.16	0.05	-0.02
LP-Seasonally wet and wet grasslands	0.03	-0.09	-0.07	-0.08	0.03	-0.11	**0.97**	0.01	-0.02
EL-Seasonally wet and wet grasslands	0.09	-0.12	0.06	0.39	0.14	-0.08	**0.83**	0.15	0.06
MPA-Seasonally wet and wet grasslands	0.00	-0.10	-0.17	-0.31	-0.04	-0.15	**0.83**	-0.17	-0.02
LP-Temperate thickets and scrub	-0.26	-0.17	**0.89**	0.07	-0.12	0.10	-0.02	0.09	0.14
EL-Temperate thickets and scrub	-0.30	-0.21	**0.82**	0.15	-0.13	0.20	0.02	0.17	0.04
MPA-Temperate thickets and scrub	-0.14	-0.17	0.48	-0.03	-0.18	0.01	0.02	0.16	**0.78**
LP-Broadleaved deciduous woodland	-0.39	-0.37	0.02	0.05	-0.17	0.05	-0.05	**0.73**	0.15
EL-Broadleaved deciduous woodland	-0.48	-0.46	0.28	0.10	-0.15	0.02	-0.05	**0.61**	-0.16
MPA-Broadleaved deciduous woodland	-0.11	-0.20	0.02	0.07	-0.15	0.03	0.01	0.55	**0.71**
LP-Coniferous woodland	-0.45	-0.29	0.54	-0.18	-0.34	-0.10	-0.23	0.22	-0.22
EL-Coniferous woodland	-0.48	-0.33	0.49	-0.19	-0.36	-0.10	-0.23	0.28	-0.22
MPA-Coniferous woodland	-0.18	-0.17	**0.84**	-0.17	-0.17	-0.07	-0.15	0.01	0.06
LP-Arable land and market gardens – intensive	**0.74**	-0.18	-0.24	-0.15	-0.25	-0.19	-0.06	-0.24	0.38
EL-Arable land and market gardens – intensive	**0.90**	-0.11	-0.24	-0.01	-0.02	-0.09	-0.07	-0.21	-0.02
MPA-Arable land and market gardens – intensive	0.17	-0.14	-0.08	-0.18	-0.11	-0.19	-0.01	-0.07	**0.90**
LP-Arable land and market gardens – low intensity	**0.90**	-0.06	-0.14	0.20	0.14	0.08	0.18	0.17	-0.10
EL-Arable land and market gardens – low intensity	**0.92**	-0.08	-0.15	0.28	-0.10	0.12	-0.01	-0.05	-0.06
MPA-Arable land and market gardens – low intensity	0.39	-0.08	-0.01	-0.03	**0.62**	-0.02	0.37	0.49	0.05

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
LP-Cultivated areas of gardens and parks	-0.13	0.01	-0.19	-0.21	**0.89**	-0.21	0.00	-0.19	-0.13
EL-Cultivated areas of gardens and parks	-0.13	-0.01	-0.23	-0.20	**0.81**	-0.21	0.13	-0.31	-0.02
MPA-Cultivated areas of gardens and parks	-0.04	-0.02	-0.11	-0.18	**0.92**	-0.17	-0.05	0.08	-0.10
LP-Constructed habitats – significant green spaces	-0.23	**0.76**	-0.28	-0.15	0.17	-0.22	-0.02	-0.37	-0.16
EL-Constructed habitats – significant green spaces	0.06	0.51	-0.36	-0.08	0.15	-0.13	-0.09	**-0.61**	-0.29
MPA-Constructed habitats – significant green spaces	-0.18	**0.89**	-0.06	-0.08	-0.14	-0.09	-0.06	0.09	-0.02
LP-Constructed habitats – high imperviousness	-0.02	**0.92**	-0.15	-0.14	0.01	-0.14	-0.11	-0.19	-0.14
EL-Constructed habitats – high imperviousness	0.02	**0.93**	-0.16	-0.13	-0.04	-0.14	-0.12	-0.16	-0.13
MPA-Constructed habitats – high imperviousness	-0.07	0.35	0.26	0.06	0.10	-0.01	0.29	-0.41	-0.27
Eigenvalue	4.78	4.78	4.06	4.02	3.68	3.43	2.83	2.74	2.66
Explained variance (%)	13.29	13.26	11.22	11.16	10.22	9.53	7.87	7.60	7.38
Cumulative variance (%)	13.29	26.55	37.77	48.93	59.15	68.68	76.55	84.15	91.53

Loading values which exceeded the lower threshold of 0.60 were marked with bold.

Table 4. Differences of habitat principal components (PCs) in Scops Owl observation points between Hungary (N=12) and Slovenia (N=18)

4. táblázat Az élőhelyre vonatkozó főkomponensek (PC) közötti különbségek a magyar (N=12) és a szlovén (N=18) területeken található füleskuvik észlelési pontok körül

	Mean rank				
Variable	**Hungary**	**Slovenia**	**U**	**Z**	
PC1	10.50	23.00	18.00	3.81	***
PC2	14.17	17.50	84.00	1.02	
PC3	15.78	15.08	103.00	-0.21	
PC4	14.44	17.08	89.00	0.80	
PC5	16.61	13.83	88.00	-0.85	
PC6	13.94	17.83	80.00	1.19	
PC7	16.22	14.42	95.00	-0.55	
PC8	15.17	16,00	102.00	0.25	
PC9	14,00	17.75	81.00	1.14	

Table 5. Differences of habitat diversity indices in Scops Owl observation points between Hungary (N=12) and Slovenia (N=18)

5. táblázat Az ökológiai diverzitás mutatószámaiban mérhető különbségek a magyarországi (N=12) és a szlovéniai (N=18) területeken található füleskuvik észlelési pontok körül

Variable	Mean rank			
	Hungary	**Slovenia**	**U**	**Z**
Shannon diversity	13.72	18.17	76.00	-1.35
Evenness	13.33	18.75	69.00	-1.65
Simpson diversity	13.22	18.92	67.00	-1.74

Using GLMs, we also explored if there is any difference in distances (from roads, settlements and water bodies) between real field observations and randomly selected points. In each GLM, one of the four distance variables was the dependent variable, country and observation type (real *vs*. randomized) were used as discrete fixed effects, and the initial model included the interaction of these factors.

Random spatial points were generated by QGIS (vector/research tools/random points inside polygons) within those 2.5 × 2.5 km UTM quadrates where Scops Owls were absent.

For GLMs, we applied backward stepwise model simplification (Hegyi *&* Laczi 2015). We performed the statistical analyses in Statistica 7.0 (Statsoft, Inc.).

Results

Environmental variables

We detected significant differences between countries in seven habitat variables: proportion and edge length of dry grasslands were lower in Hungary, as well as the mean patch area of intensively managed mesic grasslands, proportions and edge lengths of intensive and low intensity arable land and market gardens *(Table 2)*. The PCA resulted in nine PCs with eigenvalue larger than one *(Table 3)*. Higher value of a given PC means larger values in the original variables with positive loadings, and lower values in the original variables with negative loadings. According to this, e.g. higher PC1 represents larger proportions and edge lengths of intensive and low intensity arable land and market gardens. Between countries, only PC1 differed significantly, i.e. it was higher in Slovenia *(Table 4)*, which is partly in concordance with the previous results. Ecological (landscape) diversity indices did not differ between the two countries *(Table 5)*.

Distances from roads

Analyses revealed that Scops Owls occupied habitats slightly farther from roads in Hungary than in Slovenia ($F_{1,48}$ = 4.54, P = 0.038, mean ± SD: 46.74 ± 7.39 in Hungary, 44.28 ± 4.33 in Slovenia), independently of road types (primary and secondary). However, road type also had a significant effect ($F_{1,48}$ = 176.74, P<0.0001) because Scops Owls were observed further from primary roads than from secondary roads *(Figure 2)*, independently of country. The ’road type x country’ interaction was not significant ($F_{1,47}$ = 2.15, P=0.15).

Distance from settlements and water bodies

Comparing real and randomized data, GLMs revealed that distances were smaller in the case of real observations from primary roads (mean±SE, real: 66.14 ± 4.48, random: 90.84 ± 5.15), secondary roads (real: 17.73 ± 2.08, random: 31.02 ± 2.70) and settlements (real: 34.62 ± 3.52, random: 50.67 ± 4.04) irrespective of country, but there was no difference in distances from water bodies (real: 16.20 ± 1.40, random: 19.10 ± 1.58) *(Table 6)*.

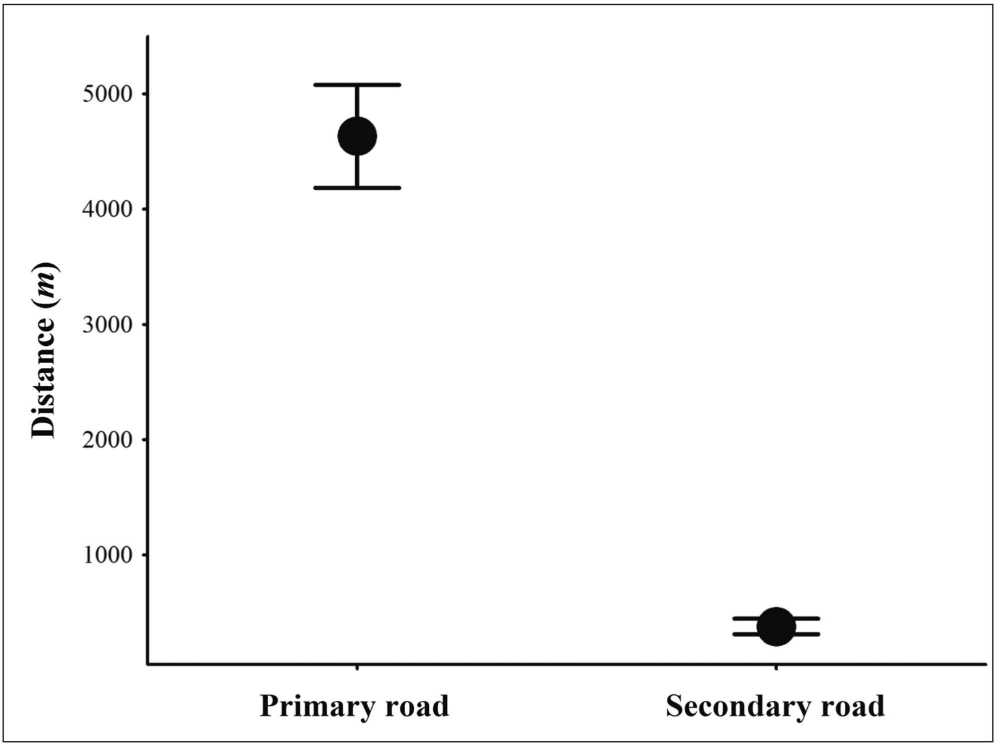


Figure 2. Distance of Scops Owl observations from different road types in Hungary and Slovenia. For illustration, we presented the raw distance data (mean±SE)

2. ábra Különböző úttípusoktól mért távolságok. A szemléltetéshez a valós távolsági adatokat (átlag±SE) ábrázoltuk

Discussion

Several studies attempted to explain the population decline of the Scops Owl in Europe (Sergio *et al.* 2009, Treggiari *et al.* 2013, Denac *et al.* 2019). Landscape transformation and the change in agricultural use undoubtedly lead the list of human induced factors, however, revealing these effects still remains a real challenge in Central Europe, outside the core Mediterranean range (Ivajnšič *et al.* 2020).

Sergio *et al.* (2009) concludes that Scops Owl abundance in the Central-Eastern Italian pre-Alps is determined by two factors. Scops Owl territories differed from randomly generated locations in two respects: (1) extensive agriculture (length of hedgerows and availability of individual trees) and (2) proximity to the Tawny Owl *Strix aluco* territories, its main predator.

It has previously been tested and proved that the abundance of the Scops Owl is associated with a mosaic of land-use categories (Denac *et al.* 2019). Although there are well visible differences in landscape structure between GNP and Vas County, we did not find evidence that these differences were associated with the difference in the Scops Owl carrying capacity of the two regions. The agricultural conditions in Slovenia allowed the preservation of the patchwork-like landscape with large number of small (<2 ha) plots managed by different farmers. This landscape structure is able to maintain high versatility of various cultivations, large network of unmanaged hedges and verges and consequently, rich biodiversity. By contrast, in Hungary more than 95% of agricultural land had become the property of collective farms between 1945 and 1961 (Swain 1985) that ultimately resulted in a transformed landscape structure dominated by large monocultures across the whole of Hungary. Vas County is regarded as one of the regions in Hungary that managed to save a remarkable proportion of the mosaic landscape, which may explain the lack of significant difference in the ecological diversity indices between GNP and Vas County in our study.

The average size of habitat plots and the total length of edges *per se* are certainly important features, but the actual composition of differently farmed plots in the landscape might tell even more about the suitability of a habitat for Scops Owls. We found that both proportion and edge length of dry grasslands and intensively managed mesic grasslands were lower in Hungary. Also, market gardens were present in a larger proportion in GNP. These landscape features all indicate that in GNP the complex cultivation is still pronounced, and less intensive cultivation modes, like rural market gardens and grasslands play a key role in Sops Owl habitat selection.

The dire decline of Scops Owl population over the past 25 years in GNP (Štumberger 2000, Denac *et al.* 2019) warns conservationists and policy makers that adverse landscape transformation reaches even the last strongholds of our sensitive iconic species. By modelling Scops Owl breeding suitability in GNP, Ivajnšič *et al.* (2020) outlined a predictable significant population decrease (by 33%) in GNP in the next 50 years. They discuss in detail that EU Common Agricultural Policy (CAP) is poorly adapted to the needs of Central and Eastern European low-intensity farming traditions, especially with regards to the high biodiversity grasslands. At the European level, an adapted CAP and specifically tailored subsidy schemes can support farmers to maintain large landscape complexity. However, to our opinion such interventions are only able to expand the agony of the post-rural countryside in Central Europe. Current food production policy, expensive agricultural technology and global trade agreements all mean impediments to a self-sustained small-scale agricultural practice that could restore biodiversity focused farming and local communities long-term.

Before such structural economic and societal changes take place, cost and time effective conservation interventions are needed to ensure the viability of endangered bird populations. In agreement with the conclusions of Sergio *et al.* (2009), who pointed out the importance of the individual trees and network of hedges, we recommend the establishment of a network of Veteran Tree Reserves (VTRs) in Vas County. The Hungarian landscape, unlike that of some other European countries as England, lack old trees. Historical, cultural and legislative factors played a role over the past two centuries in that most of the ancient tree specimens along with the network of hedges and unmanaged verges disappeared from the rural countryside. Hedges and solitary trees hold value both for biodiversity and landscape if their lifespan overarch centuries. This longevity was ensured in the United Kingdom since the early medieval era, as hedges and planted trees displayed field boundaries and the preservation of these landscape features became an organic part of the culture, up to the 1950s, when post-war industrial agriculture eliminated a great deal of these wildlife corridors (Barnes & Williamson 2006). Newly established VTRs would increase connectivity between cross-border subpopulations and between individual breeding pairs, and they would provide suitable calling, breeding and foraging habitats for Scops Owls.

The network of VTRs can be improved even if the coexistence of Tawny Owl and Scops Owl have not been investigated in Hungary yet. The Tawny Owl is a common nocturnal predator in W Hungary, whereas its presence is less pronounced in C Hungary, where the most stable Scops Owl populations exist (MME 2020). However, further investigations are needed to clarify how certain locations in Vas County serve as traditional Scops Owl breeding sites for decades, where Tawny Owls are permanently present as well.

A possible explanation can be the protection provided by the urban environment. Scops Owl observations in this study appeared to be closer to settlements than the ones randomly generated in the landscape. It can be assumed that Tawny Owls hunt less frequently in settlements. Streetlight in urban environment also can attract Scops Owls closer to settlements, although there was no correlation between spatial breeding distribution and light pollution patterns in GNP (Ivajnšič *et al.* 2020). As Sergio *et al.* (2007) pointed out, intraguild predation among owl species is density dependent. There might be a threshold of abundance, beyond which the effect of Tawny Owl predation risk on Scops Owl occurrence becomes significant.

Moreover, Scops Owls were observed farther from primary roads than from secondary roads. This is in accordance with other studies showing that corticosterone level was higher in owlets hatched closer to roads (Expósito-Granados *et al.* 2019). Šušmelj (2011) also concluded that larger distance from highways increased the likelihood of Scops Owl settlement in the Slovenian Karst.

Conservation effort should be prioritised in an era, where ecological and climate crisis sweeps thousands of species away. Conserving range edge populations is important as these populations are the best subjects for fast adaptation and speciation. However, investing disproportional capacities in the reinforcement of sink populations when the source ones are under dire threat, needs to be reconsidered. The deployment of cost-effective and sustainable conservation measures, like the introduction of VTRs network, is an obvious step to take, but ultimately the solutions must urge the halt of further large-scale landscape transformations at the policy level.

Acknowledgements

The fieldwork was funded by the INTERREG Danube Transnational Programme DTP2-007-2.3. We thank MME – BirdLife Hungary, the team of Birding.hu, Őrség National Park staff and several field ornithologists for providing Scops Owl data from Hungary. Katerine Denac (DOPPS, BirdLife – Slovenia) offered kindly data and information of the Goričko Scops Owl population.

References

Barnes, W. & Williamson, T. 2006. Hedgerow History: Ecology, History and Landscape Character. – Windgather Press, Cheshire

Barthos, Gy. 1957. Breeding Scops Owl in South-Western Hungary. – Aquila 63–64: 288–289., 344–345. (in Hungarian with English Summary)

Benjamini, Y. & Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. – Journal of the Royal Statistical Society B 57(1): 289–300.

BirdLife International 2020. Species factsheet: *Otus scops*. – http://www.birdlife.org

Davies, C. E., Moss, D. & Hill, M. O. 2004. EUNIS Habitat Classification Revised 2004. Report to the European Topic Centre on Nature Conservation, European Environment Agency, October 2004.

Denac, K., Kmecl, P. & Koce, U. 2019. Habitat use of Eurasian Scops Owls *Otus scops* in an agricultural mosaic landscape. – Ardea 107(2): 119–129. DOI: 10.5253/arde.v107i2.a1

Expósito-Granados, M., Parejo, D., Chastel, O. & Avilés, J. M. 2019. Physiological stress and behavioural responses of European Rollers and Eurasian Scops Owls to human disturbance differ in farming habitats in the south of Spain. – Bird Conservation International, Cambridge University Press, pp. 1–16. DOI: 10.1017/S0959270919000388

Gill, F. & Donsker, D. 2019. IOC World Bird List (v 9.2). – DOI: 10.14344/IOC.ML.9.2.

Gaston, K. 2009. Geographic range limits: Achieving synthesis. – Proceedings of the Royal Society B: Biological Sciences 276: 1395–1406. DOI: 10.1098/rspb.2008.1480

Hadarics, T. & Zalai, T. 2008. Nomenclator Avium Hungariae Magyarország Madarainak Névjegyzéke – An annonated list of the birds of Hungary. – MME Birdlife Hungary, Budapest (in Hungarian with English Summary)

Hegyi, G. & Laczi, M. 2015. Using full models, stepwise regression and model selection in ecological data sets: Monte Carlo simulations. – Annales Zoologici Fennici 52: 145–159. DOI: 10.5735/086.052.0502

Ivajnšič, D., Denac, D., Denac, K., Pipenbaher, N. & Kaligarič, M. 2020. The Scops Owl *(Otus scops)* under human-induced environmental change pressure. – Land Use Policy 99: 104853. DOI: 10.1016/j.landusepol.2020.104853

MME 2020 – Magyar Madártani és Természetvédelmi Egyesület. Magyarország madarai. – BirdLife Hungary, The Birds of Hungary on-line database. – https://www.mme.hu/magyarorszagmadarai/madaradatbazis (in Hungarian)

Martínez, J. A., Zuberogoitia, I., Martínez, J. E., Zabala, J. & Calvo, F. 2007. Patterns of territory settlement by Eurasian Scops-owls *(Otus scops)* in altered semi-arid landscapes. – Journal of Arid Environments 69(3): 400–409. DOI: 10.1016/j.jaridenv.2006.10.011

Randik, A. 1959. The Distribution of the Scops Owl in the Carpathian Basin. – Aquila 66: 99–106., 104–106. (in Hungarian with English Summary)

Sergio, F., Marchesi, P., Pedrini, P. & Penteriani, V. 2007. Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? – Animal Behaviour 74: 1607–1616. DOI: 10.1016/j.anbehav.2006.10.022

Sergio, F., Marchesi, L. & Pedrini, P. 2009. Conservation of Scops Owl *Otus scops* in the Alps: relationships with grassland management, predation risk and wider biodiversity. – Ibis 151(1): 40–50. DOI: 10.1111/j.1474-919X.2008.00865.x.

Štumberger, B. 2000. Veliki skovik *Otus scops* na Goričkem [Eurasian Scops Owl *Otus scops* at Goričko (NE Slovenia)]. – Acrocephalus 21: 23–29. (in Slovenian)

Šušmelj, T. 2011. The impact of environmental factors on distribution of Scops Owl *Otus scops* in the wider area of Kras (SW Slovenia). – Acrocephalus 32(148–149): 11–28.

Swain, N. 1985. Collective Farms Which Work? – Cambridge University Press, Cambridge

Treggiari, A. A., Gagliardone, M., Pellegrino, I. & Cucco, M. 2013. Habitat selection in a changing environment: the relationship between habitat alteration and Scops Owl (Aves: strigidae) territory occupancy. – Italian Journal of Zoology 80(4): 574–585. DOI: 10.1080/11250003.2013.853843

sciendo

Ornis Hungarica 2020. 28(2): 37–65.
DOI: 10.2478/orhu-2020-0016

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

Adrienn Horváth[1], László Bank[2] & Győző F. Horváth[1]*

[×] Presented at 2nd Hungarian Owl Research Conference held in Pécs on 11th September 2020.

Received: November 05, 2020 – Revised: November 22, 2020 – Accepted: November 23, 2020

Horváth, A., Bank, L. & Horváth, Gy. F. 2020. Variation in the diet and breeding biology of the Common Barn-owl *(Tyto alba)* in a demographic cycle of Common Vole *(Microtus arvalis)* between two outbreaks – Ornis Hungarica 28(2): 37–65. DOI: 10.2478/orhu-2020-0016

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

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

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

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

Kulcsszavak: reprodukciós kimenet, táplálékfogyasztás, alternatív zsákmány, gradáció

[1] *University of Pécs, Faculty of Sciences, Institute of Biology, Department of Ecology, 7624 Pécs, Ifjúság utca 6., Hungary*
[2] *Baranya County Group of BirdLife Hungary, 7632 Pécs, Siklósi út 94., Hungary BirdLife Hungary, 1121 Budapest, Költő utca 21., Hungary*
** corresponding author, e-mail: hgypte@gamma.ttk.pte.hu*

Introduction

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

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

In temperate ecosystems, Bernard *et al.* (2010) reported how the dietary response of Common Barn-owl can be affected by the density of prey species and demonstrated that the frequency of a given prey in the diet depends also on the population density or availability of other species. The feeding behaviour of Barn Owls is generally opportunistic (Bernard *et al.* 2010), but complex patterns of prey selection with switching mechanism to alternative prey were reported by studies particularly in arid environments, where food intake results supported that the Common Barn-owl is a rather selective opportunistic predator (Heywood & Pavey 2002, Tores *et al.* 2005, McDowell & Medlin 2009, Romano *et al.* 2020).

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

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

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

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

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

Material and methods

Study area and sample collection

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

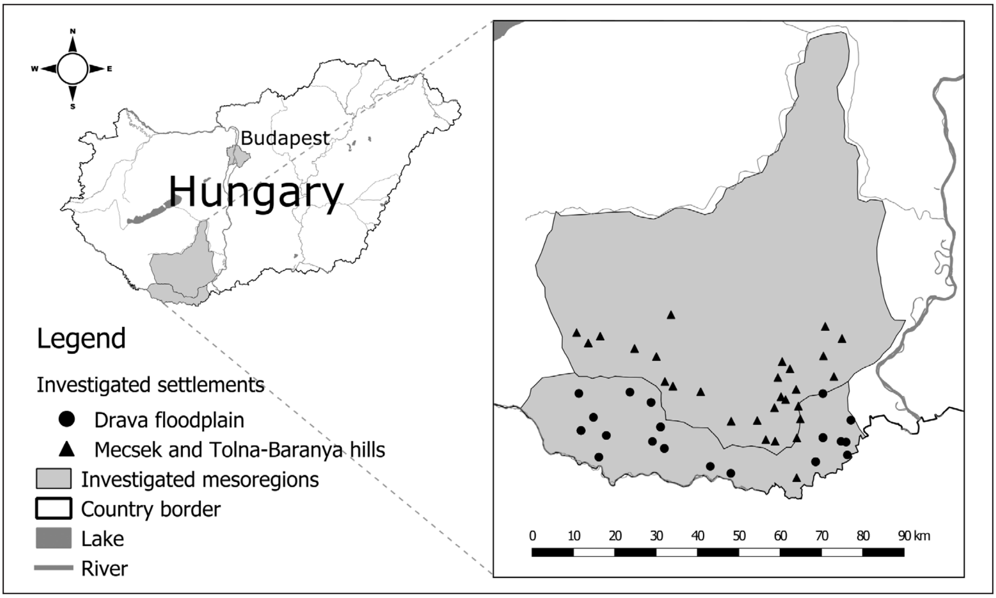


Figure 1. Study area in the South-Transdanubian region, Hungary, showing the location of the two mesoregions and the investigated nesting pairs within the examined landscape

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

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

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

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

Data analysis

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

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

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

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

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

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

Results

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

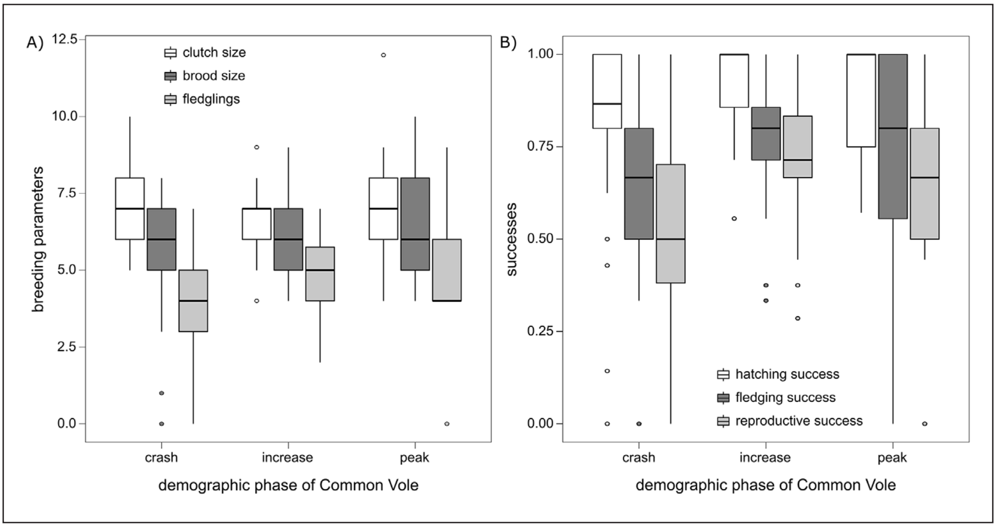


Figure 2. Variation in the values of breeding parameters (A) and breeding biology successes (B) (median, 25–75% percentiles, min-max) in the demographic phases of Common Vole

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

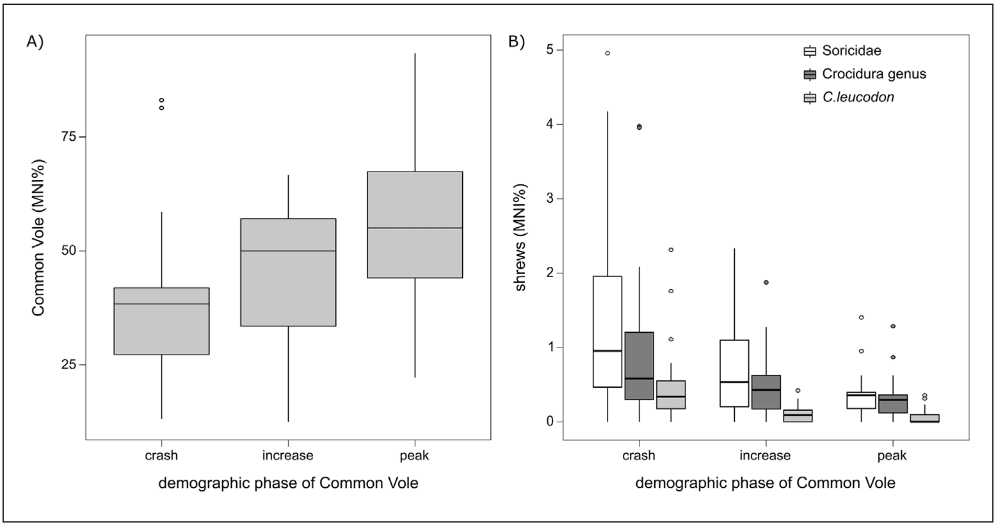


Figure 3. Variation in the relative abundance of Common Vole (A) and shrews (B) (median, 25–75% percentiles, min-max) in the demographic phases of Common Vole

3. ábra A mezei pocok (A) és a cickányok (B) gyakorisági értékeinek (medián, 25–75% percentilis, minimum-maximum) változása a mezei pocok demográfiai fázisaiban for the other two demographic phases showed no significant differences in the reproductive output values between the two mesoregions.

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

Table 1. Average values (±SE, range) of the potential alternative prey categories› proportion (MMI %), prey diversity for the whole 5-year dataset

1. táblázat A potenciális alternatív zsákmány kategóriák arányának (MMI %), valamint a zsákmány diverzitás átlaga (± SE, Min-Max) a teljes 5 éves adatkészletből

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

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

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

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

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

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

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

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

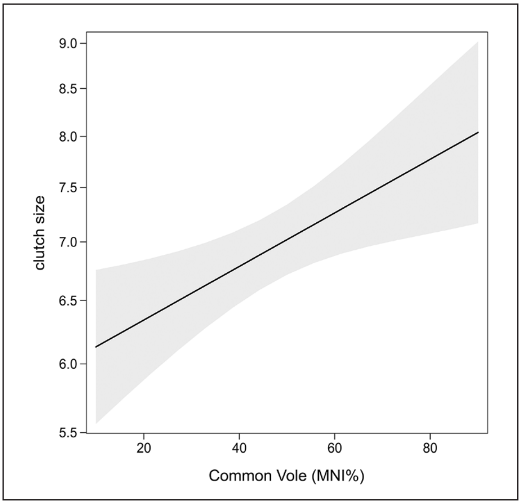


Figure 4. Relationship between clutch size and relative abundance of the Common Vole *(M. arvalis)* based on main effect of the M2 model

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

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

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

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

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

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

Brood size was affected by the proportion of the Common Vole and the Shannon diversity based on the best-fitted M2 model *(Table 4)*. In case of each three continuous predictors, the significant main effect was confirmed by Type III test (*Mar*: $\chi^2 = 6.51$, $P = 0.0108$; H’: $\chi^2 = 8.73$, $P = 0.0031$). Similar to clutch size, significant positive relationships were confirmed by the estimated parameters between brood size and the relative abundance (MNI%) of the Common Vole *(Table 5, Figure 5a)*. In contrast, a significant negative regression was detected between the prey diversity and the brood size *(Table 5,*

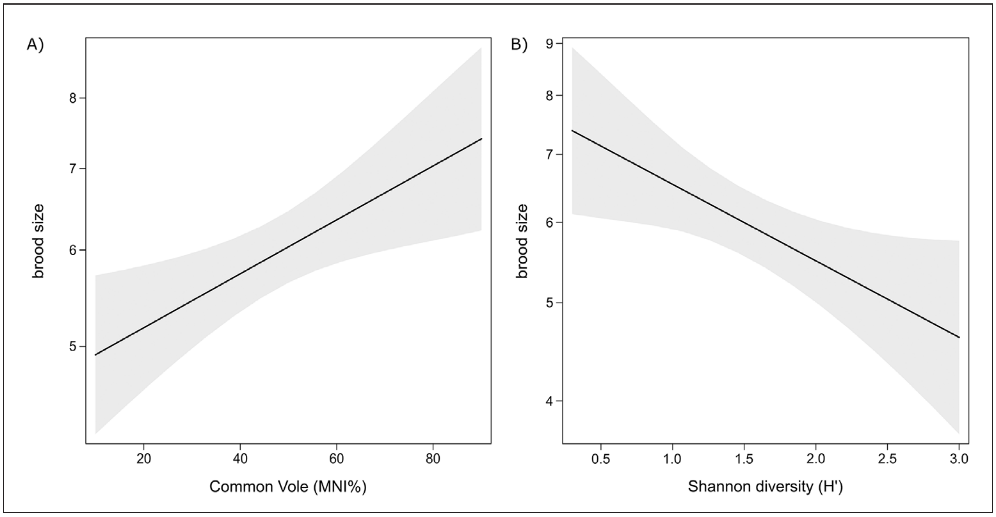


Figure 5. Relationship between brood size and relative abundance of the Common Vole *(M. arvalis)* (A) and Shannon diversity (B) based on main effects of the M2 model

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

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

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

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

QAICc: Quasi-Akaike Information Criterion corrected for small sample size
Δ_i: QAICc differences
w_i: Akaike weights

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

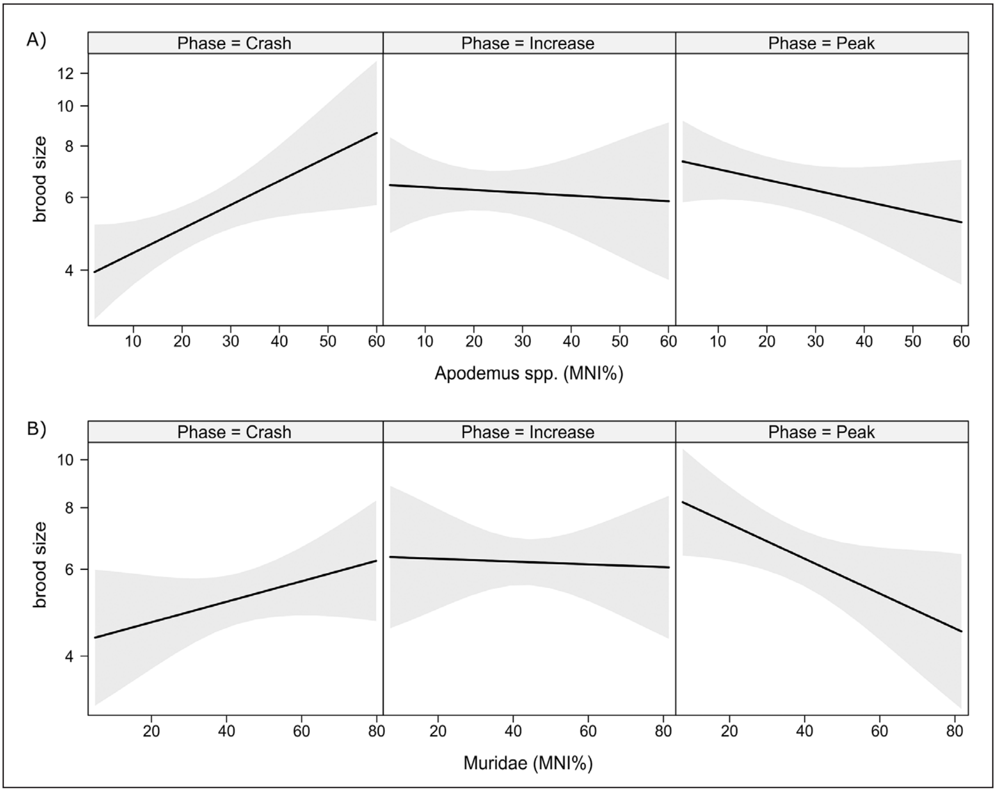


Figure 6. The interaction effect plot of the M1 model in case of *Apodemus* spp. (A) and Muridae (B) as potential alternative prey categories of the Common Barn-owl, showing the different impact of the two predictors on the variation of brood size during a given demographic phase of the Common Vole

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

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

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

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

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

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

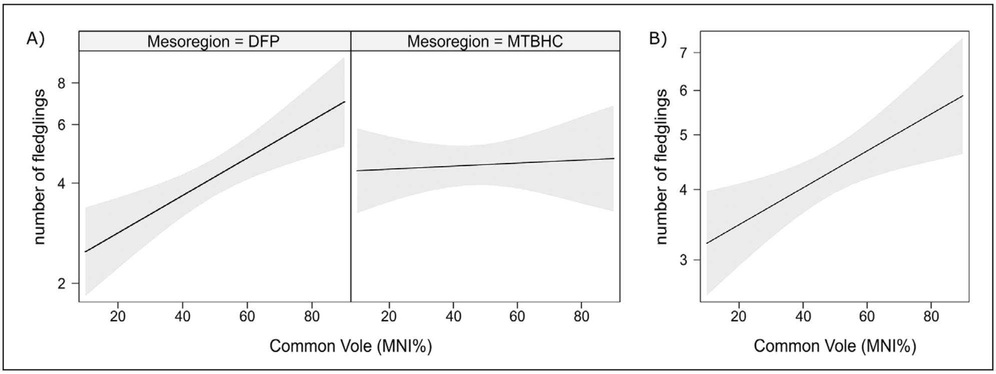


Figure 7. The interaction effect plot of the M2 model in case of the Common Vole, showing the different impact of this predictor on the variation of number of fledglings in the two investigated mesoregions (A) and the relationship between relative abundance of the Common Vole and number of fledglings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

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

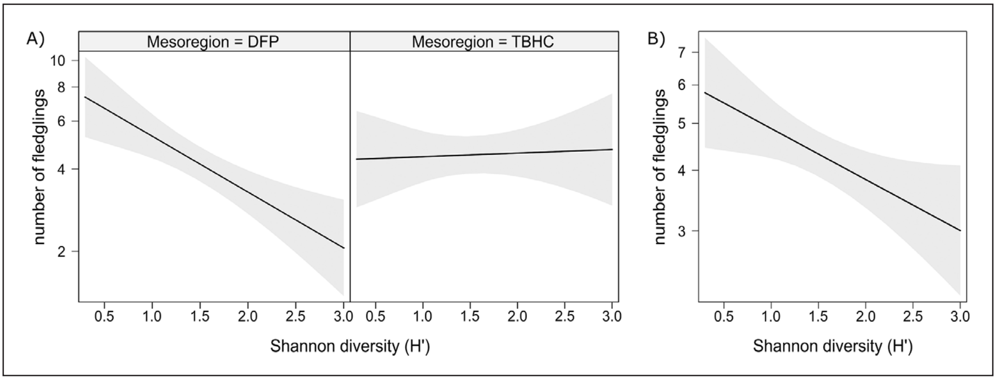


Figure 8. The interaction effect plot of the M2 model in case of Shannon diversity, showing the different impact of this predictor on the variation of number of fledglings in the two investigated mesoregions (A) and the relationship between Shannon diversity and number of fledglings based on the main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

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

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

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

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

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

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

Δ_i: QAICc differences

w_i: Akaike weights

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

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

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

Model (ID)	**Variable/Interaction**	**B**	**± SE**	**t**	**P**
hatching success					
~ Asp × Phase (M1)	Asp	0.051	0.025	2.028	< 0.05
	Phase	2.211	0.924	2.393	< 0.05
~ Cle × Region (M2)	Cle × Region-MTBHC	-0.302	0.128	-2.351	< 0.05
fledging success					
~ Mar × Region (M2)	Mar	0.026	0.012	2.096	< 0.05
	Region-MTBHC	1.967	0.845	2.329	< 0.05
~ Muridae × Region (M2)	Muridae × Region-MTBHC	0.046	0.020	2.261	< 0.05
~ Asp × Region (M2)	Asp × Region-MTBHC	0.066	0.029	2.249	< 0.05
~ LBMR × Phase (M1)	Phase	1.612	0.490	3.292	< 0.01
	Phase-Peak	1.013	0.423	2.395	< 0.05
	LBMR × Phase-Increase	-0.231	0.112	-2.069	< 0.05
	LBMR × Phase-Peak	-0.214	0.095	-2.255	< 0.05
~ D × Region (M2)	D	3.974	1.741	2.283	< 0.05
	Region-MTBHC	1.735	0.795	2.182	< 0.05
~ H′ × Region (M2)	H′	-0.967	0.462	-2.094	< 0.05
reproductive success					
~ LBMR × Phase (M1)	Phase-Increase	1.428	0.406	3.516	< 0.001
	Phase-Peak	0.835	0.362	2.306	< 0.05
	LBMR × Phase-Peak	-0.174	0.086	-2.024	< 0.05

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

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

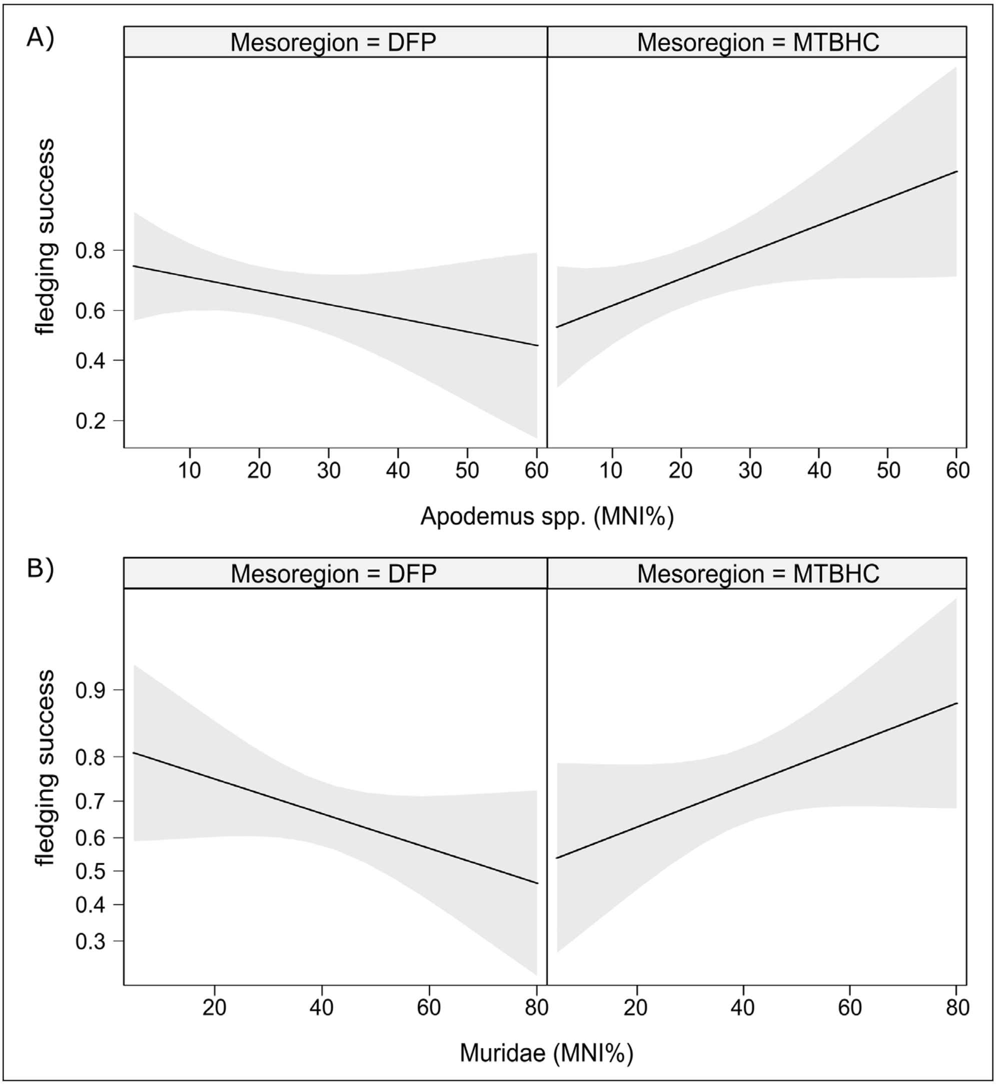


Figure 9. The interaction effect plot of the M2 model in case of *Apodemus* spp. (A) and Muridae (B) as potential alternative prey categories of the Common Barn-owl, showing the different impact of these predictors on the variation of fledging success in the two investigated mesoregions

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

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

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

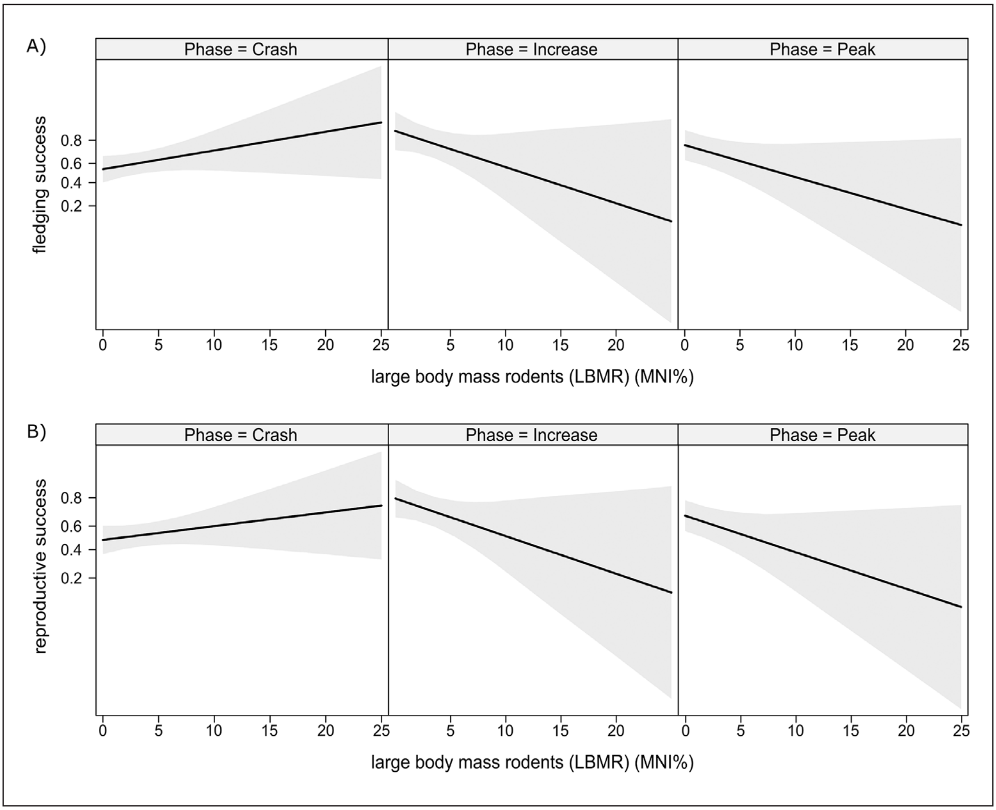


Figure 10. The interaction effect plot of the M1 model in case of fledging success (A) and reproductive success (B), showing the different impact of the abundance of large body mass rodents (LBMR) on the variation of fledging and reproductive success during a given demographic phase of the Common Vole

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

In summary, our results demonstrated that the clutch size of the Common Barn-owl is determined ultimately by the availability and consumption rate of the Common Vole as main prey, while other small mammal prey categories did not affect the clutch size. These results support the finding that the clutch size of vole-eating raptors and owls, which begin breeding in early spring, reflects the vole abundance of this early spring period. Considering the other investigated small mammal prey groups, only in case of the Murid rodent prey categories (*Apodemus* spp., Muridae) were alternative prey roles confirmed.

Acknowledgments

We thank the Churches of Baranya County, especially the Bishopric of Pécs and Reformed Congregations for providing opportunity to place nest boxes and supporting the breeding biology monitoring of owls and the systematic collection of the pellet samples. The members of the Baranya County Group of BirdLife Hungary and the enthusiastic volunteers of the 'Foundation for Natural Resources in Baranya' provided their generous help in the monitoring, cleaning and maintenance of the nest boxes. The pellet analysis of the Common Barn Owl was supported by Foundation for Natural Resources in Baranya, the Hungarian Biodiversity Monitoring System and the Duna-Dráva National Park Directorate. We thank the volunteers and university students for their dedicated work in helping us disassemble and process the owl pellets. Finally, we would like to thank the two anonymous reviewers for many helpful comments.

References

Angelstam, P., Lindström, E. & Widén, P. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. – Oecologia 62: 199–208. DOI: 10.1007/BF00379014

Bank, L., Haraszthy, L., Horváth, A. & Horváth, G. F. 2019. Nesting success and productivity of the Common Barn-owl *Tyto alba*: results from a nest box installation and long-term breeding monitoring program in Southern Hungary. – Ornis Hungarica 27(1): 1–31. DOI: 10.2478/orhu-2019-0001

Barton, K. 2016. MuMIn: multi-model inference. – R Package Vers. 1 (15), 6 http://CRAN.R-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. – Journal of Statistical Software 67(1): 1–48. DOI: 10.18637/jss.v067.i01.

Baudrot, V., Perasso, A., Fritsch, C., Giraudoux, P. & Raoul, F. 2016. The adaptation of generalist predators' diet in a multi-prey context: Insights from new functional responses. – Ecology 97(7): 1832–1841. DOI: 0.1890/15-0427.1

Baudvin, H. 1979. Les secondes nichées chex la Chouette Effraie *(Tyto alba)* en Conte-d'Or [The second clutches of the Barn Owl *Tyto alba*]. – Nos Oiseanx 35: 125–134. (in French)

Bellocq, M. I. 2000. A review of the trophic ecology of the Barn Owl in Argentina. – Journal of Raptor Research 34(2): 108–119.

Benedek, A. M., Dumitru, A. & Sbârcea, R. 2007. Correlation between diet and breeding of *Tyto alba* (Scopoli, 1769) (Aves: Tytonidae). – Travaux du Museum National d'Histoire Naturelle Grigore 1: 329–335.

Bernard, N., Michelat, D., Raoul, F., Quéré, J. P., Delattre, P. & Giraudoux, P. 2010. Dietary response of Barn Owls *(Tyto alba)* to large variations in populations of Common Voles *(Microtus arvalis)* and European Water Voles *(Arvicola terrestris)*. – Canadian Journal of Zoology 88(4): 416–426. DOI: 10.1139/Z10-011

Bohnsack, P. 1966. Über die Ernährung der Schleiereule, *Tyto alba*, insbesondere außerhalb der Brutzeit, in einem westholsteinischen Massenwechselgebiet der Feldmaus, *Microtus arvalis* [About the feeding of the Barn Owl, *Tyto alba*, especially outside the breeding season, in a West Holstein mass change area of the Field Vole, *Microtus arvalis*]. – Corax 1(17): 162–172. (in German)

Bonvicino, C. R. & Bezerra, A. M. 2003. Use of regurgitated pellets of Barn Owl *(Tyto alba)* for inventorying small mammals in the Cerrado of Central Brazil. – Studies Neotropical Fauna and Environment 38(1): 1–5. DOI: 10.1076/snfe.38.1.1.14030

Bontzorlos, V. A., Peris, S. J., Vlachos, C. G. & Bakaloudis, D. E. 2005. The diet of Barn Owl in the agricultural landscapes of central Greece. – Folia Zoologica 54(1–2): 99–110.

Braaksma, S. & de Bruijn, O. 1976. De kerkuilstand in Nederland [New data on Barn Owl in the Netherlands]. – Limosa 49: 135–187. (in Dutch with English Summary)

Bryja, J., Tkadlec, E., Nesvadbova, J., Gaisler, J. & Zejda, J. 2001. Comparison of enumeration and Jolly-Seber estimation of population size in the Common Vole *Microtus arvalis*. – Acta Theriologica 46: 279–285. DOI: 10.1007/BF03192434

Burnham, K. P. & Anderson, D. R. 2002. Model selection and Inference: a practical information-theoretic approach. – Springer-Verlag, New York, 488 pp. DOI: 10.1007/b97636

De Bruijn, O. 1979. Voedseloecologie van de Kerkuil *Tyto alba* in Nederland [Food ecology of the Barn Owl *Tyto alba* in the Netherlands]. – Limosa 52: 91–154. (in Dutch with English Summary)

De Bruijn, O. 1994. Population ecology and conservation of the Barn Owl *Tyto alba* in farmland habitats in Liermers and Achterhoek (The Netherlands). – Ardea 82(1): 1–109.

De Jong, J. 1983. De Kerkuil [The Barn Owl]. – Kosmos, Utrecht, The Netherlands (in Dutch)

Dobson, A. J. & Barnett, A. G. 2018. An introduction to generalized linear models. – Chapman & Hall/CRC Texts in Statistical Science

Caboń-Raczyńska, K. & Ruprecht, A. L. 1977. Estimation of population density of the Common Vole in Poland: an analysis of owl pellets. – Acta Theriologica 22(20–29): 349–354.

Campbell, R. W., Manuwal, D. A. & Harestad, A. S. 1987. Food habits of the Common Barn Owl in British Columbia. – Canadian Journal of Zoology 65(3): 578–586. DOI: 10.1139/z87-090

Charter, M., Izhaki, I., Meyrom, K., Motro, Y. & Leshem, Y. 2009. Diets of Barn Owls differ in the same agricultural region. – The Wilson Journal of Ornithology 121(2): 378–383. DOI: 10.1676/08-083.1

Charter, M., Izhaki, I., Leshem, Y., Meyrom, K. & Roulin, A. 2015. Relationship between diet and reproductive success in the Israeli Barn Owl. – Journal of Arid Environments 122: 59–63. DOI: 10.1016/j.jaridenv.2015.06.011

Charter, M., Izhaki, I. & Roulin, A. 2018. The relationship between intra-guild diet overlap and breeding in owls in Israel. – Population Ecology 60(4): 397–403. DOI: 10.1007/s10144-018-0633-6

Colvin, B. A. & McLean, E. B. 1986. Food habits and prey specificity of the Common Barn Owl in Ohio. – Ohio Journal of Science 86(3): 76–80.

Dementavičius, D., Rumbutis, S., Virbickas, T., Vaitkuvienė, D., Dagys, M. & Treinys, R. 2020. Spatial and temporal variations in the White-tailed Eagle *Haliaeetus albicilla* breeding diet revealed by prey remains. – Bird Study 67(2): 206– 216. DOI: 10.1080/00063657.2020.1808591

Fay, R., Michler, S., Laesser, J., Jeanmonod, J. & Schaub, M. 2020. Large-scale vole population synchrony in central Europe revealed by Kestrel breeding performance. – Frontiers in Ecology and Evolution 7: 512. DOI: 10.3389/fevo.2019.00512

Fox, J., Weisberg, S., Friendly, M., Hong, J., Andersen, R., Firth, D., Taylor, S. & R Core Team 2017. Package "effects". Effect Displays for Linear, and Other Models. Version 4.0-0. – https://cran.rproject.org/web/packages/effects/ effects.pdf

Frey, C., Sonnay, C., Dreiss, A. & Roulin, A. 2011. Habitat, breeding performance, diet and individual age in Swiss Barn Owls *(Tyto alba)*. – Journal of Ornithology 152(2): 279–290. DOI: 10.1007/s10336-010-0579-8

Gubanyi, J. A., Case, R. M. & Wingfield, G. 1992. Diet and nesting success of Barn Owls breeding in western Nebraska. – American Midland Naturalist 127(2): 224–232. DOI: 10.2307/2426528

Hartig, F. 2017. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. – R package version 0.1, 5(5).

Heywood, M. R. & Pavey, C. R. 2002. Relative importance of plague rodents and dasyurids as prey of Barn Owls in central Australia. – Wildlife Research 29(2): 203–207. DOI: 10.1071/WR01104

Hindmarch, S. & Elliott, J. E. 2015. A specialist in the city: the diet of Barn Owls along a rural to urban gradient. – Urban Ecosystems 18(2): 477–488. DOI: 10.1007/s11252-014-0411-y

Horváth, G., Molnár, D., Németh, T. & Csete, S. 2005. Landscape ecological analysis of Barn Owl pellet data from the Drava lowlands, Hungary. – Natura Somogyiensis 7: 179–189.

Horváth, A., Morvai, A. & Horváth, G. F. 2018. Food-niche pattern of the Barn Owl *(Tyto alba)* in intensively cultivated agricultural landscape. – Ornis Hungarica 26(1): 27–40. DOI: 10.1515/orhu-2018-0002

Ille, R. 1991. Preference of prey size and profitability in Barn Owls *Tyto alba guttata*. – Behaviour 116(3–4): 180–189. DOI: 10.1163/156853991X00021.

Jacob, J. & Tkadlec, E. 2010. Rodent outbreaks in Europe: dynamics and damage. – In: Singleton, G., Belmain, S., Brown, P. R. & Hardy, B. (eds.) Rodent outbreaks: Ecology and impacts – IRRI (International Rice Research Institute): Los Banos (Philippines), pp. 207–224.

Jacob, J., Manson, P., Barfknecht, R. & Fredricks, T. 2014. Common Vole *(Microtus arvalis)* ecology and management: implications for risk assessment of plant protection products. – Pest Management Science 70(6): 869–878. DOI: 10.7325/Galemys.2016.A2

Jacob, J., Imholt, C., Caminero-Saldaña, C., Couval, G., Giraudoux, P., Herrero-Cófreces, S., Horváth, G. F., Luque-Larena, J. J., Tkadlec, E. & Wymenga, E. 2020. Europe-wide outbreaks of Common Voles in 2019. – Journal of Pest Science 93(2): 703–709. DOI: 10.1007/s10340-020-01200-2

Jędrzejewski, W., Jędrzejewska, B., Zub, K., Ruprecht, A. L. & Bystrowski, C. 1994. Resource use by Tawny Owls *Strix aluco* in relation to rodent fluctuations in Białowieża National Park, Poland. – Journal of Avian Biology 25(4): 308–318. DOI: 10.2307/3677278

Kaus, D. 1977. Zur Populationsdynamik, Ökologie und Brutbiologie der Schleiereule *Tyto alba* in Franken [On the population dynamics, ecology and breeding biology of the Barn Owl *Tyto alba* in Franconia]. – Anzeiger der Omithologische Gesellschaft in Bayern 16: 18–44. (in German with English Summary)

Kitowski, I. 2013. Winter diet of the Barn Owl *(Tyto alba)* and the Long-eared Owl *(Asio otus)* in Eastern Poland. – North-western Journal of Zoology 9(1): 16–22.

Kleiber, C. & Zeileis, A. 2008. Applied econometrics with R. – Springer-Verlag, New York DOI: 10.1007/978-0-387-77318-6

Kleiber, C. & Zeileis, A. 2009. AER: Applied Econometrics with R. – R package version 1.1.

Klok, C. & De Roos, A. M. 2007. Effects of vole fluctuations on the population dynamics of the Barn Owl *Tyto alba*. – Acta Biotheoretica 55: 227–241. DOI: 10.1007/s10441-007-9013-x

Korpimäki, E. & Norrdahl, K. 1989. Predation of Tengmalm's Owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. – Oikos 54(2): 154–164. DOI: 10.2307/3565261

Korpimäki, E., Huhtala, K. & Sulkava, S. 1990. Does the year-to-year variation in the diet of Eagle and Ural Owls support the alternative prey hypothesis? – Oikos 58(1): 47–54. DOI: 10.2307/3565359

Korpimäki, E. & Hakkarainen, H. 1991. Fluctuating food supply affects the clutch size of Tengmalm's Owl independent of laying date. – Oecologia 85(4): 543–552. DOI: 10.1007/BF00323767

Korpimäki, E. & Norrdahl, K. 1991. Numerical and functional responses of Kestrels, Short-eared Owls, and Long-eared Owls to vole densities. – Ecology 72(3): 814–826. DOI: 10.2307/1940584

Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N. C. 2002. Dynamic effects of predators on cyclic voles: Field experimentation and model extrapolation. – Proceedings: Biological Sciences 269: 991–997. DOI: 10.1098/rspb.2002.1972

Kotler, B. P., Brown, J. S., Smith, R. J. & Wirtz, W. O. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. – Oikos 53(2): 145–152. DOI: 10.1007/BF00328733

Kreiderits, A., Gamauf, A., Krenn, H. W. & Sumasgutner, P. 2016. Investigating the influence of local weather conditions and alternative prey composition on the breeding performance of urban Eurasian Kestrels *Falco tinnunculus*. – Bird Study 63(3): 369–379. DOI: 10.1080/00063657.2016.1213791

Kryštufek, B. & Macholán, M. 1998. Morphological differentiation in *Mus spicilegus* and the taxonomic status of mound-building mice from the Adriatic coast of Yugoslavia. – Journal of Zoology 245(2): 185–196. DOI: 10.1111/j.1469-7998.1998.tb00086.x

Lack, D. 1947. The significance of clutch-size. I and II. – Ibis 89: 302–352. DOI: 10.1111/j.1474-919X.1947.tb04155.x

Lambin, X., Bretagnolle, V. & Yoccoz, N. G. 2006. Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? – Journal of Animal Ecology 75(2): 340–349. DOI: 10.1111/j.1365-2656.2006.01051.x

Leonardi, G. & Dell'Arte, G. L. 2006. Food habits of the Barn Owl *(Tyto alba)* in a steppe area of Tunisia. – Journal of Arid Environments 65(4): 677–681. DOI: 10.1016/j.jaridenv.2005.10.007

Luque-Larena, J. J., Mougeot, F., Vinuela, J., Jareno, D., Arroyo, L., Lambin, X. & Arroyo, B. 2013. Recent large-scale range expansion and outbreaks of the Common Vole *(Microtus arvalis)* in NW Spain. – Basic and Applied Ecology 14(5): 432–441. DOI: 10.1016/j.baae.2013.04.006

Macholán, M. 1996. Key to European House Mice *(Mus)*. – Folia Zoologica 45(3): 209–217.

Marti, C. D. 1988. A long-term study of food-niche dynamics in the Common Barn Owl: comparisons within and between populations. – Canadian Journal of Zoology 66(8): 1803–1812. DOI: 10.1139/z88-261

Marti, C. D. 1994. Barn Owl reproduction: patterns and variation near the limit of the species' distribution. – The Condor 96(2): 468–484. DOI: 10.2307/1369329

Marti, C. D. 2010. Dietary trends of Barn Owls in an agricultural ecosystem in Northern Utah. – Wilson Journal of Ornithology 122(1): 60–67. DOI: 10.1676/09-025.1

Martínez, J. A. & López, G. 1999. Breeding ecology of the Barn Owl *(Tyto alba)* in Valencia (SE Spain). – Journal für Ornithologie 140(1): 93–99. DOI: 10.1007/BF02462093

McDowell, M. C. & Medlin, G. C. 2009. The effects of drought on prey selection of the Barn Owl *(Tyto alba)* in the Strzelecki Regional Reserve, north-eastern South Australia. – Australian Mammalogy 31(1): 47–55. DOI: 10.1071/AM08115

Milchev, B. 2015. Diet of Barn Owl *Tyto alba* in Central South Bulgaria as influenced by landscape structure. – Turkish Journal of Zoology 39(5): 933–940. DOI: 10.3906/zoo-1409-24

Milchev, B., Boev, Z. & Kodjabashev, N. 2006. Breeding distribution and diet composition of the Barn Owl *Tyto alba* (Scopoli, 1769), (Aves: Strigiformes) in the North-Western Upper Thracian plain (Bulgaria). – Acta Zoologica Bulgarica 58(1): 83–92.

Millon, A. & Bretagnolle, V. 2008. Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. – Oikos 117: 1500–1510. DOI: 10.1111/j.0030-1299.2008.16458.x

Paspali, G., Oruci, S., Koni, M., Wilson, I. F., Krystufek, B. & Bego, F. 2013. Seasonal variation of small mammals in the diet of the Barn Owl *(Tyto alba)* in the Drinos River valley, southern Albania. – Turkish Journal of Zoology 37(1): 97–105. DOI: 10.3906/zoo-1203-25

Pavluvčík, P., Poprach, K., Machar, I., Losík, J., Gouveia, A. & Tkadlec, E. 2015. Barn Owl productivity response to variability of vole populations. – PloS One 10(12): e0145851. DOI: 10.1371/journal.pone.0145851

Petrovici, M., Molnár, P. & Sándor, A. D. 2013. Trophic niche overlap of two sympatric owl species (*Asio otus* Linnaeus, 1758 and *Tyto alba* Scopoli, 1769) in the North-Western part of Romania. – North-Western Journal of Zoology 9(2): 250–256.

Pezzo, F. & Morimando, F. 1995. Food habits of the Barn Owl, *Tyto alba*, in a Mediterranean rural area: Comparison with the diet of two sympatric carnivores. – Italian Journal of Zoology 62(4): 369–373. DOI: 10.1080/11250009509356091

Price, T. & Liou, L. 1989. Selection on clutch size in birds. – The American Naturalist 134(6): 950–959. DOI: 10.1086/285023

Purger, J. J. 2014. Survey of the small mammal fauna in north-western Somogy County (Hungary), based on Barn Owl *Tyto alba* (Scopoli, 1769) pellet analysis. – Natura Somogyiensis 24: 293–304.

Pyke, G. K., Pulliam, H. R. & Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. – Quarterly Review of Biology 52: 137–154. DOI: 10.1086/409852

R Core Team 2019. R: a language and environment for statistical computing. – Vienna, Austria: R Foundation for Statistical Computing. Available at https://www.R-project.org/

Reif, V., Tornberg, R., Jungell, S. & Korpimäki, E. 2001. Diet variation of Common Buzzards in Finland supports the alternative prey hypothesis. – Ecography 24(3): 267–274. DOI: 10.1034/j.1600-0587.2001.240304.x

Reif, V., Jungell, S., Korpimäki, E., Tornberg, R. & Mykrä, S. 2004. Numerical response of Common Buzzards and predation rate of main and alternative prey under fluctuating food conditions. – Annales Zoologici Fennici 41(4): 599–607.

Riegert, J., Lövy, M. & Fainová, D. 2009. Diet composition of Common Kestrels *Falco tinnunculus* and Long-eared Owls *Asio otus* coexisting in an urban environment. – Ornis Fennica 86(4): 123–130.

Romano, A., Séchaud, R. & Roulin, A. 2020. Global biogeographical patterns in the diet of a cosmopolitan avian predator. – Journal of Biogeography 47(7): 1467–1481. DOI: 10.1111/jbi.13829

Rodríguez-Pastor, R., Escudero, R., Vidal, D., Mougeot, F., Arroyo, B., Lambin, X., Vila-Coro, A. M., Rodrígez-Moreno, I., Anda, P. & Luque-Larena, J. J. 2017. Density-dependent prevalence of *Francisella tularensis* in fluctuating vole populations, northwestern Spain. – Emerging Infectious Diseases 23(8): 1377–1379. DOI: 10.3201/eid2308.161194

Romanowski, J. & Zmihorski, M. 2008. Effect of season, weather and habitat on diet variation of a feeding-specialist: a case study of the Long-eared Owl, *Asio otus* in Central Poland. – Folia Zoologica 57(4): 411–419.

Roulin, A. 2002. Short-and long-term fitness correlates of rearing conditions in Barn Owls *Tyto alba*. – Ardea 90(2): 259–267.

Roulin, A. 2004a Covariation between plumage colour polymorphism and diet in the Barn Owl *(Tyto alba)*. – Ibis 146(3): 509– 517. DOI: 10.1111/j.1474-919x.2004.00292.x

Roulin, A. 2004b Effects of hatching asynchrony on sibling negotiation, begging, jostling for position and within-brood food allocation in the Barn Owl *Tyto alba*. – Evolutionary Ecology Research 6(7): 1083–1098.

Salamolard, M., Butet, A., Leroux, A. & Bretagnolle, V. 2000. Responses of an avian predator to variations in prey density at a temperate latitude. – Ecology 81(9): 2428–2441. DOI: 10.1890/0012-9658(2000)081[2428:ROAAPT] 2.0.CO;2

Sasvári, L., Hegyi, Z., Csörgő, T. & Hahn, I. 2000. Age-dependent diet change, parental care and reproductive cost in Tawny Owls *Strix aluco*. – Acta Oecologica 21(4–5): 267–275. DOI: 10.1016/S1146-609X(00)01080-8

Schoener, T. W. 1971. Theory of feeding strategies. – Annual Review of Ecology and Systematics 11: 369–404. DOI: 10.1146/annurev.es.02.110171.002101

Schönfeld, M. & Girbig, G. 1975. Beiträge zur Brutbiologie der Schleiereule, *Tyto alba*, unter besonderer Berücksichtigung der Abhängigkeit von der Feldmausdichte [Contribution to the breeding biology of the Barn Owl, *Tyto alba*, with special regard to the dependence on field density]. – Hercynia 12: 257– 319. (in German with English Summary)

Shehab, A. H. & Al Charabi, S. M. 2006. Food of the Barn Owl *Tyto alba* in the Yahmool Area, Northern Syria. – Turkish Journal of Zoology 30(2): 175–179.

Sokal, R. R. & Rohlf, F. J. 1997. Biometry. – W. H. Freeman and Co., New York

Solonen, T., Ahola, K. & Karstinen, T. 2015. Clutch size of a vole-eating bird of prey as an indicator of vole abundance. – Environmental Monitoring and Assessment 187(9): 588–588. DOI: 10.1007/s10661-015-4783-0

Szép, D., Klein, Á. & Purger, J. J. 2017. The prey composition of the Barn Owl *(Tyto alba)* with respect to landscape structure of its hunting area (Zala County, Hungary). – Ornis Hungarica 25(2): 51–64. DOI: 10.1515/orhu-2017-0015

Szép, D., Klein, Á. & Purger, J. J. 2019. Investigating the relationship between the prey composition of Barn Owls *(Tyto alba)* and the habitat structure of their hunting range in the Marcal Basin (Hungary), based on pellet analysis. – Ornis Hungarica 27(1): 32–43. DOI: 10.2478/orhu-2019-0002

Szűcs, D., Horváth, K. & Horváth, G. F. 2014. Comparing small mammal faunas based on Barn Owl *(Tyto alba)* pellets collected in two different lowland landscapes. – Natura Somogyiensis 24: 305–320.

Taylor, I. 1994. Barn Owls. Predator-prey relationships and conservation. – Cambridge University Press, Cambridge

Terraube, J., Arroyo, B., Madders, M. & Mougeot, F. 2011. Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. – Oikos 120(2): 234–244. DOI: 10.1111/j.1600-0706.2010.18554.x

Tkadlec, E. & Stenseth, N. C. 2001. A new geographical gradient in vole population dynamics. – Proceedings of the Royal Society of London, Series B: Biological Sciences 268(1476): 1547–1552. DOI: 10.1098/rspb.2001.1694

Tome, D. 2003. Functional response of the Long-eared Owl *(Asio otus)* to changing prey numbers: a 20-year study. – Ornis Fennica 80(2): 63–70.

Toms, M. P., Crick, H. Q. & Shawyer, C. R. 2001. The status of breeding Barn Owls *Tyto alba* in the United Kingdom 1995–97. – Bird Study 48(1): 23–37. DOI: 10.1080/00063650109461200

Tores, M. & Yom-Tov, Y. 2003. The diet of the Barn Owl *Tyto alba* in the Negev Desert. –Israel Journal of Ecology and Evolution 49(2–3): 233–236. DOI: 10.1560/JU3E-EWK4-13QY-CGRF

Tores, M., Motro, Y., Motro, U. & Yom-Tov, Y. 2005. The Barn Owl – a selective opportunist predator. – Israel Journal of Ecology and Evolution 51(4): 349–360. DOI: 10.1560/7862-9E5G-RQJJ-15BE

Torre, I., Gracia-Quintas, L., Arrizabalaga, A., Baucells, J. & Díaz, M. 2015. Are recent changes in the terrestrial small mammal communities related to land use change? A test using pellet analyses. – Ecological Research 30(5): 813–819. DOI: 10.1007/s11284-015-1279-x

Tóth, L. 2014. Numerical response of the Common Buzzard *Buteo buteo* to the changes in abundance of small mammals. – Ornis Hungarica 22(1): 48–56. DOI: 10.2478/orhu-2014-0010

Tulis, F., Baláž, M., Obuch, J. & Šotnár, K. 2015. Responses of the Long-eared Owl *Asio otus* diet and the numbers of wintering individuals to changing abundance of the Common Vole *Microtus arvalis*. – Biologia 70(5): 667–673. DOI: 10.1515/biolog-2015-0074

Varuzza, P., Capizzi, D., Santini, L. & Apollonio, M. 2001. Barn Owl *Tyto alba* predation on small mammals in relation to the Mediterranean environment (Pisa Province, Italy). – Acta Ornithologica 36(2): 153–160. DOI: 10.3161/068.036.0208

Veselovský, T., Bacsa, K. & Tulis, F. 2017. Barn Owl *(Tyto alba)* diet composition on intensively used agricultural land in the Danube Lowland. – Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis 65(1): 225–233. DOI: 10.11118/actaun201765010225

Yom-Tov, Y. & Wool, D. 1997. Do the contents of Barn Owl pellets accurately represent the proportion of prey species in the field? – The Condor 99(4): 972–976. DOI: 10.2307/1370149

Zar, J. H. 2010. Biostatistical Analysis, 5th ed. – Pearson Prentice-Hall, Upper Saddle River, NJ.

Zagoršek, T. 2018. A contribution to the knowledge of diet composition of the Barn Owl *Tyto alba* in the area of Pisa (Italy). – Acrocephalus 39(178–179): 171–176.

Zárybnická, M., Sedláček, O., Salo, P., Šťastný, K. & Korpimäki, E. 2015. Reproductive responses of temperate and boreal Tengmalm's Owl *Aegolius funereus* populations to spatial and temporal variation in prey availability. – Ibis 157(2): 369–383. DOI: 10.1111/ibi.12244

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. 2009. Mixed Effects Models and Extensions in Ecology with R. – Springer-Verlag, New York

Ornis Hungarica 2020. 28(2): 66–73.
DOI: 10.2478/orhu-2020-0017

European Hamster at the edge: declining in nature and rare in owl pellets[×]

Jenő J. Purger[1,2*], Kornélia Kurucz[1], Dávid Szép[1], Dragica Purger[2,3], Boris Kryštufek[4], Danijel Ivajnšič[5], Tina Klenovšek[5] & Franc Janžekovič[5]

[×] Presented at 2nd Hungarian Owl Research Conference held in Pécs on 11th September 2020.

Received: October 31, 2020 – November 06, 2020 – November 09, 2020

Purger, J. J., Kurucz, K., Szép, D., Purger, D., Kryštufek, B., Ivajnšič, D., Klenovšek, T. & Janžekovič, F. 2020. European Hamster at the edge: declining in nature and rare in owl pellets. – Ornis Hungarica 28(2): 66–73. DOI: 10.2478/orhu-2020-0017

Abstract Over the last decades, the European Hamster *(Cricetus cricetus)* has been declining in many parts of its European range. Due to the lack of recent information on the occurrence and status of the European Hamster in the south-western Carpathian Basin west of the Danube, we used information gathered from prey remains in Common Barn-owl *(Tyto alba)* pellets. In spite of considerable sampling effort, we retrieved only few hamster remnants. Two skulls were found in Podolje (Croatia) in 2007 and 2016, respectively. Further five hamsters were retrieved from pellets collected in 2017, 11 km to the northwest in Udvar (Hungary). In Sátorhely, 5 km north from Udvar, one roadkill male was found on 27.07.2019. Testimonies from local inhabitants confirmed the current presence of the European Hamster in the area. Our results suggest the presence of a small isolated population in the border area of Croatia (UTM 10 km grid square CR27) and Hungary (CR18, CR19). This small isolated population is on the south-western limit of the range of the species. We presume that the population requires conservation attention because of its isolated position at the edge of the species' range, its small size and low abundance. We call for a transboundary action by nature conservation authorities in Croatia and Hungary.

Keywords: Baranja, *Cricetus cricetus*, Croatia, Hungary, *Tyto alba*

Összefoglalás A mezei hörcsög *(Cricetus cricetus)* az utóbbi néhány évtizedben európai elterjedési területének egy jelentős részéről visszaszorult. Aktuális előfordulási adatok hiányában a Dunától nyugatra, a Kárpát-medence délnyugati részén gyöngybagoly *(Tyto alba)* köpetekből előkerülő zsákmánymaradványok alapján nyert információkat használtuk a mezei hörcsög elterjedésének és státuszának megállapítására. A mintavételezésbe fektetett jelentős erőfeszítések ellenére csak kevés hörcsög maradványa került elő. A horvátországi Podolje terepülésről 2007-ben és 2016-ban összesen két koponyát, majd 11 km-re északnyugatra a magyarországi Udvar településen 2017-ben gyűjtött köpetekből 5 mezei hörcsög maradványait mutattuk ki. Udvartól mindössze 5 km-re északi irányban, Sátorhelynél az úton 2019.07.27-én egy elgázolt hím példányt találtunk. A mezei hörcsög aktuális jelenlétét a területen a helyi lakosság megfigyelései is alátámasztották. Az összegyűlt adatok arra utalnak, hogy Horvátország (CR27 a 10 km-es UTM háló alapján) és Magyarország (CR18, CR19) határmenti területén él egy kis elszigetelt populáció, mely a faj elterjedési területének délnyugati határán van. Megítélésünk szerint ez a populáció megérdemli a természetvédelem figyelmét, mivel a faj elterjedési területének peremén található, helyzete elszigetelt, mérete kicsi, és a hörcsögök előfordulási gyakorisága alacsony. Horvátország és Magyarország természetvédelmi hatóságait határon átnyúló fellépésre hívjuk fel.

Kulcsszavak: Baranya, *Cricetus cricetus*, Horvátország, Magyarország, *Tyto alba*

[1] *Department of Ecology, Institute of Biology, University of Pécs, 7624 Pécs, Ifjúság útja 6., Hungary*
[2] *BioRes Limited Partnership, 7624 Pécs, Barackvirág utca 27., Hungary*
[3] *Department of Pharmacognosy, Faculty of Pharmacy, University of Pécs, 7624 Pécs, Rókus utca 2., Hungary*

[4] Slovenian Museum of Natural History, 1000 Ljubljana, Prešernova 20., Slovenia
[5] Faculty of Natural Sciences and Mathematics, University of Maribor, 2000 Maribor, Koroška cesta 160., Slovenia
*corresponding author, e-mail: purgerjj@gmail.com

Introduction

The European Hamster *(Cricetus cricetus)* has been a common inhabitant of agricultural landscape in many parts of Europe and Asia. During population outbreaks, hamsters were serious pests to crops (Nechay 2000). Since the 1950s, populations in western and central parts of Europe experienced gradual decline, which was observed also in the western Carpathian Basin (Surov *et al.* 2016, Banaszek *et al.* 2020, Kryštufek *et al.* 2020). Chain of events like habitat fragmentation and degradation, including a decline in food supplies, also damped down its population cycles (Nechay 2008). An increase in winter precipitation and widespread monocultures further contributed to population decline (Tissier *et al.* 2016). Small, fragmented and isolated populations are vulnerable to various threats, which accelerate their further decline and finally lead to extinction (Weinhold 2008). Improvements in land management are a crucial step to avoid further decline (Tissier *et al.* 2016). The IUCN status of the species is Critically Endangered which was justified by a decline in reproductive rate, population size and distributional range.

Recent surveys retrieved local hamster extinctions in certain parts of Hungary, including Southern Transdanubia (e.g. Bihari 2004, 2007, Cserkész 2017, Kondor & Cserkész 2017). In this communication, we address the situation in the Baranya region. Baranya (also Baranja) is a flat plain between the Drava and Danube Rivers and is administratively divided between Hungary and Croatia. European Hamsters used to be widespread and common throughout the Croatian part of the region (Petrov 1992) but are now restricted to the southern part of the Hungarian Baranya (Nechay 2000). The hamster population in Baranya is of particular conservation interest for at least two reasons. Because of recent decline (Bihari 2007, Cserkész 2017, Kondor & Cserkész 2017), it requires conservation management on its own. Equally important, Baranya anchors the entire hamster population along the Drava in Croatia and Slovenia. This population is in a shape of a long (c. 200 km) and very narrow stripe (up to 20 km) which stretches – presumably continuously – on the right bank of the river. Gene flow in this narrow corridor can become disrupted at any point and at any time, making the right bank of the Drava a deadly effective population trap for hamsters. The area is densely populated and heavily used for agriculture. The majority of information on hamsters is from the early 1970s (Ružić 1978, Petrov 1992) and is therefore primarily of historical interest. There are no hamsters on the left bank of the Drava River in Hungary (Bihari 2007, Cserkész 2017), however, during an outbreak in the 1980s, the hamster population spread toward the Drava Plain till the western edge of Baranya County, Hungary (Nechay 2000).

The presence of European Hamsters at the far end of the Drava in Slovenia was confirmed for the first time in May 1980. Two specimens were found in the vicinity of the village Obrež, situated alongside the road Ormož – Središče ob Dravi (Kryštufek 1987). This tiny population is very marginal and restricted to a narrow strip of agricultural habitat between the hilly area to the north and the river to the south. The last individual was recorded in late 1990s and recent observations yielded no positive evidence on the animal. The conservation status in Croatia was reviewed by Tvrtković (2006), but this account includes hardly any new evidence. Tvrtković mainly stressed the lack of recent scientific information. While the current situation in Croatia is enigmatic, the European Hamster presumably still has considerable populations in the lowland to the east of the Danube in Hungary and Voivodina (the northern part of Serbia) (Banaszek *et al.* 2020).

In the Hungarian Baranya, the European Hamster is very rare (Bihari 2007, Cserkész 2017, Kondor & Cserkész 2017), hence its detection is a difficult task. In such cases, mammalogists frequently collect information from remnants found in pellets of avian predators, particularly owls. Owl pellet analysis is an important supplementary method in small mammal surveys (Mikuska *et al.* 1979, Horváth *et al.* 2007). In contrast to trapping, it can be particularly effective in monitoring difficult-to-detect small mammals (Torre *et al.* 2004, Heisler *et al.* 2016). The method has its limitations, e.g. the exact location of a small mammal prey can only be assumed. Despite this, the information gathered from the owl pellets can facilitate and direct further research, which can utilize different field techniques.

Research in Hungary retrieved the European Hamster as an important and frequent prey of the large-bodied Eurasian Eagle-owl *(Bubo bubo)*, while the smaller Common Barn-owl *(Tyto alba)* and the Northern Long-eared Owl *(Asio otus)* preyed on hamsters only rarely or extremely rarely (Bihari *et al.* 2008). The Common Barn-owl prefers open areas during hunting (Taylor 1994) and, as an opportunistic feeder, consumes prey in proportion to its abundance in the hunting habitat (Tores *et al.* 2005). Although the European Hamster is not an easy prey due to its comparatively large and robust body and aggressive behaviour (Kryštufek *et al.* 2020), we still presumed that the Common Barn-owl should be able to capture juvenile European Hamsters, e.g. at the time they start feeding above ground.

Our goal in this study was twofold. Firstly, we aimed to re-evaluate the current distribution of the European Hamster in Southern Transdanubia, relying primarily on the results of owl pellet analyses. In order to complete the distributional picture, we also used unpublished observations and literature data. Another goal was to re-draw attention to the importance of owl pellet collections and analyses in the detection of elusive small mammals and in performing a non-invasive monitoring.

Material and methods

Our database on prey composition of Common Barn-owl pellets contains information gained between the years 2007–2017 (Croatian part of Baranya, and Udvar in Hungary) and is based on remnants of 11,792 small mammal individuals. The database is stored at the Department of Ecology, University of Pécs. We extracted the information on the occurrence of hamster present in the study area, as well as on their relative abundance (Yom-Tov & Wool 1997). We completed the list of hamster records by interviews carried out among local ornithologists and upon sporadical inspection of roadkills (one skeleton is preserved in the

Natural History Museum of Slovenia). The four persons were included in searching for typical hamster holes (burrows) in agricultural habitats. Walking in transects about 5 meters apart, we examined the agricultural plots suggested by the hamster observers and also those areas, which we considered as potential habitats based on our own experience. In the period between 2018 and 2020, searching was performed two times in spring and three times in autumn in the areas north of the Croatian settlement of Podolje, and five times in Hungary in the area enclosed by the Udvar, Sátorhely, Nagynyárád and Majs settlements.

Results and discussion

Positive records of European Hamsters in Baranya are summarized in *Table 1*. All sites are located close to the international border between Croatia and Hungary *(Figure 1)*. Three records are from Common Barn-owl pellets, one observation was a road casualty, and two were reliable verbal reports *(Table 1)*. One of the records is historic (1988) but we still list it to document more thoroughly the status of the hamster in this part of Baranya.

For the hamster from Podolje, we were not certain if it had been preyed by the Common Barn-owl near its resting site *(Table 1)*. In 2007, we carefully sampled owl pellets in Croatia between the Drava and Danube rivers and the Hungarian border but found no further hamsters (Szép *et al.* 2018). Earlier detailed surveys in this part of Croatia (e.g. Mikuska *et al.* 1978, Mikuska & Vuković 1980, Tórizs 2010, 2011) similarly did not detect a single European Hamster. The species, however, was reported for the area prior to the mid-1970s (Ružić 1978, Petrov 1992). Despite this, we concluded that a single skull does not provide

Table 1. Occurrences of European Hamster *(Cricetus cricetus)* in the border region of Croatia and Hungary

1. táblázat Mezei hörcsög *(Cricetus cricetus)* előfordulások Horvátország és Magyarország határmenti régiójában

Map Id	Locality, Country	Latitude	Longitude	Date	Mode	Material	Source
1	Podolje, Croatia	45.815394	18.728147	28.09.2007	Owl pellets	1, juv, skull and mandible	Szép *et al.* 2018
1	Podolje, Croatia	45.815394	18.728147	29.10.2016	Owl pellets	1, juv, skull and mandible	own data
2	Udvar, Hungary	45.900367	18.659647	16.03.2017	Owl pellets	5, juv, skull and mandible	own data
3	Sátorhely, Hungary	45.942702	18.643589	27.07.2019	Roadkill	1, male, carcass	own data
4	Majs, Hungary	45.917971	18.632420	2015–2020	Observation in nature		Csaba László, pers. comm.
5	Babarc, Hungary	46.002709	18.551715	1988	Observation in nature		Tamás Treitz, pers. comm.

Figure 1. Occurrences of European Hamster *(Cricetus cricetus)* in the border region of Croatia and Hungary (1–5), on the south-western limit of its distribution range

1. ábra A mezei hörcsög *(Cricetus cricetus)* előfordulási helyszínei Horvátország és Magyarország határmenti régiójában (1–5), elterjedési területének délnyugati határán

indisputable evidence on the presence of the hamster but instead left open the possibility that the owls might prey the hamster to the east of the Danube in the nearby Serbia.

A subsequent survey, repeated in 2016, revealed a young hamster skull from the same location *(Table 1, Figure 1)*. A year later a large pellet sample was collected from the attic of a family house in Udvar (the Hungarian side of Baranya), which contained skeletal remnants of five hamsters *(Table 1, Figure 1)*. The site was so close to the Hungarian-Croatian border that hamsters could be preyed upon on either side.

Intensive owl pellet surveys have been continuously undertaken in Baranya (the southern county of Hungary) since 1985. European Hamster remains were not found either in the first ten years (Horváth 1999) or in subsequent surveys (e.g. Horváth 1998). Such a lack of evidence is surprising, as hamsters were present in Southern Transdanubia during the last decades of the 20th century (Nechay 2000, Bihari 2004). Near the current finding site *(Figure 1),* it was observed in Babarc (CR19) in spring 1988 (Tamás Treitz, pers. comm.). We accepted the presence of the European Hamsters in Hungary as proven after a road casualty was found at Sátorhely *(Table 1, Figure 1)*. Mr. Csaba László drew our attention to the carcass of the hamster that he collected. He recollected another observation of European Hamster nearby a few years earlier. In his testimony, hunters also observed hamsters on nearby fields (in the area of settlement Majs) several times during the last five years (Csaba László, pers. comm.). In 2019, we surveyed the vicinity of the site of the road casualty, as well as potentially suitable habitats in Croatia, but found no sign on the presence of the European Hamster.

Our survey covered only a small surface area in the border between Croatia and Hungary. The question remains whether there are still hamster habitats in the southern section of

Drava in Slavonia and further west. In Hungary, no hamsters were found in Common Barn-owl pellets collected along the Drava and Mura (e.g. Horváth 1998, Purger 1998, Szép *et al.* 2017), but similar surveys have never been conducted on the Croatian side (Tvrtković 2006). It would therefore be important to urgently perform this task.

Conclusion

Results of the Common Barn-owl pellet analyses and further data from field observations proved that a small isolated population of the European Hamster is still present in the Croatian-Hungarian border area. The habitat patch, which is estimated to cover an area of 20 × 10 km is on the south-western limit of the hamster's distribution range. Without proper attention and timely conservation measures, and in the absence of further population monitoring, hamsters can easily vanish from this area in the near future, just like they did in many parts of their European range. To counterbalance the negative population trend, a joint coordinated action by the relevant nature conservation authorities and cross-border cooperation is urgently needed, here and now.

Acknowledgements

We are grateful to Csaba László, Tamás Treitz and Béla Simonkovics for their information and help during the work and Ákos Halmai for his help in preparing the map. The project "Bilateral Scientific and Technological (TéT) Cooperation Hungarian-Slovenian Relation (2018-2.1.11-TÉT-SI-2018-00015)" was implemented with the support of the National Research, Development and Innovation Office from the NKFIH Fund and Slovenian Research Agency project nb. BI-HU/19-20-009.

References

Banaszek, A., Bogomolov, P., Feoktistova, N., La Haye, M., Monecke, S., Reiners, T. E., Rusin, M., Surov, A., Weinhold, U. & Ziomek, J. 2020. *Cricetus cricetus*. – The IUCN Red List of Threatened Species 2020: e. T5529A111875852. DOI: 10.2305/IUCN.UK.2020-2.RLTS.T5529A111875852.en (Downloaded on 04 October 2020.)

Bihari, Z. 2004. A hörcsög *(Cricetus cricetus)* magyarországi elterjedésének változása az elmúlt 50 év alatt [Changes in the distribution of Hamster *(Cricetus cricetus)* in Hungary during the past fifty years]. – Természetvédelmi Közlemények 11: 559−566. (in Hungarian with English Summary)

Bihari, Z. 2007. Mezei hörcsög *Cricetus cricetus* (Linnaeus, 1758) [European Hamster]. – In: Bihari, Z., Csorba, G. & Heltai, M. (eds.) Magyarország emlőseinek atlasza [Atlas of mammals in Hungary]. – Kossuth Kiadó, Budapest, pp. 176−178. (in Hungarian with English Summary)

Bihari, Z., Horváth, M., Lanszki, J. & Heltai, M. 2008. Role of the Common Hamster *(Cricetus cricetus)* in the diet of natural predators in Hungary. – In: Millesi, E., Winkler, H. & Hengsberger, R. (eds.) The Common Hamster *(Cricetus cricetus)*: Perspectives on an endangered species. Austrian Academy of Sciences, Wien. – Biosystematics and Ecology Series 25: 61–68.

Cserkész, T. 2017. A mezei hörcsög aktuális helyzete [The current distribution of the European Hamster]. – In: Holes, A. (ed.) Magyarország környezeti állapota 2016 [The state of the environment in Hungary in 2016]. – Herman Ottó Intézet, Budapest, pp. 76–81. (in Hungarian)

Heisler, L. M., Somers, C. M. & Poulin, R. G. 2016. Owl pellets: a more effective alternative to conventional trapping for broad-scale studies of small mammal communities. – Methods in Ecology and Evolution 7(1): 96–103. DOI: 10.1111/2041-210X.12454

Horváth, G., Jurčević Agić, I., Merdić, E., Tórizs, I. & Purger, J. J. 2007. Small mammal monitoring based on the analysis of owl pellets. – In: Purger, J. J. (ed.) Manual for the investigation of biodiversity along the Drava River. – University of Pécs, pp. 203–217. (in Croatian)

Horváth, Gy. 1998. Kisemlős (Mammalia) faunisztikai vizsgálatok a gyöngybagoly *(Tyto alba)* köpetanalízise alapján a Dráva mentén (1995–1997) [The investigation of the small mammal fauna of the River Dráva plain region, based on the analysis of Barn Owl *(Tyto alba)* pellets between 1995–1997]. – Dunántúli Dolgozatok (Publicationes Transdanubiensis) Természettudományi Sorozat (Studia Pannonica) 9: 475–488. (in Hungarian with English Summary)

Horváth, Gy. 1999. A gyöngybagoly (*Tyto alba* Scop., 1769) köpetvizsgálatának tíz éve Baranya megyében (1985–1994) [Ten years of Barn Owl (*Tyto alba* Scop., 1769) pellet analysis in county Baranya]. – Állattani Közlemények 84: 63–77. (in Hungarian with English Summary)

Kondor, T. & Cserkész, T. 2017. A mezei hörcsög *(Cricetus cricetus)* populációs trendjének és elterjedésének változása Magyarországon [Changes in the population trend and distribution of the European Hamster *(Cricetus cricetus)* in Hungary]. – Bükki Emlőstani Kutatócsoport Egyesület, Eger, pp. 18. (in Hungarian)

Kryštufek, B. 1987. Hrček (*Cricetus cricetus* Linnaeus, 1758; Rodentia, Mammalia) edini stepski sesalec v slovenski favni [Hamster (*Cricetus cricetus* Linneaeus, 1785; Rodentia, Mammalia) the only steppe mammal in the Slovene fauna]. – Varstvo Narave 13: 93–98. (in Slovenian with English Summary)

Kryštufek, B., Hoffmann, I. E., Nedyalkov, N., Pozdnyakov, A. & Vohralík, V. 2020. *Cricetus cricetus* (Rodentia: Cricetidae). – Mammalian Species 52(988): 10–26. DOI: 10.1093/mspecies/seaa001

Mikuska, J. & Vuković, S. 1980. Kvalitativna i kvantitativna analiza ishrane kukuvije drijemavice, *Tyto alba* Scop. 1769, na području Baranje, sa posebnim osvrtom na rasprostranjenost sitnih sisavaca [Qualitative and quantitative analysis of the diet of Common Barn-owl, *Tyto alba* Scop. 1769, in Baranja region, with a focus on the distribution of small mammals]. – Larus (31–32): 269–288. (in Croatian with German Summary)

Mikuska, J., Pivar, G. & Pančić, S. 1978. Analiza ishrane kukuvije drijemavice, *Tyto alba* Scop. 1769, na području Specijalnog zoološkog rezervata „Kopački rit" i okoline s posebnim osvrtom na faunu sitnih sisavaca [Diet analysis of Common Barn-owl, *Tyto alba* Scop. 1769, in the area of the Special Zoological Reserve "Kopački rit" and the surrounding area, with a focus on the fauna of small mammals]. – Priroda Vojvodine 4: 45–46. (in Serbo-Croatian).

Mikuska, J., Tvrtković, N. & Džukić, G. 1979. Collecting and analysis of bird pellets as one more important methods for studying the fauna of Mammals in Yugoslavia. – Archives of Biological Sciences 29(3–4): 157–160.

Nechay, G. 2000. Status of Hamsters: *Cricetus cricetus, Cricetus migratorius, Mesocricetus newtoni* and other hamster species in Europe. – Council of Europe Publishing, Strasbourg, France, Nature and Environment Series 106.

Nechay, G. 2008. Peak numbers of *Cricetus cricetus* (L.): do they appear simultaneously? – In: Millesi, E., Winkler, H. & Hengsberger, R. (eds.) The Common Hamster *(Cricetus cricetus)*: Perspectives on an endangered species. – Austrian Academy of Sciences, Wien. – Biosystematics and Ecology Series 25: 69–77.

Petrov, B. M. 1992. Mammals of Yugoslavia: Insectivores and Rodents. – Natural History Museum in Belgrade, Special issues 37: 1–186.

Purger, J. J. 1998. A Dráva mente Somogy megyei szakaszának kisemlős (Mammalia) faunája, gyöngybagoly, *Tyto alba* (Scopoli, 1769) köpetek vizsgálata alapján [Small mammal fauna of the region of Drava river in county Somogy (Hungary), obtained by Barn Owl, *Tyto alba* (Scopoli, 1769) pellet analysis]. – Dunántúli Dolgozatok (Publicationes Transdanubiensis) Természettudományi Sorozat (Studia Pannonica) 9: 489–500. (in Hungarian with English Summary)

Ružić, A. 1978. Distribution and abundance of the Common Hamster (*Cricetus cricetus* Linnaeus, 1758; Rodentia, Mammalia) in Yugoslavia. – Biosistematika 4(1): 203–208. (in Serbo-Croatian with English Summary)

Surov, A., Banaszek, A., Bogomolov, P., Feoktistova, N. & Monecke, S. 2016. Dramatic global decrease in the range and reproduction rate of the European Hamster *Cricetus cricetus*. – Endangered Species Research 31: 119–145. DOI: 10.3354/esr00749

Szép, D., Horváth, G. F., Krčmar, S. & Purger, J. J. 2018. Connection between prey composition and the landscape structure in the hunting area of Barn Owls *(Tyto alba)* in Baranja (Croatia). – Periodicum Biologorum 120(2–3): 125–233. DOI: 10.18054/pb.v120i2-3.6650

Szép, D., Klein, Á. & Purger, J. J. 2017. The prey composition of the Barn Owl *(Tyto alba)* with respect to landscape structure of its hunting area (Zala County, Hungary). – Ornis Hungarica 25(2): 51–64. DOI: 10.1515/orhu-2017-0015

Taylor, I. R. 1994. Barn Owls: Predator – Prey Relationships and Conservation. – Cambridge University Press, Cambridge, 304 p.

Tissier, M. L., Handrich, Y., Robin, J-P., Weitten, M., Pevet, P., Kourkgy, C. & Habold, C. 2016. How maize monoculture and increasing winter rainfall have brought the hibernating European Hamster to the verge of extinction. – Scientific Reports 6: 25531. DOI: 10.1038/srep25531

Tores, M., Motro, Y., Motro, U. & Yom-Tov, Y. 2005. The Barn Owl – a selective opportunist predator. – Israel Journal of Zoology 51(4): 349–360. DOI: 10.1560/7862-9E5G-RQJJ-15BE

Tórizs, I. 2010. A gyöngybagoly [*Tyto alba* (Scop.) 1769] monitorozása a Drávaszögben, különös tekintettel a táplálkozásbiológiára [Monitoring of the Common Barn-owl (*Tyto alba* (Scop.) 1769) in Baranja, with special regard to feeding biology]. – MS Thesis, University of West Hungary, Sopron, 67 p. (in Hungarian)

Tórizs, I. 2011. Gyöngybagolyvédelem a Drávaszögben [The conservation of Common Barn-owl in Baranja]. – Rovátkák 3: 34–54. (in Hungarian)

Torre, I., Arrizabalaga, A. & Flaquer, C. 2004. Three methods for assessing richness and composition of small mammal communities. – Journal of Mammalogy 85(3): 524–530. DOI: 10.1644/BJK-112

Tvrtković, N. 2006. Hrčak / Common Hamster *Cricetus cricetus* (Linnaeus, 1758). – In: Tvrtković, N. (ed.) Crvena knjiga sisavaca Hrvatske [Red book of mammals of Croatia]. – Ministry of Culture, State Institute for Nature Protection, Republic of Croatia, Zagreb, pp. 87–88. (in Croatian)

Weinhold, U. 2008. Draft European action plan for the conservation of the Common Hamster (*Cricetus cricetus* L., 1758). – Convention on the conservation of European wildlife and natural habitats, 28th Meeting of the Standing Committee, Council of Europe, Strasbourg, France, 36 p.

Yom-Tov, Y. & Wool, D. 1997. Do the Contents of Barn Owl Pellets Accurately Represent the Proportion of Prey Species in the Field? – The Condor 99(4): 972−976. DOI: 10.2307/1370149

Ornis Hungarica 2020. 28(2): 74–84.
DOI: 10.2478/orhu-2020-0018

Impact of agriculture irrigation on the habitat structure and use by Great Bustards *(Otis tarda)* in a Natura 2000 site

Péter Spakovszky* & Rainer Raab

Received: October 16, 2020 – Revised: November 09, 2020 – Accepted: November 11, 2020

Spakovszky, P. & Raab, R. 2020. Impact of agriculture irrigation on the habitat structure and use by Great Bustard *(Otis tarda)* in a Natura 2000 site. – Ornis Hungarica 28(2): 74–84. DOI: 10.2478/orhu-2020-0018

Abstract As the whole Palearctic steppe system, its iconic bird, the Great Bustard has also suffered from the expansion of intensive agriculture. The species now typically has stable or growing populations only in protected areas, but negative processes are still prevalent even there. In this study, we present a recent change in a part of the Natura 2000 site designated for the isolated West Pannonian population. In recent years, a total of 2.3 km Center-pivot and laterally moving linear irrigation systems have been built and 4.7 km of underground pipelines have been laid, with which more than 52% of the 1245,5 ha study area was irrigated by 2020. In comparison to 2009, when the study period has started, the sown area of autumn cereals, one of the main breeding habitats, was roughly halved and the proportion of crops unsuitable for breeding was increased. New crops requiring irrigation have emerged with a rate of 30.6% in the last year. Despite the available support, the area of alfalfa, which is the most significant breeding habitat, and is grown almost exclusively in the agri-environmental scheme, has decreased. As a result of habitat degradation, the number of Great Bustard females observed in the area in spring decreased to a small fraction of the beginning. Irrigation farming is expected to increase, as a response to the climate change, but in order to save agro-steppe habitats and their species, the adverse effects of agricultural intensification need to be urgently addressed at both local and European levels.

Keywords: intensive agriculture, agri-environmental scheme, agro-steppe habitat, West Pannonian Great Bustard population, agricultural policy

Összefoglalás Ahogy a palearktikus sztyepp övezet egésze, úgy annak emblematikus madara, a túzok is elszenvedte az intenzív mezőgazdálkodás elterjedését. A fajnak ma már jellemzően csak védett területen vannak stabil vagy növekvő állományai, de negatív folyamatok még ott is jellemzőek. A tanulmányunkkal az elszigetelődött nyugat-pannon populáció számára kijelölt Natura 2000 terület egy részén, a közelmúltban bekövetkezett változást mutatjuk be. Az 1245,5 ha nagyságú vizsgálati területen az utóbbi években 2,3 km összhosszúságú forgó és oldalazó lineár öntözőberendezést építettek, illetve 4,7 km hosszan hidránsrendszereket fektettek, melyekkel 2020-ban a terület 52%-át öntözték. Ennek hatására 2009-hez, vagyis a vizsgálati időszak kezdetéhez képest az egyik fő költőhabitat, az őszi gabonák vetésterülete nagyjából a felére csökkent, és nőtt a költésre alkalmatlan élőhelyek aránya. Új, öntözést igénylő növénykultúrák jelentek meg, melyek területi részaránya az utolsó évben már 30,6% volt. Az elérhető támogatás ellenére csökkent a költőhelyként jelentős lucerna vetésterülete, melyet szinte csak az agrár-környezetgazdálkodási program miatt termesztenek. Az élőhely romlásának következményeként a területen tavasszal megfigyelhető túzoktyúkok száma a korábbi töredékére esett. A klímaváltozás hatására várható az öntözéses gazdálkodás terjedése, de az agrár-sztyepp élőhelyek és fajaik megmentése érdekében a mezőgazdaság intenzifikációjának káros hatásait sürgősen kezelni kell mind helyi, mind európai szinten.

Kulcsszavak: intenzív mezőgazdaság, agrár-környezetgazdálkodás, agro-sztyepp élőhely, nyugat-pannon túzokállomány, agrárpolitika

Technisches Büro für Biologie Mag. Dr. Rainer Raab, Quadenstraße 13 A-2232 Deutsch-Wagram, Austria
** corresponding author, e-mail: spakovszky@yahoo.com*

Introduction

Agriculture is the primary cause of biodiversity loss worldwide (Dudley & Alexander 2017). One of the most endangered habitats by land use is the Palearctic steppe (Török *et al.* 2020). In addition to the loss of original habitats, the population of species that can adapt somewhat to the changed conditions (so-called farmland birds) is affected also by the intensity of farming in cultivated areas (Donald *et al.* 2001, Reidsma *et al.* 2006, Jerrentrup *et al.* 2017, Traba & Morales 2019). This is especially true for species that are specialized for open habitats (Teillard *et al.* 2015). Irrigation is one of the most common elements of intensive farming practice, and in areas where it is widespread, steppe bird populations are in a less favorable position (Brotons *et al.* 2004, De Frutos *et al.* 2015).

The Great Bustard is an emblematic bird of the agro-steppe habitat, and it has also suffered the negative effects of the spread of intensive agriculture (Horreo *et al.* 2013). It bred in many European countries in the Middle Ages (Glutz *et al.* 1973), since then only isolated populations have survived (Szabó *et al.* 2007, Alonso *et al.* 2009a), and the primary reason for the eradication of countless populations was the agricultural activity (Alonso *et al.* 2003, Faragó 2006, Alonso 2014). Today, stable or possibly growing populations occur only in areas of comparatively better quality, that are usually protected, where near-natural habitats can also be found among patches of arable land (Pinto *et al.* 2005, Pitra *et al.* 2011, Szenek & Végvári 2018), or where significant habitat protection measures have been taken to repress intensive farming, typically by launching an agri-environmental scheme (AES hereinafter) (Martín *et al.* 2012a, Alonso 2014, Faragó *et al.* 2014, Raab *et al.* 2014b), but usually the two are present together.

In agricultural areas, irrigation is particularly detrimental to habitat quality, which also affects Great Bustards. An abundance model tested in Spain (Martín *et al.* 2012b) showed that non-irrigated herbaceous vegetation cover was higher in places visited by Great Bustards than in places where the species was absent, and one of the defining component of the final abundance model was the non-irrigated area. This was confirmed by a study from Gameiro *et al.* (2020) showing that the abundance of Great Bustards is highly dependent on the extent of the agro-steppe habitat in the Iberian Peninsula, and the recent negative change affecting these habitats was the expansion of plantations and irrigated crops. Moreover, a significant reduction or extinction of some Portuguese Great Bustard populations was largely due to irrigation (Pinto *et al*. 2005).

The world's largest nature conservation network, the Natura 2000 network, has been established to protect Europe's endangered habitats and species in order to eliminate harmful processes such as those mentioned above. When designing the network, the Great Bustards received special attention and the 91 Special Protected Areas (SPA) designated for the species under the Birds Directive cover the core areas of the species' most important habitats (EC 2009).

Recently, the burgeon of irrigated crop production in Hungary has accelerated, sometimes even affecting protected areas. This trend is significantly catalyzed by a large-scale agricultural irrigation development program (Hungarian Government 2017). In the present study, we demonstrate what negative change irrigation farming causes in the breeding site of an isolated Great Bustard population, using a particular example.

Material and method

Study species and area

The global population of our study species, the Great Bustard amounts to 44,000–57,000 individuals (Alonso 2014) and is classified as vulnerable (BirdLife International 2020). The size of the isolated West Pannon population exceeds 600 individuals (Raab *et al.* 2010. Faragó *et al.* 2014 and own data), whose central habitat is located in the area of the Hungarian-Austrian-Slovak triple border (Raab *et al.* 2010). Natura 2000 sites have been designated in all three countries, which intersect along national borders. The study area is the most northern continuous part of the Moson Plain Natura 2000 site (HUFH10004) in Hungary, which is mainly in conventional field cultivation *(Figure 1)*. It is bordered on the east by a motorway, on the north-west by the Slovak and Austrian state borders, and on the south-west by fallow lands, a planted forest and, on a short section, a canal. It covers an area of 1245.5 hectares. Here, the calcareous chernozem soil is typical, which is excellent for crop production, although due to the shallow soil layer, the crops can suffer from drought early, but with the application of irrigation, however, it is easy and safe to achieve good yields even in dry years (Miklay & Molnár 1968). The main crops grown are cereals, maize and oilseed rape. The area is part of the 'High Nature Value Area', so local farmers can receive compensations for Great Bustard-friendly farming within the Hungarian Agri-Environmental Scheme. The total area of land cultivated in this way in the study area does not currently reach 100 ha (<10% of the study area), these are typically extensively cultivated alfalfa fields.

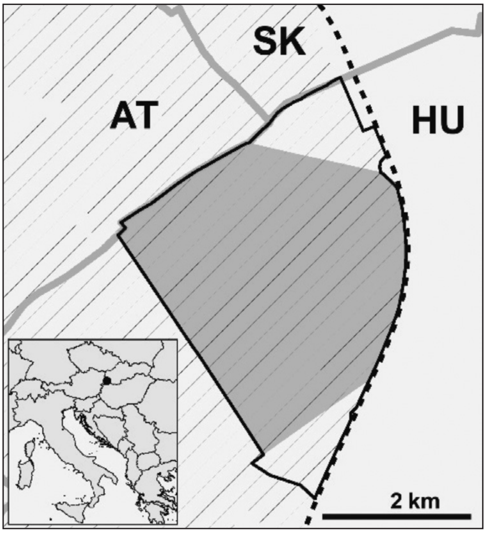


Figure 1. Schematic map and location of the study area. Solid black line – the study area; grey area – 'bustard counting area'; hatched area – Natura 2000 site; grey line – state border; dashed black line –highway; HU – Hungary; AT – Austria; SK – Slovakia

1. ábra A vizsgálati terület térképvázlata és elhelyezkedése. Folytonos fekete vonal – a vizsgálati terület; szürke mező – túzokszámolási terület; vonalkázott mező – Natura 2000 terület; szürke vonal – államhatár; szaggatott fekete vonal – autópálya; HU – Magyarország; AT – Ausztria; SK – Szlovákia

The Great Bustard is an extremely sexually dimorphic bird (Alonso *et al*. 2009b), with lek mating system (Morales *et al*. 2001), and the parental care is exclusively undertaken by the females (Morales *et al*. 2002). In the spring, their favored habitat is usually cereals throughout their European range (Faragó 1987, Pescador & Peris 1996, Moreira *et al*. 2004), and depending on whether they are available in their habitat: alfalfa, vetch, pastureland and fallow land (Faragó 1987, Pescador & Peris 1996, Lane *et al*. 2001, Rocha *et al*. 2013). These are also the main breeding habitats (Petrick 1996, Morgado & Moreira 2000, Rocha *et al*. 2013, Janó & Végvári 2016).

The area fidelity to the breeding sites in female Great Bustards is very high (Alonso *et al*. 2000) and the natal dispersion is low (Martín *et al.* 2008). The Central European Great Bustard populations are considered as facultative migratory, indicating that their migration is triggered by harsh weather (Faragó 1990, Streich *et al.* 2006), however, a kind of seasonal movement is characteristic even for sedentary females (Alonso *et al.* 2000). Female Great Bustards can be observed in the study area from spring to autumn and they are not present in winter (own unpublished data), i.e. the place is of primary importance for reproduction.

Method

A direct and an indirect indicator are used for the spread of agricultural irrigation in the study area. The direct metric is the size of the irrigated area, which was measured only in 2019 and in 2020. The indirect metric is the length of permanently installed irrigation pipes which includes the Center-pivot (also called water-wheel or circle irrigation) and the lateral move (linear move, wheel move or side-roll) irrigation systems and furthermore the underground pipeline with hydrants supplying hose reel irrigation systems. These were measured during their construction. The accuracy of these data, thanks to intensive fieldwork, is estimated to be close to 100%.

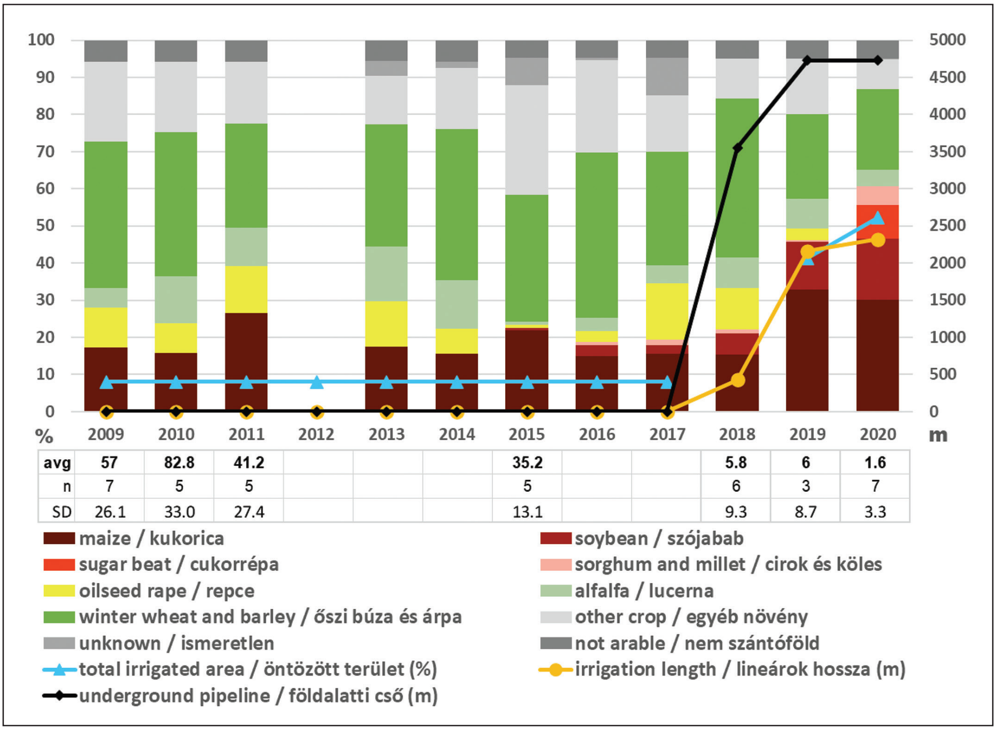
Habitat mapping was carried out in the study area every year between 2009 and 2020, during which we identified the main crop grown. Taking into account the irrigation characteristics and breeding site characteristics of a given crop, we grouped or treated them separately as follows: (1) soybean, (2) sugar beet, (3) sorghum species and millet (so far not suitable for breeding and grown almost exclusively by irrigation), (4) maize (not suitable for breeding, can be grown without irrigation, but is irrigated more and more frequently in recent years), (5) oilseed rape (the main winter food for Great Bustards in this region, but not suitable for breeding and recently increasingly irrigated), (6) autumn cereals (one of the most favored crop for breeding, typically grown without irrigation; only winter wheat and winter barley were included, other autumn cereals are usually sown for green fodder, which is not suitable for successful breeding), (7) alfalfa (perhaps the most important cultivated crop for breeding site in our area, the fields included in the study area are mainly supported by AES), (8) other crops (all other crops grown on smaller proportion, most of which are not preferred types of breeding habitats or cultivated in a not-Great Bustard-friendly way), (9) non-arable land (roads, wooded areas, water surface, orchard etc.), (10) unknown (the main crop grown is not known in that year). A suitable data set is not available from 2012.

At least once a month, a complete Great Bustard count was performed in the study area, classifying the individuals according to their sex (Spakovszky 2009). The study area is mainly significant as a breeding site, therefore we examined the spring presence of females. Most females appear at the breeding site in late March (Alonso *et al.* 2000), so only the counts after March 14th were considered. The detection probability of the breeding females is limited due to the concealing behavior (Magaña *et al.* 2010). Therefore, in order to avoid a distortion (Sanz-Pérez *et al.* 2020), the results of the censuses after April 30th, when the majority of the females in our area are already incubating (Faragó 1983, Petrik 1996), were not taken into account. Despite the relatively small size of the study area, during the active spring period of the females, the whole area cannot be patrolled in such a way that double counting of individuals can be definitely excluded due to visual obstacles, thus the censuses of females were performed only in the 'bustard counting area' *(Figure 1)*. This equals 83.7% of the study area. We provided the average and the standard deviation of the results of repeated censuses for the 15th March – 30th April period, and omitted the years (2012–2014, 2016, 2017), when the number of censuses covering the 'bustard counting area' was less than 3. The association of the number of Great Bustard females with the extent of irrigated area was measured by Pearson's correlation coefficient.

Results

Prior to 2018, the proportion of irrigated surface was below 10% of the study area each year as an estimated maximum according to our field observations. Since 2018, the area of irrigated lands increased rapidly, and by 2020, 52% of the study area had been irrigated *(Figure 2).* The construction of Center-pivot and laterally moving linear irrigation systems as well as underground pipeline-hydrant systems began in 2017, of which the total length reached 2.3 km and 4.7 km in the study area till 2020, respectively. Since 2016, there has been an interest from farmers in irrigation, resulting in several water wells having been drilled in the study area, but these were not generally used at first (pers. obs.).

In the study area, new plant species appeared in the crop composition, such as soybeans, sugar beets, sorghum species and millet, which were mostly grown with irrigation (pers. obs.). The area proportion of these new crops was 30.6% in 2020 *(Figure 2)*. The sown area of maize was significant in the past, too, but increased slightly as a result of irrigation. A major change in relation to maize is the widespread use of irrigation, with 84% of the maize fields area being irrigated in 2019 and 75.6% in 2020. The sown area of oilseed rape has decreased, which is assumed not to be related to irrigation, but to market processes making its cultivation less and less profitable in our region, however, it is also grown mainly with irrigation in recent years (pers. obs.). The area of autumn cereals has decreased from 30–40% per year to about 20%. The cultivation area of alfalfa is highly dependent on the AES, as alfalfa is grown almost exclusively on AES-supported arable land. In 2015, it barely reached 1% of the study area because that was an "interim year" between two periods when the AES was out of order. Nevertheless, despite being subsidized, it has never been grown in significant proportions and is even declining in the long run, which shows the competitiveness of intensive farming, including irrigation, against the AES. Furthermore, it was observed that in locations where a significant investment was made to build the new irrigation facility, crops typically grown without irrigation were also irrigated in many cases. For example, in 2020, 40.3% of the winter wheat cultivation area was irrigated, which crop was typically not irrigated formerly.



	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
avg	57	82.8	41.2				35.2			5.8	6	1.6
n	7	5	5				5			6	3	7
SD	26.1	33.0	27.4				13.1			9.3	8.7	3.3

Figure 2. The crop composition and the proportion of the irrigated surface of the study area, the total length of the two main irrigation system, and the average number of the observed Great Bustard females (avg) in the counting area in the given years. n – the number of the Great Bustard counting events between 15th March and 30th April in the given year, SD – standard deviation. The proportion of the irrigated surface before 2018 is expert estimation maximum

2. ábra A vizsgálati terület vetésszerkezete és az öntözött földek aránya, valamint a két fő öntözési rendszer hossza, illetve a túzokszámolási területen észlelt túzoktyúkok átlagos egyedszáma (avg) a vizsgálat éveiben. n – a túzokszámolási alkalmak száma március 15. és április 30. között az adott évben, SD – szórás. Az öntözött terület 2018 előtti értékei tapasztalati becsült maximumok

The number of Great Bustard females observed in the area in the spring decreased significantly during the study period. At the beginning of the study period, dozens of female Great Bustards were usually present in the study area in spring, on average 57 in 2009 (SD = 26.1, n=7), 32.8 in 2010 (SD=33, n=5) and 41.2 in 2011 (SD=27.4, n=5). In contrast, it was seldom possible to count a dozen females at the end of the study period, on average 5.8 in 2018 (SD=9.3, n=6), 6 in 2019 (SD=8.7, n=3) and 1.6 in 2020 (SD=3.3, n=7), respectively *(Figure 2)*. No significant change other than the spread of irrigation and consequently the alteration of habitat structure was observed in the study area, and the decrease in the number of females is strongly correlated with it (*Pearson's* $r = -0.91$, $p = 0.011$).

Discussion

As a result of our work, we demonstrate that irrigation farming in the study area has significantly increased in recent years, resulting to an increase in the proportion of crops that are unsuitable for breeding. In contrast, the proportion of favored breeding habitats has decreased, and thus it can be stated, that the quality of the bustard habitat has effectively deteriorated as a result of irrigation. Although only approximately half of the study area was irrigated, its negative effects are clearly detected on the intervening and adjacent non-irrigated lands, thus reducing the quality of the whole area (Brotons *et al.* 2004). Great Bustards are a long-lived species (Morales *et al.* 2002), so presumably individuals missing from the study area have been forced to other places, and a shrinking habitat may increase mortality and reduce reproduction rates (Morales *et al.* 2002). In the last two years, females have occurred mainly in the south-western and southern parts of the study area in the spring (pers. obs.), where better quality habitats are still available in the nearby fields. Great Bustards are expected to move less and less towards the study area, similarly to the experiences in Villafáfila, Spain, where less bustards moved south from the center compared to other directions because there were irrigated unsuitable habitats in significant extent (Alonso *et al.* 1995).

The West Pannonian Great Bustard population was driven to the verge of extinction in the second half of the 20th century (Raab *et al.* 2010), but by investing a significant amount of energy and resources, we managed to reverse the declining trend and multiply the population in a short time (Faragó *et al.* 2014, Raab *et al.* 2014a). This unique result (Alonso 2014) is now threatened by an incompetently controlled agro-economic development (Palacín *et al.* 2012). Although the habitat-destroying effect of the spread of irrigated farming is clear, it is still feasible that it will remain hidden for a while at population level because the positive effects of diversified conservation activity may outweigh it (Gameiro *et al.* 2020).

As a kind of response to today's climate change, an increase in irrigated areas is expected in some parts of Europe (Riediger *et al.* 2014), e.g. in Hungary the goal is to quadruple the currently irrigated agricultural surface (Hungarian Government 2017). This direction is worrying in two ways. On the one hand, it means a further intensification of agriculture, which is already a serious problem for the ecosystem in general. On the other hand, climate change is expected to reduce access to irrigation water across Europe although to varying extent from region to region (Iglesias & Garrote 2015), leading to an unsustainable shift in agriculture and generating conflicts by using limited water resources (Olesen *et al.* 2011, Moore & Lobell 2014).

The situation of agro-steppe habitats and their species in Natura 2000 areas is more favorable than outside, but negative processes also take place there (Silva *et al.* 2018, Gameiro *et al.* 2020). The general objectives of the Directives (Birds Directive 79/409/EEC, Habitats Directive 92/43/EEC) have not yet been met, but remain highly relevant and are still fit for the protection of species and habitats, as was recently concluded by an evaluation of the Natura 2000 protection system (EC 2016). Therefore, the system needs to be maintained, further developed and supported (Gameiro *et al.* 2020). The authorities and organizations concerned must not disregard the original objectives in their management activities and procedures and must protect agro-steppe species and their habitats (Lane *et al.* 2001, Palacín *et* *al.* 2012). In Hungary, the sustainable land use of natural grasslands in Natura 2000 sites has been regulated since 2007 (269/2007 government decree), which prohibits the irrigation of these grasslands. However, similar legislation on the sustainable management of Natura 2000 arable land has not yet been implemented, which has to happen as soon as possible. Within this legislation, it is necessary to provide solutions for the appropriate reductions of harmful effects caused by an intensive agriculture, including irrigation.

Today, the Common Agriculture Policy of the EU is being redesigned, which is perhaps the main tool for moving European agriculture in the right direction. If we are to take biodiversity conservation seriously, the new agricultural policy must reflect on the challenges and take serious steps (Palacín & Alonso 2018, Traba & Morales 2019, Pe'er *et al.* 2020).

Acknowledgements

The study was completed thanks to the Fertő-Hanság National Park Directorate through the support of the long-term monitoring of the Great Bustard in the Mosoni-plain and with the partial contribution of the EU through the LIFE09 NAT/AT/000225 and LIFE15 NAT/AT/000834 projects. We thank Clara Freytag, Alexander Bek and Maximilian Raab for their help during writing the article.

References

Alonso, J. C. 2014. The Great Bustard: past, present and future of a globally threatened species. – Ornis Hungarica 22(2): 1–13. DOI: 10.2478/orhu-2014-0014

Alonso, J. C., Alonso, J. A. & Morales, M. 1995. Range and patterns of Great Bustard movements at Villafafila, NW Spain. – Ardeola 42(1): 69–76.

Alonso, J. C., Morales, M. B. & Alonso, J. A. 2000. Partial migration, and lek and nesting area fidelity in female Great Bustards. – The Condor 102: 127–136.

Alonso, J. C., Palacín, C. & Martín, C. A. 2003. Status and recent trends of the Great Bustard *(Otis tarda)* population in the Iberian peninsula. – Biological Conservation 110(2): 185–195. DOI: 10.1016/S0006-3207(02)00188-X

Alonso, J. C., Martín, C. A., Alonso, J. A., Palacín, C., Magaña, M., Lieckfeldt, D. & Pitra, C. 2009a Genetic diversity of the Great Bustard in Iberia and Morocco: Risks from current population fragmentation. – Conservation Genetics 10(2): 379–390. DOI: 10.1007/s10592-008-9605-2

Alonso, J. C., Magaña, M., Alonso, J. A., Palacín, C., Martín, C. A. & Martín, B. 2009b The most extreme sexual size dimorphism among birds: allometry, selection, and early juvenile development in the Great Bustard *(Otis tarda)*. – The Auk 126(3): 657–665. DOI: 10.1525/auk.2009.08233

BirdLife International 2020. Species factsheet: *Otis tarda*. – Downloaded from http://www.birdlife.org on 25/09/2020.

Brotons, L., MaÑosa, S. & Estrada, J. 2004. Modelling the effects of irrigation schemes on the distribution of steppe birds in Mediterranean farmland. – Biodiversity and Conservation 13(5): 1039–1058. DOI: 10.1023/B:BIOC.0000014468.71368.35

De Frutos, A., Olea, P. P. & Mateo-Tomás, P. 2015. Responses of medium- and large-sized bird diversity to irrigation in dry cereal agroecosystems across spatial scales. – Agriculture, Ecosystems & Environment 207: 141–152. DOI: 10.1016/j.agee.2015.04.009

Donald, P. F., Green, R. E. & Heath, M. F. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. – Proceedings of the Royal Society of London. Series B: Biological Sciences 268(1462): 25–29. DOI: 10.1098/rspb.2000.1325

Dudley, N. & Alexander, S. 2017. Agriculture and biodiversity: A review. – Biodiversity, 18(2–3): 45–49. DOI: 10.1080/14888386.2017.1351892

EC (European Commission) 2009. Great Bustard, *Otis tarda* factsheet. – EU Wildlife and Sustainable Farming project 2009

EC (European Commission) 2016. Fitness check of the EU Nature Legislation (Birds and Habitats Directives). – Downloaded from: https://ec.europa.eu/environment/nature/legislation/fitness_check/docs/nature_fitness_check.pdf on 25/09/2020.

Faragó, S. 1983. A túzok (*Otis t. tarda* L.) fészkelésbiológiája Magyarországon [The breeding ecology of Great Bustard (*Otis t. tarda* L.) in Hungary]. – Állattani Közlemények 70: 33–38. (in Hungarian)

Faragó, S. 1987. A növényzet szerepe a túzok (*Otis tarda tarda* Linné, 1785) elterjedésében és költésbiológiájában Magyarországon [The role of the vegetation in the spreading and hatching biology of Bustard (*Otis tarda* Linné, 1785) in Hungary]. – Erdészeti és Faipari Tudományos Közlemények 1986(1): 177–213. (in Hungarian with English Summary)

Faragó, S. 1990. A kemény telek hatása Magyarország túzok (*Otis tarda* L.) állományára [The effect of heavy winters on Bustard (*Otis tarda* L.) populations in Hungary]. – Állattani Közlemények 76: 51–62. (in Hungarian with English Summary)

Faragó, S. 2006. One-hundred-year trend of the Great Bustard *(Otis tarda)* population in the Kisalföld Region. – Aquila 112: 153–162.

Faragó, S., Spakovszky, P. & Raab, R. 2014. Conservation of Great Bustard *(Otis tarda)* population of the Mosoni-Plain - A success story. – Ornis Hungarica 22(2): 14–31. DOI: 10.2478/orhu-2014-0015

Gameiro, J., Silva, J. P., Franco, A. M. A. & Palmeirim, J. M. 2020. Effectiveness of the European Natura 2000 network at protecting Western Europe's agro-steppes. – Biological Conservation 248: 108681. DOI: 10.1016/j.biocon.2020.108681

Glutz, U. N., Bauer, K. M. & Bezzel, E. 1973. *Otis tarda* Linné 1758 – Großtrappe [*Otis tarda* Linné 1758 – Great Bustard]. – In: Handbuch der Vögel Mitteleuropas, Vol. 5. Aula Verlag Wiesbaden (2nd reviewed ed. 1994), pp. 649–688. (in German)

Horreo, J. L., Palacín, C., Alonso, J. C. & Milá, B. 2013. A link between historical population decline in the threatened Great Bustard and human expansion in Iberia: Evidence from genetic and demographic data. – Biological Journal of the Linnean Society 110(3): 518–527. DOI: 10.1111/bij.12152

Hungarian Government 2017. Nemzeti Vízstratégia (Kvassay Jenő Terv) [National Water Strategy (Jenő Kvassay Plan)]. – Budapest – Downloaded from: https://www.kormany.hu/download/6/55/01000/Nemzeti%20V%C3%ADzstrat%C3%A9gia.pdf on 25/09/2020. (in Hungarian)

Iglesias, A. & Garrote, L. 2015. Adaptation strategies for agricultural water management under climate change in Europe. – Agricultural Water Management 155: 113–124. DOI: 10.1016/j.agwat.2015.03.014

Janó, G. & Végvári, Zs. 2016. Nest site selection of the Great Bustard *(Otis t. tarda)* in Körös-Maros National Park, Eastern Hungary. – Ornis Hungarica 24(2): 32–45. DOI: 10.1515/orhu-2016-0013

Jerrentrup, J. S., Dauber, J., Strohbach, M. W., Mecke, S., Mitschke, A., Ludwig, J. & Klimek, S. 2017. Impact of recent changes in agricultural land use on farmland bird trends. – Agriculture, Ecosystems & Environment 239: 334–341. DOI: 10.1016/j.agee.2017.01.041

Lane, S. J., Alonso, J. C. & Martín, C. A. 2001. Habitat preferences of Great Bustard *Otis tarda* flocks in the arable steppes of central Spain: Are potentially suitable areas unoccupied? – Journal of Applied Ecology 38: 193–203. DOI: 10.1046/j.1365-2664.2001.00577.x

Magaña, M., Alonso, J. C., Martín, C. A., Bautista, L. M. & Martín, B. 2010. Nest-site selection by Great Bustards *Otis tarda* suggests a trade-off between concealment and visibility: Nesting habitat selection by Great Bustards. – Ibis 152(1): 77–89. DOI: 10.1111/j.1474-919X.2009.00976.x

Martín, C. A., Alonso, J. C., Alonso, J. A., Palacín, C., Magaña, M. & Martín, B. 2008. Natal dispersal in Great Bustards: The effect of sex, local population size and spatial isolation. – Journal of Animal Ecology 77(2): 326–334. DOI: 10.1111/j.1365-2656.2007.01349.x

Martín, C. A., Martínez, C., Bautista, L. M. & Martin, B. 2012a Population increase of the Great Bustard *Otis tarda* in its main distribution area in relation to changes in farming practices. – Ardeola 59(1): 31–42. DOI: 10.13157/arla.59.1.2012.31

Martín, B., Alonso, J. C., Martín, C. A., Palacín, C., Magaña, M. & Alonso, J. 2012b Influence of spatial heterogeneity and temporal variability in habitat selection: A case study on a Great Bustard metapopulation. – Ecological Modelling 228: 39–48. DOI: 10.1016/j.ecolmodel.2011.12.024

Miklay, F. & Molnár, L. 1968. A Mosoni-síkság talajviszonyai [Soil characteristics of the Mosoni-plain]. – Agrokémia és Talajtan 17(4): 495–506. (in Hungarian)

Moore, F. C. & Lobell, D. B. 2014. Adaptation potential of European agriculture in response to climate change. – Nature Climate Change 4(7): 610–614. DOI: 10.1038/nclimate2228

Morales, M. B., Alonso, J. C. & Alonso, J. 2002. Annual productivity and individual female reproductive success in a Great Bustard *Otis tarda* population. – Ibis 144: 293–300. DOI: 10.1046/j.1474-919X.2002.00042.x

Morales, M. B., Jiguet, F. & Arroyo, B. 2001. Exploded leks: what Bustards can teach us. – Ardeola 48(1): 85–98.

Moreira, F., Morgado, R. & Arthur, S. 2004. Great Bustard *Otis tarda* habitat selection in relation to agricultural use in southern Portugal. – Wildlife Biology 10(1): 251–260. DOI: 10.2981/wlb.2004.030

Morgado, R. & Moreira, F. 2000. Seasonal population dynamics, nest site selection, sex-ratio and clutch size of the Great Bustard *Otis tarda* in two adjacent lekking areas. – Ardeola 47(2): 237–246.

Olesen, J. E., Trnka, M., Kersebaum, K. C., Skjelvåg, A. O., Seguin, B., Peltonen-Sainio, P., Rossi, F., Kozyra, J. & Micale, F. 2011. Impacts and adaptation of European crop production systems to climate change. – European Journal of Agronomy 34(2): 96–112. DOI: 10.1016/j.eja.2010.11.003

Palacín, C., Alonso, J. C., Martín, C. A. & Alonso, J. A. 2012. The importance of traditional farmland areas for steppe birds: A case study of migrant female Great Bustards *Otis tarda* in Spain. – Ibis 154(1): 85–95. DOI: 10.1111/j.1474-919X.2011.01183.x

Palacín, C. & Alonso, J. C. 2018. Failure of EU Biodiversity Strategy in Mediterranean farmland protected areas. – Journal for Nature Conservation 42: 62–66. DOI: 10.1016/j.jnc.2018.02.008

Pe'er, G., Bonn, A., Bruelheide, H., Dieker, P., Eisenhauer, N., Feindt, P. H., Hagedorn, G., Hansjürgens, B., Herzon, I., Lomba, Â., Marquard, E., Moreira, F., Nitsch, H., Oppermann, R., Perino, A., Röder, N., Schleyer, C., Schindler, S., Wolf, C., Zinngrebe, Y. & Lakner, S. 2020. Action needed for the EU Common Agricultural Policy to address sustainability challenges. – People and Nature 2(2): 305–316. DOI: 10.1002/pan3.10080

Pescador, M. & Peris, S. J. 1996. Selección del hábitat por la Avutarda *(Otis tarda)* en campos agrícolas del centro-oeste de la Península Ibérica [Habitat selection of Great Bustard *(Otis tarda)* in agricultural environment in West-Central Iberian Peninsula]. – Ecología 10: 471–480. (in Spanish with English Summary)

Petrick, S. 1996. Zur Brutplatzwahl der Großtrappe (*Otis t. tarda* L., 1758) im Land Brandenburg [Breeding habitat selection of Great Bustard (*Otis t. tarda* L., 1758) in Brandenburg State, Germany]. – Naturschutz und Landschaftspflege in Brandenburg 5(1–2): 99–102. (in German with English Summary)

Pinto, M., Rocha, P. & Moreira, F. 2005. Long-term trends in Great Bustard *(Otis tarda)* populations in Portugal suggest concentration in single high quality area. – Biological Conservation 124(3): 415–423. DOI: 10.1016/j.biocon.2005.01.047

Pitra, C., Suárez-Seoane, S., Martín, C. A., Streich, W-J. & Alonso, J. C. 2011. Linking habitat quality with genetic diversity: A lesson from Great Bustards in Spain. – European Journal of Wildlife Research 57(3): 411–419. DOI: 10.1007/s10344-010-0447-0

Raab, R., Julius, E., Greis, L., Schütz, C., Spakovszky, P., Steindl, J. & Schönemann, N. 2014a Endangering factors and their effect on adult Great Bustards *(Otis tarda)*. – Conservation efforts in the Austrian LIFE and LIFE+ projects. – Aquila 121: 49–63.

Raab, R., Julius, E., Greis, L., Schütz, C., Spakovszky, P., Steindl, J. & Schönemann, N. 2014b The Austrian agri-environmental scheme for Great Bustard *(Otis tarda)*. – Aquila 121: 95–102.

Raab, R., Kollar, H. P., Winkler, H., Faragó, S., Spakovszky, P., Chavko, J., Maderič, B., Škorpíková, V., Patak, E., Wurm, H., Julius, E., Raab, S. & Schütz, C. 2010. Die Bestandsentwicklung der westpannonischen Population der Großtrappe, *Otis tarda* Linnaeus 1758, von 1900 bis zum Winter 2008/2009 [Development of the West Pannonian population of the Great Bustard, *Otis tarda* Linnaeus 1758, from 1900 to the winter 2008/2009]. – Egretta 51: 74–99. (in German with English Summary)

Reidsma, P., Tekelenburg, T., van den Berg, M. & Alkemade, R. 2006. Impacts of land-use change on biodiversity: An assessment of agricultural biodiversity in the European Union. – Scenario-Based Studies of Future Land Use in Europe 114(1): 86–102. DOI: 10.1016/j.agee.2005.11.026

Riediger, J., Breckling, B., Nuske, R. S. & Schröder, W. 2014. Will climate change increase irrigation requirements in agriculture of Central Europe? A simulation study for Northern Germany. – Environmental Sciences Europe 26(1): 18. DOI: 10.1186/s12302-014-0018-1

Rocha, P., Morales, M. B. & Moreira, F. 2013. Nest site habitat selection and nesting performance of the Great Bustard *Otis tarda* in southern Portugal: Implications for conservation. – Bird Conservation International 23(3): 323–336. DOI: 10.1017/S0959270912000202

Sanz-Pérez, A., Sollmann, R., Sardà-Palomera, F., Bota, G. & Giralt, D. 2020. The role of detectability on bird population trend estimates in an open farmland landscape. – Biodiversity and Conservation 29(6): 1747–1765. DOI: 10.1007/s10531-020-01948-0

Silva, J. P., Correia, R., Alonso, H., Martins, R. C., D'Amico, M., Delgado, A., Sampaio, H., Godinho, C. & Moreira, F. 2018. EU protected area network did not prevent a country wide population decline in a threatened grassland bird. – PeerJ 6: e4284. DOI: 10.7717/peerj.4284

Spakovszky, P. 2009. Túzok *(Otis tarda)* állományának monitoringja a LIFE programban [Monitoring of the Great Bustard *(Otis tarda)* population in the LIFE-project]. – Szélkiáltó 14: 21. (in Hungarian with English Summary)

Streich, W. J., Litzbarski, H., Ludwig, B. & Ludwig, S. 2006. What triggers facultative winter migration of Great Bustard *(Otis tarda)* in Central Europe? – European Journal of Wildlife Research 52(1): 48–53. DOI: 10.1007/s10344-005-0007-1

Szabó, K., Bozsó, M., Boros, E. & Pénzes, Z. 2007. A túzok hazai populációinak genetikai változatossága [Genetic diversity of the Hungarian Great Bustard populations]. – In: Forró, L. (ed.) A Kárpát-medence állatvilágának kialakulása [The evolution of the fauna in Carpathian Basin]. – Magyar Természettudományi Múzeum, Budapest, pp. 297–302. (in Hungarian)

Szenek, Z. & Végvári, Zs. 2018. Habitat selection of the Great Bustard *(Otis tarda)* in Körös-Maros National Park. – Ornis Hungarica 26(1): 89–94. DOI: 10.1515/orhu-2018-0006

Teillard, F., Jiguet, F. & Tichit, M. 2015. The response of farmland bird communities to agricultural intensity as influenced by its spatial aggregation. – PLOS ONE 10(3): e0119674. DOI: 10.1371/journal.pone.0119674

Török, P., Neuffer, B., Heilmeier, H., Bernhardt, K-G. & Wesche, K. 2020. Climate, landscape history and management drive Eurasian steppe biodiversity. – Flora 271: 151685. DOI: 10.1016/j.flora.2020.151685

Traba, J. & Morales, M. B. 2019. The decline of farmland birds in Spain is strongly associated to the loss of fallowland. – Scientific Reports 9(1): 9473. DOI: 10.1038/s41598-019-45854-0

Ornis Hungarica 2020. 28(2): 85–110.
DOI: 10.2478/orhu-2020-0019

Bird species assemblages in railway stations: variations along an urban-rural gradient

Anupam Chakraborty[1], Sayan Das[1], Anirban Ash[2], Goutam K. Saha[1] & Gautam Aditya[1*]

Received: June 23, 2020 – Revised: October 23, 2020 – Accepted: October 24, 2020

Chakraborty, A., Das, S., Ash, A., Saha, G. K. & Aditya, G. 2020. Bird species assemblages in railway stations: variations along an urban-rural gradient. – Ornis Hungarica 28(2): 85–110. DOI: 10.2478/orhu-2020-0019

Abstract The transportation infrastructures like railway tracks and roads bear negative impacts on natural environment. However, the opposite effects are also true in some instances where the man-made constructions have positive effect on faunal assemblages. This proposition was justified through the assessment of bird species using railway stations as model man-made structures in an urban-rural gradient, in the suburbs of Kolkata, India. During the entire study period along nine different railway stations, a total of 43 bird species belonging to 12 orders and 26 families were observed. Among these, the order Passeriformes was predominant in its species composition having 18 different species from 11 different families. In urban railway stations, a total of 23 bird species under 22 genera and 14 families were observed. In suburban railway stations, a total of 35 bird species under 32 genera and 22 families were documented. The railway stations from rural region showed the maximum number of species and abundance of bird families, where a total of 36 bird species under 32 genera and 23 families were observed. The railway stations from the suburban and rural regions were more similar in species composition. Irrespective of the locations, during the entire study period, the House Crow *(Corvus splendens)* was the dominant species followed by the Common Myna *(Acridotheres tristis)*. About 18 bird species exhibited a decreasing population trend observed through the global population trend analysis. In all the railway stations, the abundance of omnivores were dominant while, the number of granivores were higher in the rural regions and the nectarivores were absent in the urban regions. It was apparent that the railway stations bear a positive effect on the bird species assemblages, which can be sustained through proper environmental management planning inclusive of urban greening.

Keywords: bird species, positive effects, railway network, habitat heterogeneity

Összefoglalás A közlekedési infrastruktúra – például a vasút- és úthálózat – legtöbbször negatív hatással van a természetes környezetre. Ezeknek az ember alkotta létesítményeknek a faunákra nézve azonban pozitív hozadéka is lehet, melyet e vizsgálat is igazol. A kutatás során azt tanulmányozták, hogy az egyes madárfajok hogyan használják a vasútállomásokat – mint az ember által létrehozott struktúrákat – egy városi-vidéki gradiens mentén, az indiai Kolkata külvárosában. A teljes vizsgálati időszak alatt kilenc különböző vasútállomás mentén összesen 12 rendbe tartozó 43 madárfajt és 26 családot figyeltek meg. A fajösszetételben az énekesmadár-alakúak rendje (Passeriformes) dominált 18 különböző fajjal, 11 különböző családból. A városi vasútállomásokon összesen 23 madárfajt (22 nemzetség és 14 család), az elővárosi vasútállomásokon összesen 35 madárfajt (32 nemzetség és 22 család) dokumentáltak. A vidéki régió vasútállomásai mutatták a legmagasabb fajszámot, a családokat tekintve pedig a legnagyobb abundancia értéket: ebben a térségben összesen 36 madárfajt észleltek 32 nemzetségből és 23 családból. Az elővárosi és a vidéki vasútállomások fajösszetételükben hasonlóbbak voltak. A helyszínektől függetlenül a teljes vizsgálati időszak alatt az indiai varjú *(Corvus splendens)* volt az uralkodó faj, amelyet a pásztormejnó *(Acridotheres tristis)* követett. Körülbelül 18 faj mutatott csökkenő populációs tendenciát a globális populáció trendelemzés alapján. Valamennyi vasútállomáson a mindenevők domináltak. A vidéki régiókban nagyobb számban voltak jelen magevők, a városi régiókból hiányoztak a nektárevők. Nyilvánvalóvá vált, hogy a vasútállomások pozitív hatást gyakorolnak a madárfajok együtteseire, és a kedvező állapot megfelelő környezetvédelmi tervezéssel és környezetgazdálkodással – beleértve a városok zöldítését is – hosszú távon is fenntartható lehet.

Kulcsszavak: madárfajok, pozitív hatás, vasúthálózat, élőhely-heterogenitás

[1] Department of Zoology, University of Calcutta, 35 Ballygunge Circular Road, Kolkata 700019. India
[2] Department of Zoology, The University of Burdwan, Golapbag, Burdwan 713104. India
**corresponding author, e-mail: gautamaditya2001@gmail.com*

Introduction

Birds are one of the most suitable species to monitor the short and the long-term environmental changes (Koskimies 1989, Bibby 1999, Khan & Naher 2009). Use of birds as indicators for habitat conditions (Canterbury *et al.* 2000, Browder *et al.* 2002,Vallecilo *et al.* 2016), including forests (Pain *et al*. 2004, Venier & Pearce 2004, Aich & Mukhopadhyay 2008, Chatterjee *et al*. 2014), agro-ecosystems (Dhindsa & Saini 1994, Borad *et al*. 2001, Basavarajappa 2006, Sundar & Kittur 2013, Hossain & Aditya 2016) and aquatic bodies (Kumar *et al*. 2006, Kumar & Gupta 2013), biological diversity (Gregory *et al.* 2003, Fraixedas *et al.* 2020) and urbanization (Pollack *et al.* 2017) are well-recognized, apart from the application of birds as flagship species in conserving diversity (Williams *et al.* 2000) and enhancing tourism (Veríssimo *et al.* 2009). Due to an increasing appreciation of the ecosystem services provided by the birds (Whelan *et al*. 2008, Şekercioğlu 2012a, 2012b), the focus for the monitoring, conservation and ecological studies on birds are continued at different biogeographical context (Bradford *et al*. 1998, Browder *et al*. 2002, Lee *et al*. 2004, Sundar & Kittur 2013, Hossain & Aditya 2016). Initiation for the conservation strategies for the birds requires idea about the assemblage pattern at varied spatio-temporal scales. This applies particularly for the conservation initiative in the urban landscapes, which offer habitats for the birds in the form of gardens, parks and green lanes (Chamberlain *et al*. 2009). In comparison to the limited attention given to human-dominated urban biodiversity earlier (Melles *et al*. 2003), in the last few decades, there is an increasing awareness about the faunal biodiversity including birds of urban landscapes and their importance in bio-monitoring and conservation perspectives.

Urban landscapes differ substantially and extensively from natural and semi-natural habitats (Marzluff 2001, Chace & Walsh 2006), in terms of food resources, predator communities (Haskell *et al*. 2001, Sorace 2002), weather conditions (Haggard 1990), and pollution disturbance (Eeva *et al*. 2000). As a consequence, the bird assemblages vary considerably revealed through studiesfrom urban areas of India (Sengupta *et al.* 2014, Kale *et al.* 2018a, 2018b, Pal *et al.* 2019) and elsewhere (Chace & Walsh 2006, Chamberlain *et al.* 2009). In many instances, the rapid urbanization in association with infrastructural revolution leads to extensive modification of natural landscapes that eventually results in a profound restructuring of the preferred habitats of birds (Blair 1996, Chamberlain *et al*. 2009, Morelli *et al.* 2014). As a result, an alteration in the bird species assemblages may be observed along the urbanization gradient with varying levels of the habitat conditions and the degree of disturbances (Gering & Blair 1999, Kale *et al.* 2018a, 2018b, Rodrigues *et al.* 2018, Filloy *et al.* 2019, Pal *et al.* 2019). Although the effects of urbanization on the environmental processes are usually complex and poorly understood, the birds can be considered as bio-monitoring tool to retrieve the consequences on human and wildlife biota (Chace & Walsh 2006, Pollack *et al.* 2017).

An inherent aspect of the urbanization is the increased transportation network in the form of metallic roads and railroads that pose a complete different extent of challenges on the biota (Gilbert 2012), including birds (Beissinger & Osborne 1982, Benítez-López *et al.* 2010, Morelli *et al.* 2014). In addition to the continuous increase of global human population, the improvement in transportation network is now getting more compulsory, therefore, the enlargement of urban regions and associated railway networks is indisputable. Thus, proper knowledge and understanding of the relationships between avian species and railway networks and associated human structures should be beneficial for conservation-focused landscape management (Morelli *et al.* 2014, Wiącek *et al.* 2015). Railways play an essential role in the global transportation service and currently being promoted by various governments because of their superior economic and environmental advantages relative to other transportation means. Apart from economic benefits, railways also present several environmental advantages in contrast to roads, such as lower pollution and reduced land occupancy (Profillidis 2006, Pereira *et al.* 2012), resulting in the growth of the railway network, globally and emergence of the research on railway ecology (Borda-de-Água *et al.* 2017). As a consequence of an increased railway network, the wildlife faces severe challenges in the form of habitat loss, habitat fragmentation, anthropogenic interference, and audio-visual disorder, mortality by collisions, barrier effect, and chemical pollution (Morelli *et al.* 2014, Borda-de-Água *et al.* 2017). Thus, the railway network emerges as a prospective and perceived threat to the wildlife biota, including birds. However, the potential positive consequences of the railway network as well as the rail-associated construction structures on birds are increasingly appreciated (Li *et al.* 2010, van der Ree *et al.* 2011, Morelli *et al.* 2014, Wiącek *et al.* 2015, 2019, 2020, Kaiser-Bonk *et al.* 2019). Some of the plausible positive effects of rail-associated structures includes the marginal vegetation along railways (bridges, shrubs etc.) may provide nesting sites for several species of birds (Wiącek *et al.* 2015, 2019, 2020, Kaiser-Bonk *et al.* 2019), high structures like electricity posts and cables are extensively utilized by many passerine species for perching (DeGregorio *et al.* 2014, Morelli *et al.* 2014), singing and relaxing. The railway platform can also act as a good foraging ground for several species of birds and lastly, some birds utilize railway tracks as a resting site as it becomes heated rapidly during the day and thereby providing protection from cold and windy situations during winter (Morelli *et al.* 2014, Wiącek *et al.* 2015). All these factors render a positive effect on birds and possibly the reason why they are found in higher aggregations near rail-associated structures than in the deeper forest (Wiącek *et al.* 2015, 2019, 2020).

In view of the positive effects of the railway network on the bird species assemblages (Li *et al.* 2010, Morelli *et al.* 2014, Wiącek *et al.* 2015, 2019, 2020, Kaiser-Bonk *et al.* 2019), it would be worthy to evaluate for any variations in the effect against the urban-rural gradient. As a mode of transport, the railway network extends beyond the urban landscapes and more commonly dissects the rural areas including forests. A gradient of urbanization results in a differntial level of bird species richness, including variations in the foraging guilds and similarity in species composition (Kale *et al.* 2018a, 2018b, Pal *et al.* 2019), which may also apply for the railway network connecting urban and rural destinations. In order to justify this proposition, a pioneer attempt was made to explore the bird species diversity in railway stations of urban, semi-urban, and rural landscapes of West Bengal, India. The primary objectives of the study were (1) to make a checklist of the birds observed in railway stations, (2) to evaluate the species diversity and the functional diversity of the birds in the railway stations along an urban rural gradient and (3) to evaluate species specific differences in abundance in the railway stations along an urban rural gradient. Elucidation of the species specific benefits derived from the railway network will enhance the sustenance of diversity (Grimmett *et al.* 2016) and the ecosystem services (Whelan *et al*. 2008, Şekercioğlu 2012a, 2012b) of birds, especially in an Indian context. Apart from substantiating the urbanization effect, the results will validate the role of railway stations in supporting bird assemblages and thus, prospects in conservation management.

Materials and methods

Study area

Our present study on avian biodiversity was carried out between March and May in 2019 in railway stations in West Bengal, India. To carry out the study, nine railway stations were selected randomly in between Howrah railway junction and Barddhaman railway junction *(Figure 1)* of the Eastern Railways section of Indian Railways. Three railway stations [Talandu (23°0'38.43"N; 88°20'44.15"E), Khanyan (23°2'48.03"N; 88°18'55.92"E) and Simlagarh (23°5'46.95"N; 88°13'53.38"E)] were located in rural areas (R), three stations [Baidyabati (22°47'43.28"N; 88°19'55.26"E), Bhadreswar (22°49'42.24"N; 88°20'29.99"E) and Mankundu (22°50'48.99"N; 88°20'48.90"E)] were selected from suburban areas (SU), and the remaining three railway stations [Liluah (22°37'14.88"N; 88°20'21.84"E), Belur (22°38'8.88"N; 88°20'23.27"E) and Uttarpara (22°40'2.99"N; 88°20'28.33"E)] were chosen from urban areas (U). The categorization of urban, suburban, and rural areas was designated based on population size and density. The surroundings of U areas were enriched mainly with large buildings and small factories while the SU areas were surrounded by relatively smaller houses, discrete vegetation as well as small water bodies at the vicinity. The R areas were encircled mainly by agricultural lands and jungles. All of these nine stations covered three districts (Howrah, Hooghly, and Purba Bardhaman) of West Bengal, India. The average temperature in the studied areas varied from 35–45 ºC in summer (March to May), relative humidity lied between 50 and 75%, depending on weather conditions with an average annual rainfall of 150 mm for the concerned area.

Methodology

The birds were observed and counted in sampling sites for three consecutive months from March to May in 2019. Each site was intensely surveyed twice every month at an interval of two weeks. Adopting line transect method and maintaining constant transect length the surveys were carried out in each selected railway station in the morning time (between 6:00 AM to 9:00 AM) and in the afternoon (from 3:00 PM to 6:00 PM) depending on the

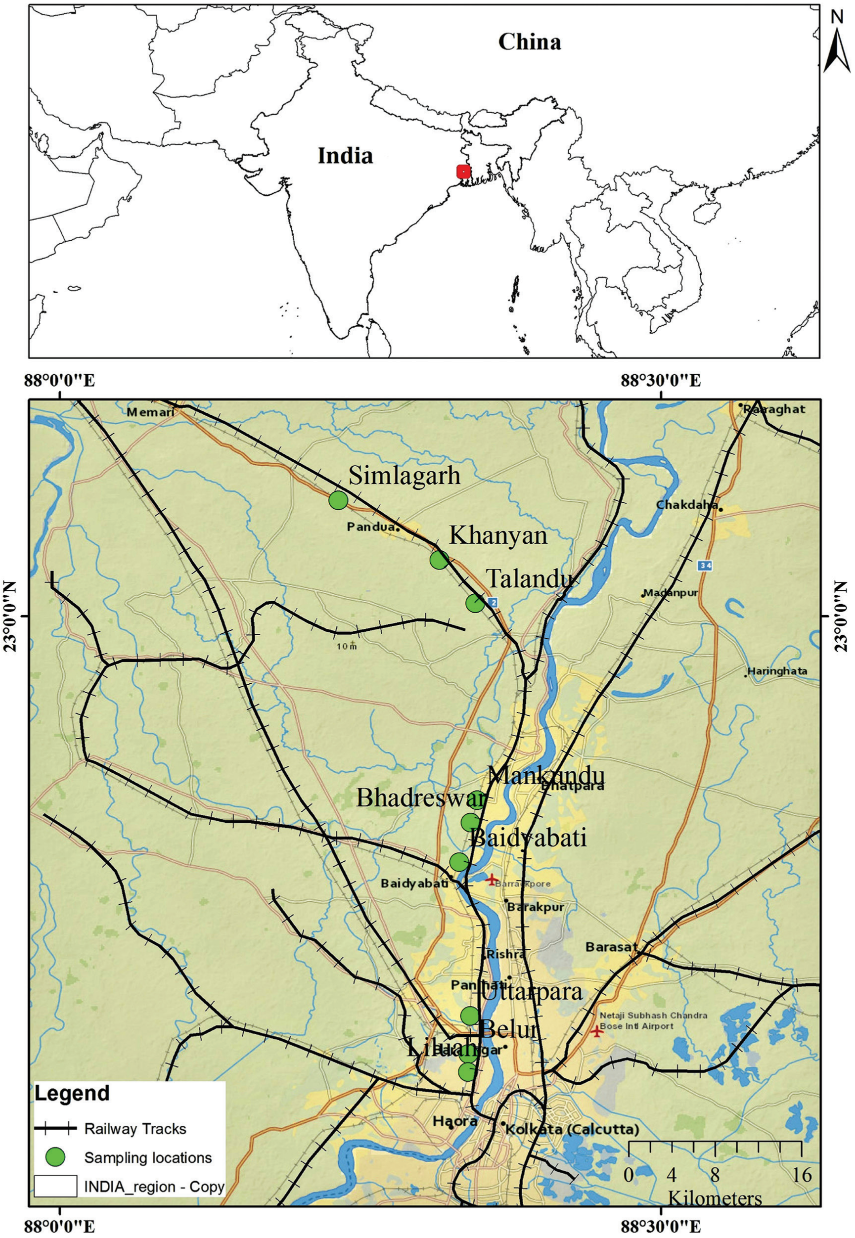


Figure 1. Map of India with the study areas including nine railway stations in West Bengalbeing highlighted. Three stations (Talandu, Khanyan and Simlagarh) were chosen from rural areas (R), three stations (Baidyabati, Bhadreswar and Mankundu) were from suburban areas (SU) and other three railway stations (Liluah, Belur and Uttarpara) were taken from urban areas (U)

1. ábra A vizsgálati terület térképe, 9 nyugat-bengáliai vasútállomás megjelölésével. Három állomás (Talandu, Khanyan és Simlagarh) vidéki (R), három állomás (Baidyabati, Bhadreswar és Mankundu) elővárosi (SU) és három állomás (Liluah, Belur és Uttarpara) városi (U) területről lett választva day length when the birds were found to be more active (Buckland *et al.* 1993, Bibby *et al.* 2000). The starting point and the direction of transects were often arbitrary. Each survey site was visited six times throughout the study period, three times in the morning time and three times in the afternoon. Cloudy and overcast days were strictly avoided for a field visit. The birds were observed either by unaided eyes or by binocular (Olympus 7x21 PS III) depending upon distance and photographs were captured by Nikon P900 for documentation of the avifauna. Based on observations and captured photographs, birds were identified (Ali 1996, Grimmett *et al.* 2016) and recorded for tabulation and statistical analysis. In some cases, birds' calls were used as an identifying key. The taxonomic categorization of bird species was made by following Praveen *et al.* 2016. During the survey period, the foraging behaviours, nesting and resting positions, areas of displaying and singing as well as their overall activities were observed.

Data analysis

The information about the status of global population trends for each observed bird species was collected from the IUCN Red List (del Hoyo *et al.* 1996). Foraging guilds were determined by examining their feeding habitat and categorized into six feeding guilds i.e. carnivore (Car), omnivore (Omn), nectarivore (Nect), granivore (Gran), insectivore (Ins) and frugivore (Frug) (Ali & Ripley 1980, Hutto 1986). To obtain the diversity indices of bird abundance, the data taken from each study site from three areas (U, SU and R) were analyzed separately by using Biodiversity Pro software (McAleece *et al.* 1997, Biodiversity Professional; Scottish Association for Marine Science and the Natural History Museum, London, UK). Species richness (S) was calculated by summing the number of different species present in that area (Mukherjee *et al.* 2015, Issa 2019). Diversity of species was represented by calculating Shannon diversity index $[H'=-\sum (P_i \ln P_i)]$, Simpson's Index of diversity $[(1-D)=1-\frac{\sum n(n-1)}{N(N-1)}]$, where P_i is the proportion of total samples belonging to the i^{th} species, n is the total number of birds belongs to a particular species and N includes the total number of birds of all species (Magurran 1988). To compare the similarity of population size of each bird species in an area, the evenness $[J=H'/H_{max}]$ was calculated. Fisher's alpha (α) is a parametric diversity index was estimated to analyse diversity within the population. The Margalef's richness was estimated as $[D_{Mg}=(S-1)/\ln N]$, (Margalef 1958), where S is the total number of avian species and N is the total number of individuals. The relationship among species richness (S), information (H), and evenness (J) in the samples was made by SHE analysis (Buzas & Hayek 1998). The proximity and similarity of avifaunal community structures of three different habitats (U, SU and R), in terms of species composition was estimated by the Jaccard coefficient $(Jc=\frac{M}{M+N})$ and Sorensen coefficient $(Sc=\frac{2\times C}{A+B})$, where M denotes the number of common species between communities, N is the total number of unique species present in both communities, C is the common species between two habitats, whereas the components A and B are the number of bird species at two different habitats proposed to be compared for similarity (Ludwig & Reynolds 1988, Krebs 1999). Agglomerative hierarchical clustering (AHC) was carried out based on the Pearson's similarity coefficient of habitat types and avian species richness associated to these habitats. To comment on the variation in abundance of different species along the urban gradients, a mixed model ANOVA was performed with the species as the repeated factors and the urban, suburban and rural regions as the fixed factors. In order to specify if there were any difference in their abundance related to time of the day variation, ANOVA was performed (Zar 1999). All abundance data were presented as mean±SE and significance were tested at $p<0.05$. Diversity index, species richness, evenness and associated analysis were performed by using Biodiversity Pro (2.0) software. The statistical analyses were performed following Zar (1999) using the XLSTAT software (Addinsoft 2010).

Result

Bird species records and their relative abundance

During the entire study along the nine different railway stations irrespective of urban to rural gradient, a total of 43 bird species belong to 12 orders and 26 families were observed *(Table 1)*. Among the recorded birds, the order Passeriformes was predominant on its species composition having 18 different species from 11 different families. In urban railway stations (U), a total of 23 bird species belongs to 22 genera and 14 families were observed. The maximum number of bird species recorded in U sites were under family Columbidae with 4 species (17.40%) followed by Sturnidae with 3 species (13.04%), Apodidae, Cuculidae, Corvidae, and Ardeidae, each containing 2 species (8.70% each) and Accipitridae, Cisticolidae, Dicruridae, Passeridae, Pycnonotidae, Phalacrocoracidae, Picidae, Psittaculidae, each with 1 species (4.35% each). In suburban railway stations (SU), a total of 35 bird species belongs to 32 genera and 22 families were documented. The maximum number of species recorded in SU were under the families Columbidae, Corvidae, Sturnidae, and Ardeidae, each having 3 species (8.60% each), followed by Apodidae, Cuculidae, Cisticolidae, Nectariniidae, and Pycnonotidae, with 2 species (5.71% each) and Accipitridae, Jacanidae, Alcedinidae, Rallidae, Dicruridae, Hirundinidae, Leiothrichidae, Muscicapidae, Oriolidae, Passeridae, Phalacrocoracidae, Megalaimidae and Picidae, each having 1 species (2.85% each). Nevertheless, railway stations from rural regions (R) showed the highest number of species and abundance of bird families, where a total of 36 bird species were recorded throughout the study period which belongs to 32 genera and 23 families. In rural regions (R) the maximum number of species listed under families Columbidae, Corvidae, and Sturnidae each of which has 3 species (8.3% each), followed by Apodidae, Alcedinidae, Cuculidae, Nectariniidae, Pycnonotidae, Ardeidae, and Megalaimidae, each with 2 species (5.6% each), and Anatidae, Rallidae, Cisticolidae, Dicruridae, Leiothrichidae, Muscicapidae, Oriolidae, Passeridae, Ciconiidae, Phalacrocoracidae, Threskiornithidae, Picidae, and Psittaculidae, each having 1 species (2.8% each). The possible variations in the relative abundance of different observed families in three different sites (U, SU and R) might be due to the alterations in habitat conditions. The relative abundance of bird species *(Figure 2)* and the abundance of families *(Figure 3)* were highest in the rural railway stations followed by suburban and urban areas.

Table 1. List of bird species with their relative abundance (mean ± SE) in urban railway station (U), suburban railway station (SU) and rural railway station (R) sites of West Bengal, India, recorded during study period, together with their feeding guilds (Car = carnivore, Omn = omnivore, Nect = nectarivore, Gran = granivore, Ins = insectivore and Frug = frugivore) and global population trend (ST= stable, IN= increasing, DE= decreasing and UN= unknown)

1. táblázat A madárfajok relatív abundancia értékei (átlag ±standard hiba) városi (U), elővárosi (SU) és vidéki (R) vasútállomásokon, Nyugat-Bengália, India területén, a táplálkozási guildek (Car = ragadozó, Omn = mindenevő, Nest = nektárfogyasztó, Gran = magevő, Ins = rovarevő, Frug = gyümölcsevő) és a globális populációs trendek (ST = stabil, IN = növekvő, DE = csökkenő, UN = ismeretlen) feltüntetésével

Family	Common and Scientific Name	Feeding Guild	Global Trend	U	SU	R
Order: Accipitriformes						
Accipitridae	Black Kite *Milvus migrans* (Boddaert, 1783)	Omn	UN	4.33±0.65	0.44±0.18	0
Order: Anseriformes						
Anatidae	Lesser Whistling-duck *Dendrocygna javanica* (Horsfield, 1821)	Omn	DE	0	0	0.17±0.17
Order: Caprimulgiformes						
Apodidae	Asian Palm Swift *Cypsiurus balasiensis* (Gray, 1829)	Ins	ST	1.61±0.51	1.11±0.32	1.28±0.35
	Indian House Swift *Apus affinis* (Gray, 1830)	Ins	IN	1.28±0.46	0.94±0.29	0.39±0.16
Order: Charadriiformes						
Jacanidae	Bronze-winged Jacana *Metopidius indicus* (Latham, 1790)	Omn	UN	0	0.22±0.12	0
Order: Columbiformes						
Columbidae	Rock Dove *Columba livia* (Gmelin, 1789)	Gran	DE	7.22±2.21	2.56±0.73	8±0.95
	Eurasian Collared Dove *Streptopelia decaocto* (Frivaldszky, 1838)	Gran	IN	0.11±0.07	1.17±0.47	3.17±0.58
	Spotted Dove *Spilopelia chinensis* (Scopoli, 1786)	Gran	IN	1.72±0.45	1.17±0.34	1.94±0.39
	Yellow-footed Green Pigeon *Treron phoenicopterus* (Latham, 1790)	Gran	IN	0.44±0.35	0	0

Family	Common and Scientific Name	Feeding Guild	Global Trend	U	SU	R
Order: Coraciiformes						
Alcedinidae	Stork-billed Kingfisher *Pelargopsis capensis* (Linnaeus, 1766)	Car	DE	0	0	0.06±0.05
	White-breasted Kingfisher *Halcyon smyrnensis* (Linnaeus, 1758)	Car	IN	0	0.22±0.22	0.28±0.1
Order: Cuculiformes						
Cuculidae	Greater Coucal *Centropus sinensis* (Stephens, 1815)	Omn	ST	0.17±0.09	0.06±0.05	0
	Asian Koel *Eudynamys scolopaceus* (Linnaeus, 1758)	Omn	ST	1.78±0.41	0.61±0.14	1±0.16
	Common Hawk-cuckoo *Hierococcyx varius* (Vahl, 1797)	Ins	ST	0	0	0.11±0.07
Order: Gruiformes						
Rallidae	White-breasted Waterhen *Amaurornis phoenicurus* (Pennant, 1769)	Omn	UN	0	0.11±0.11	0.11±0.07
Order: Passeriformes						
Cisticolidae	Plain Prinia *Prinia inornata* (Sykes, 1832)	Ins	ST	0	0.11±0.07	0
	Common Tailorbird *Orthotomus sutorius* (Pennant, 1769)	Ins	ST	1.11±0.40	1.06±0.28	1±0.16
Corvidae	Rufous Treepie *Dendrocitta vagabunda* (Latham, 1790)	Ins	DE	0.33±0.19	0.78±0.24	0.06±0.05
	House Crow *Corvus splendens* (Vieillot, 1817)	Omn	ST	16.5±2.02	17.44±2.55	16.17±1.91
	Large-billed Crow *Corvus macrorhynchos* (Wagler, 1827)	Omn	ST	0	0.06±0.05	0.67±0.21

Family	**Common and Scientific Name**	**Feeding guild**	**Global Trend**	**U**	**SU**	**R**
Order: Passeriformes						
Dicruridae	Black Drongo *Dicrurus macrocercus* (Vieillot, 1817)	Ins	UN	0.33±0.11	0.50±0.21	1.17±0.27
Hirundinidae	Barn Swallow *Hirundo rustica* (Linnaeus, 1758)	Ins	DE	0	0.44±0.44	0
Leiothrichidae	Jungle Babbler *Turdoides striata* (Dumont, 1823)	Omn	ST	0	0.83±0.35	0.22±0.22
Muscicapidae	Oriental Magpie-robin *Copsychus saularis* (Linnaeus, 1758)	Ins	ST	0	0.33±0.18	0.28±0.11
Nectariniidae	Purple-rumped Sunbird *Leptocoma zeylonica* (Linnaeus, 1766)	Nect	ST	0	0.44±0.27	0.56±0.44
	Purple Sunbird *Cinnyris asiaticus* (Latham, 1790)	Nect	ST	0	0.17±0.09	0.11±0.11
Oriolidae	Black-hooded Oriole *Oriolus xanthornus* (Linnaeus, 1758)	Omn	ST	0	0.22±0.10	0.06±0.05
Passeridae	House Sparrow *Passer domesticus* (Linnaeus, 1758)	Omn	DE	0.33±0.14	1.50±0.42	1.56±0.47
Pycnonotidae	Red-whiskered Bulbul *Pycnonotus jocosus* (Linnaeus, 1758)	Omn	DE	0	1.00±0.49	0.11±0.11
	Red-vented Bulbul *Pycnonotus cafer* (Linnaeus, 1766)	Omn	IN	1.44±0.44	2.72±0.55	6.00±1.11
Sturnidae	Asian Pied Starling *Gracupica contra* (Linnaeus, 1758)	Omn	IN	0.56±0.22	3.44±0.84	13.33±1.30
	Common Myna *Acridotheres tristis* (Linnaeus, 1766)	Omn	IN	10.39±0.98	11.00±1.48	12.94±1.00
	Jungle Myna *Acridotheres fuscus* (Wagler, 1827)	Omn	DE	0.17±0.16	0.22±0.13	1.00±0.32

Family	Common and Scientific Name	Feeding guild	Global Trend	U	SU	R
Order: Pelecaniformes						
Ardeidae	Indian Pond-heron *Ardeola grayii* (Sykes, 1832)	Car	UN	0.06±0.05	2.22±0.56	0.06±0.05
	Cattle Egret *Bubulcus ibis* (Linnaeus, 1758)	Car	IN	2.06±0.90	10.56±7.40	6.39±1.72
	Little Egret *Egretta garzetta* (Linnaeus, 1766)	Car	IN	0	0.11±0.08	0
Ciconiidae	Asian Openbill *Anastomus oscitans* (Boddaert, 1783)	Car	UN	0	0	0.56±0.33
Phalacrocoracidae	Little Cormorant *Microcarbo niger* (Vieillot, 1817)	Car	UN	2.94±1.67	1.56±0.49	2.00±0.32
Threskiornithidae	Glossy Ibis *Plegadis falcinellus* (Linnaeus, 1766)	Car	DE	0	0	0.50±0.25
Order: Piciformes						
Megalaimidae	Coppersmith Barbet *Psilopogon haemacephalus* (Statius Müller, 1776)	Frug	IN	0	0.44±0.29	0.11±0.11
	Lineated Barbet *Psilopogonl ineatus* (Vieillot, 1816)	Frug	ST	0	0	0.06±0.05
Picidae	Lesser Golden-backed Woodpecker *Dinopium benghalense* (Linnaeus, 1758)	Ins	ST	0.06±0.05	0.11±0.11	0.28±0.12
Order: Psittaciformes						
Psittaculidae	Rose-ringed Parakeet *Psittacula krameri* (Scopoli, 1769)	Frug	IN	1.44±0.62	0	0.56±0.35

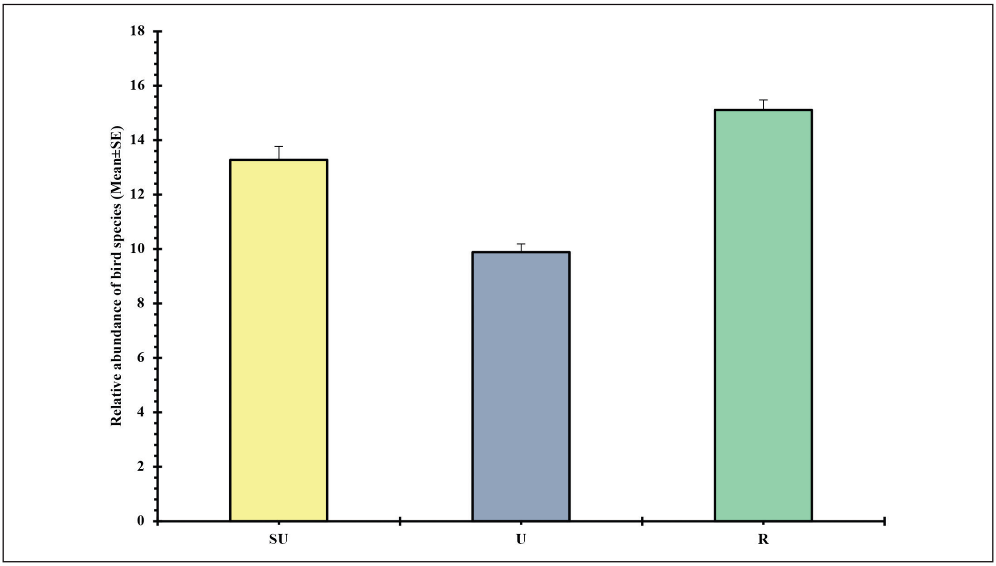


Figure 2. Relative abundance of bird species recorded from three different sites (SU, U and R)
2. ábra A madárfajok relatív abundanciája három különböző területtípusban (elővárosi (SU), városi (U) és a vidéki (R))

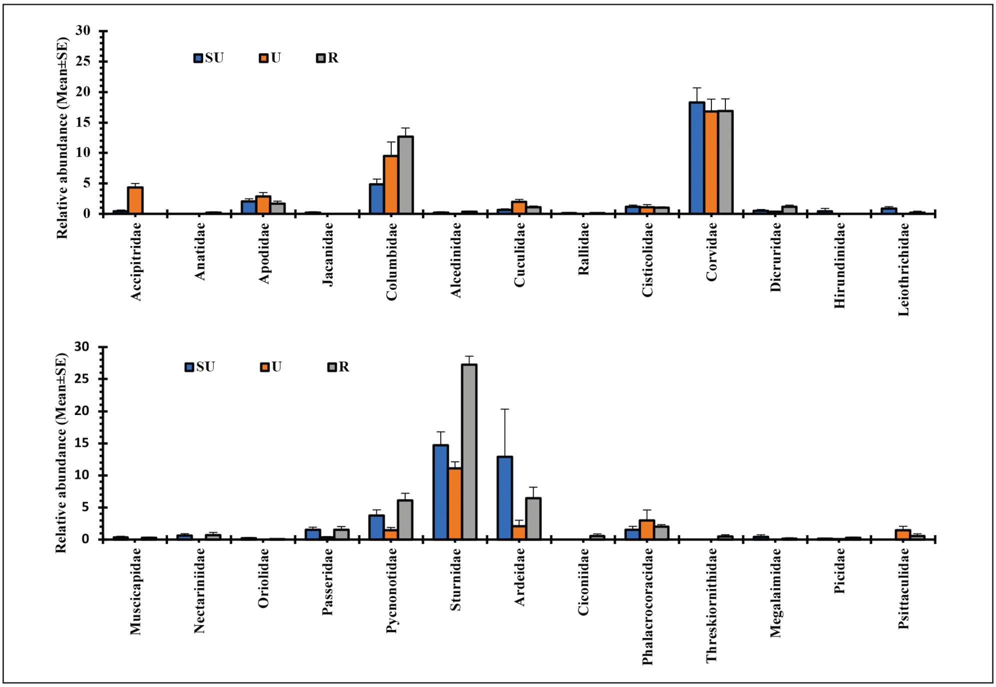


Figure 3. The relative abundance of the different bird family in the suburban (SU), urban (U) and rural (R) station areas sampled during the study period
3. ábra A különböző madárcsaládok relatív abundanciája az elővárosi (SU), városi (U) és a vidéki (R) állomásokon

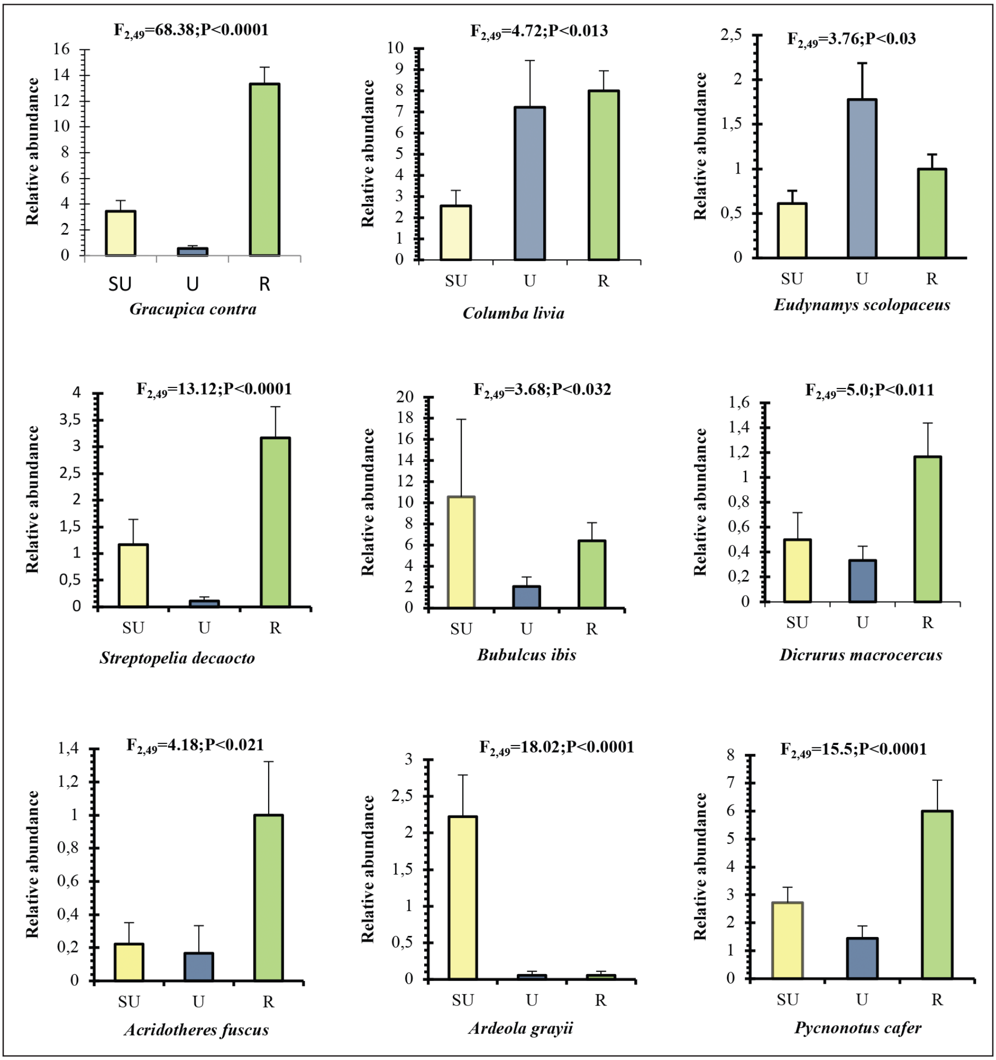


Figure 4. Selected bird species, which were available in each habitat (SU = suburban, U = urban and R = rural) and are known to differ significantly ($P < 0.05$) in their relative abundance

4. ábra A relatív abundanciájukban jelentősen különböző madárfajok összehasonlítása terület típusonként (elővárosi (SU), városi (U) és a vidéki (R))

During the entire study period, House Crow *(Corvus splendens)* was the most predominant species in all railway stations irrespective of three different landscapes with a relative abundance (mean±SE) of 16.5±2.0 for U, 17.4±2.5 for SU and 16.2±1.9 for R areas. Compared to House Crows, in U the abundance of the total number of species was higher for Common Myna *(Acridotheres tristis)* (10.4±0.9) and lowest for *Ardeola grayii* and *Dinopium benghalense* (0.06±0.1 for each). In addition to that, *Acridotheres tristis* was also found in higher abundance (11.0±1.5) in SU followed by *Bubulcus ibis* (10.6±7.4) whereas, minimum relative abundance recorded from species *Centropus sinensis* and *Corvus* *macrorhynchos* with 0.1±0.1, for each. In addition to *Corvus splendens,* the relative abundance of *Gracupica contra* and *Acridotheres tristis* were also higher in R with an abundance of 13.3±1.3 and 12.9±1.0, respectively, although, least relative abundance recorded from species *Pelargopsis capensis, Dendrocitta vagabunda, Oriolus xanthornus, Ardeola grayii, Psilopogon lineatus* each which mean abundance value of 0.06±0.05.

Species based relative abundance in three different areas *(Figure 4)* were analyzed. Significant difference ($F_{2,49}$=68.38, $P<0.0001$) was found on the distribution of Asian Pied Starling *(Gracupica contra)* in higher number in rural railway areas and in lowest number in urban railway stations. Rock Dove *(Columba livia)* was found to be more abundant in Rural railway stations and relatively moderate number in urban railway stations and lowest number in suburban railway stations ($F_{2.49}$=4.72, P=0.013). Abundance of Red-vented Bulbul *(Pycnonotus cafer)* was found in higher number in rural railway stations and lowest in urban railway station ($F_{2,49}$=15.5, $P<0.0001$), as well as Jungle Myna *(Acridotheres fuscus)* was also found in higher number in rural railway stations and lowest in urban railway stations ($F_{2,49}$=4.18, P=0.021). Eurasian Collared Dove *(Streptopelia decaocto)* ($F_{2,49}$=13.12, $P<0.0001$) and Black Drongo *(Dicrurus macrocercus)* ($F_{2,49}$=5.0, P=0.011) were found in higher number in the rural area and relative moderate number in semi urban area and were found lowest in urban area. Significant difference in the abundance ($F_{2,49}$=3.76, P=0.03) of Asian Koel *(Eudynamys scolopaceus)* was found in higher number in urban area and lowest in the semi-urban area. Significant difference in the abundance of Cattle Egret *(Bubulcus ibis)* ($F_{2,49}$=3.68, P=0.032), Indian Pond-Heron *(Ardeola grayii)* ($F_{2,49}$=18.02, $P<0.0001$), Rufous Treepie *(Dendrocitta vagabunda)* ($F_{2,49}$=4.34, P=0.018) were also noticed along the urban gradient with their higher availability in suburban railway station areas.Considering the time of surveys that were carried out in the morning (6:00 AM to 9:00 AM) and in the afternoon (3:00 PM to 6:00 PM), depending on the day length when birds were found to be most active, it was reported that expect of two species *(Cypsiurus balasiensis, Halcyon smyrnensis)*, other species did not show significant differences ($P>0.05$) in both morning and afternoon time irrespective of urban-rural gradient *(Figure 5)*.The number of Asian Palm Swift ($F_{1,52}$=4.7, $P<0.05$) and White Throated Kingfisher ($F_{1,52}$=5.49, $P<0.05$) are significantly differ in their abundance in

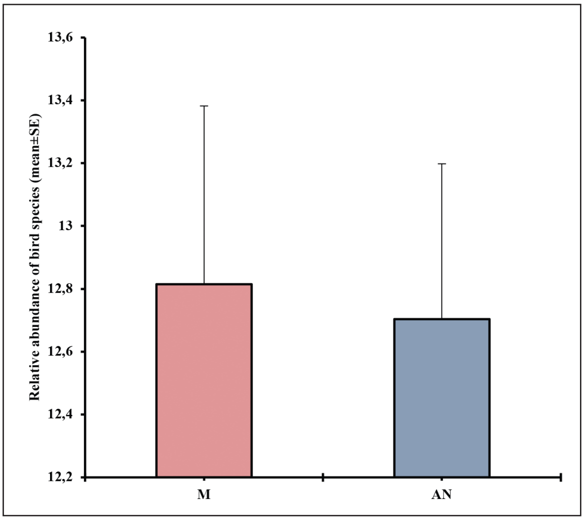


Figure 5. Relative abundance of bird species observed during different sampling time (M=Morning, AN = Afternoon) from all stations irrespective of rural-urban gradient

5. ábra A reggeli (M) és délutáni (AN) mintavételi órákban megfigyelt relatív abundancia értékek

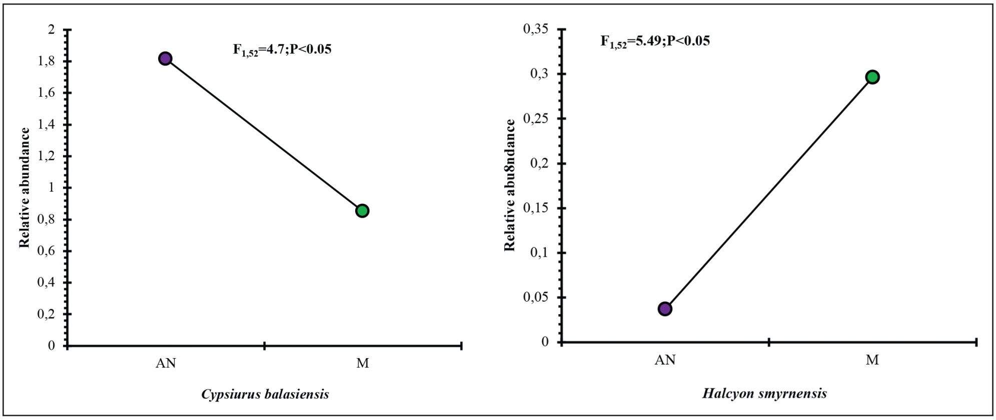


Figure 6. Relative abundance of selected bird species differ significantly ($P<0.05$) in different sampling time (M = Morning, AN = Afternoon)

6. ábra A mintavételi időszakokban (M = reggel, AN = délután) jelentősen eltérő relatív abundanciájú madárfajok összehasonlítása

between the two times *(Figure 6)*. Asian Palm Swift *(Cypsiurus balasiensis)* is more frequent in number at afternoon than in morning whereas the White Throated Kingfisher *(Halcyon smyrnensis)* is more frequent in morning times ($P=0.023$).

Global population trends of the recorded species

By analysing the global population trend it was noted that the railway stations belong to urban regions includes 6 such species of birds known to follow the stable population trend (ST), 9 increasing (IN), 4 with unknown (UN) and notably other 4 species marked to follow the decreasing (DE) population trend, whereas railway stations from suburban regions with 13 such species that are following the ST population trend, 10 with IN, 6 with UN and other 6 species known follow the DE population trend. On the contrary, railway stations from rural regions include 13 bird species that are known to follow the ST population trend, 10 IN, 5 with UN, and remaining 8 species are following the DE population trend (del Hoyo *et al.* 1996).

Analysis of diversity indices

Along the railway stations of urban-rural gradient, the values of diversity indices recorded *(Table 2)* for bird species as Species richness (S), Shannon diversity index (H'), Simpson's Index of diversity (1-D), evenness (J), Fisher's alpha (α), Margalef's Richness index (D_{Mg}). The highest Shannon diversity index (H') of birds recorded in railway stations belongs to rural regions (2.24±0.03), followed by suburban regions (2.07±0.08) and urban regions (1.81±0.05). Species richness (S) was higher in the rural (15±0.38) and suburban (13.28±0.49) rail stations than in the urban rail stations (9.89±0.30), which showed the lowest species richness amongst three sampling regions. The Simpson's

Table 2. Diversity indices of the bird communities recorded from three different habitats
2. táblázat A három különböző élőhelyet jellemző diverzitási indexek összehasonlítása

Diversity Indices	**SU**	**U**	**R**
Species richness_(S)	13.28±0.49	9.89±0.30	15.00±0.38
Simpson's index of diversity_(1-D)	0.82±0.02	0.79±0.01	0.86±0.01
Shannon diversity index _ (H')	2.07±0.08	1.81±0.05	2.24±0.03
Evenness_(J)	0.80±0.02	0.79±0.01	0.83±0.01
Fisher_ α	5.64±0.47	3.59±0.16	5.54±0.18
Margalef_ (D_{Mg})	1.73±0.07	1.28±0.04	1.93±0.05

Index, which measures community diversity found to be highest in the railway stations in rural (0.86±0.01) regions, followed by the suburban (0.82±0.02) regions and the urban (0.79±0.01) regions. Shannon evenness (J) is the ratio of H' to H_{max}, a measure of species evenness found higher in the railway stations that come under rural (0.83±0.01) and suburban (0.8±0.02) regions as compared to urban (0.79±0.01) regions. The results revealed that railway stations from rural and suburban regions were highly species-rich as compared to urban regions and further demonstrate that from rural to urban matrices, species diversity and richness decreases, showing influences of urbanization on the avian community. Fisher's alpha (α) is a parametric diversity index to estimate the diversity within the population found to be highest in the suburban (5.64±0.47) railway stations, followed by the rural (5.54±0.18) and urban (3.59±0.16) railway stations. The Margalef's Richness index (D_{Mg}), which was used as another measure of species richness also is the highest in rural (1.93±0.05) sampling sites than that of the suburban (1.73±0.07) and urban (1.28±0.04) sites. As revealed through the results of SHE analysis *(Figure 7)*, the relationship among S (species richness), H (information), and E (evenness) in the samples can interpret well and represents higher species richness in the railway stations from the rural and suburban regions than in the urban regions. In addition to the species abundance in samples as a variable for comparison, the rank abundance curves also generated for rail stations belonging to urban-rural gradient *(Figure 8)*, where the species count plotted in descending order for all the species and found to be highest in rural railways, followed by suburban and urban railway station areas. The railway stations from the suburban and rural landscapes were the regions with the most similar species composition. The Jaccard and Sorensen similarity coefficients for these two sampling sites were 0.69 and 0.817, respectively, and were the highest. In contrast, the rural and urban rail stations had Jaccard and Sorensen similarity coefficients of 0.512 and 0.678 respectively, and were the least similar in terms of species composition *(Figure 9a)*. Dendrogram based on the species richness along different railway stations areas of urban, semi-urban and rural landscapes formed two distinct clusters where rural stations and suburban stations clustered together, whereas urban habitat was in a separate cluster *(Figure 9b)*.

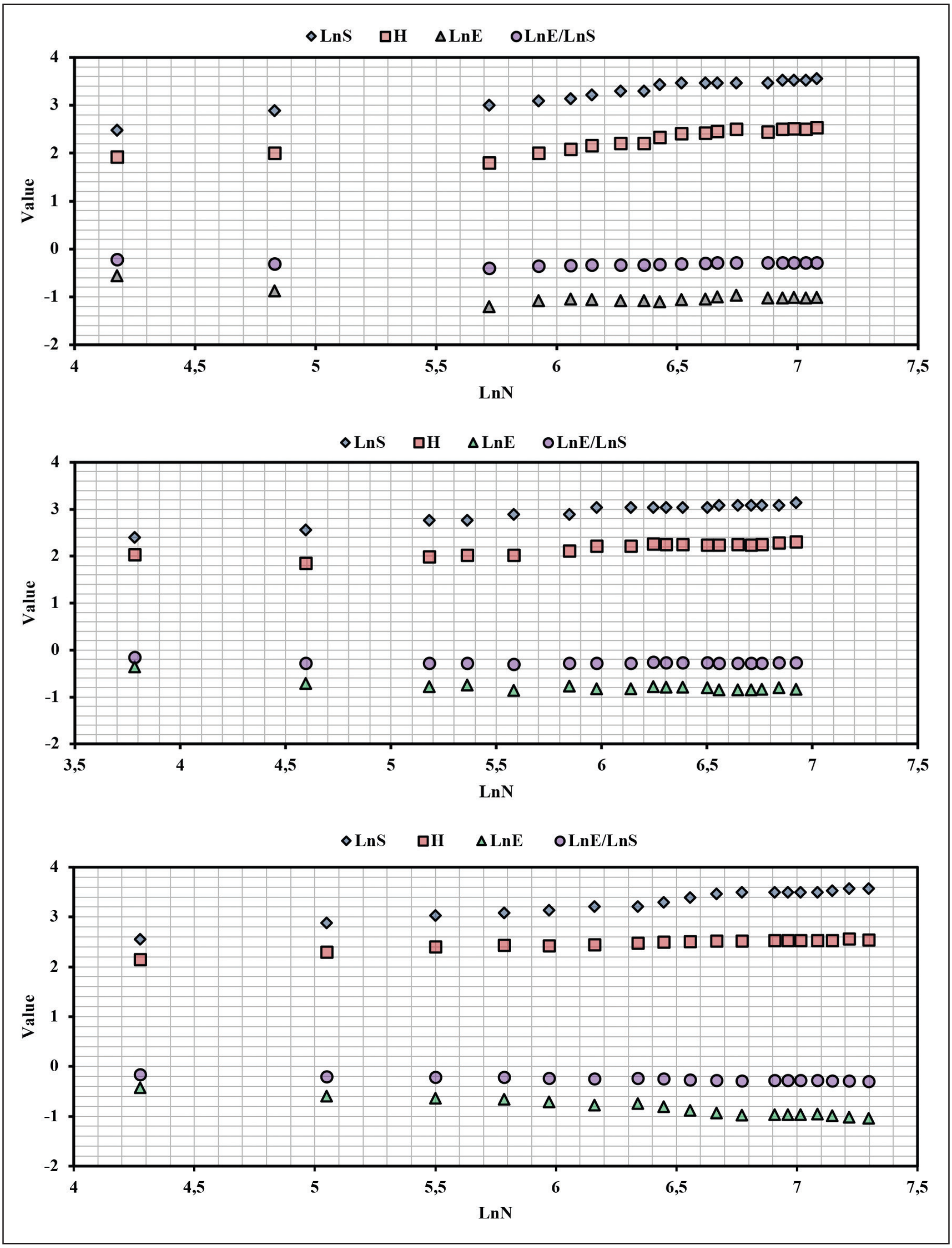


Figure 7. Plot of SHE analysis [S (species richness), H (information) and E (evenness) in the samples] calculated on relative abundance of 43 bird species of three different sites of (A) suburban; (B) urban; (C) rural railway station areas. These represent the turnover of species between sites

7. ábra Az SHE elemzés eredményei (S – fajgazdagság, H – információtartalom, E – egyenletesség) 43 madárfaj relatív abundancia adatainak felhasználásával. A – elővárosi, B – városi, C – vidéki területek

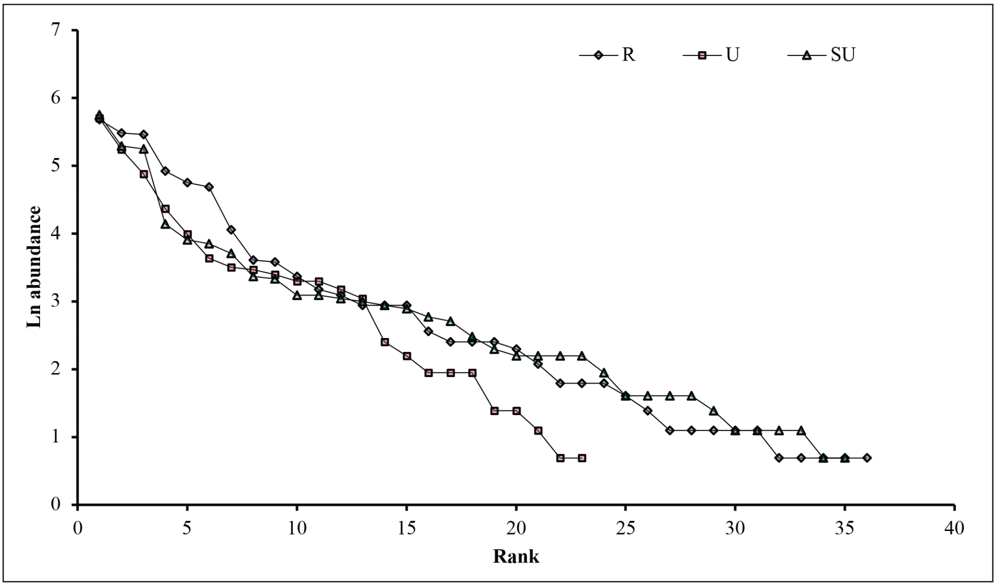


Figure 8. Rank-abundance curve of log (n+1) transformed data of bird species abundance were used to show the rank of bird in suburban, urban and rural sites

8. ábra Rank-abundancia görbe az elővárosi (SU), vidéki (R) és városi (U) madárfajok összehasonlítására

(A)

	U		R	
	Jc	**Sc**	**Jc**	**Sc**
SU	0.567	0.724	0.69	0.817
U	–	–	0.512	0.678

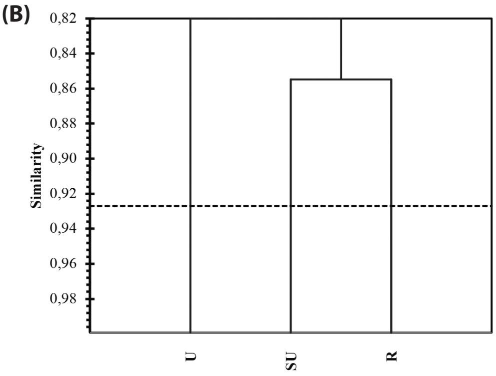


Figure 9. (A) Sorenson's (Sc) and Jaccard's (Jc) similarity coefficients calculated for different habitats in the study area (U = Urban station areas, SU = Suburban station areas and R = Rural station areas); (B) Hierarchical cluster analysis of similarity in species composition among the three study areas (SU, U and R)

9. ábra (A) Sorenson és Jaccard hasonlósági koefficiensek a három területtípusban. (B) A hierarchikus klaszterelemzés eredménye. U – városi terület, SU – elővárosi terület, R – vidéki terület

Feeding guilds of birds

Analysis of feeding guilds revealed that among the 43 species observed during the entire study period in selected railway stations irrespective of the urban-rural gradient, 16 species (37.2%) were omnivorous, 10 (23.25%) were insectivorous, 8 (18.6%) were carnivorous, 4 (9.3%) were granivorous, 3 (6.98%) were frugivorous, and the remaining 2 bird species (4.65%) were nectarivorous. Omnivores were the most dominant species in suburban (42.86%), urban (39.13%), and rural (36.11%) rail stations, followed by insectivores, with 26.08%, 25.71% and 22.22%, for U, SU and R stations, respectively. Nonetheless, the carnivore bird species recorded in the rural, suburban and urban station areas were 19.44%, 14.28% and 13.04%, respectively, while the granivorous species were highest in rural (17.4%) regions as compared to urban (8.57%) and suburban (8.33%) regions. Nectarivorous species were recorded only from the suburban (5.71%) and rural (5.5%) railways *(Figure 10)*.

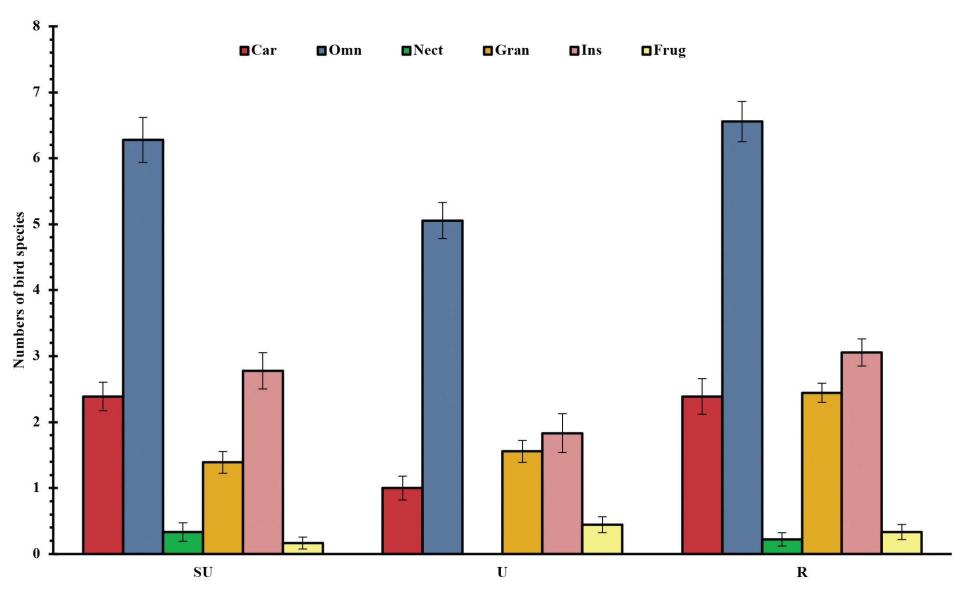


Figure 10. Numbers of bird species belong to six foraging guilds (i.e. Car=carnivore, Omn=omnivore, Nect=nectarivore, Gran=granivore, Ins=insectivore and Frug=Frugivore) recorded from the railway stations of suburban, urban and rural areas

10. ábra A hat különböző táplálkozási guildbe (Car = ragadozó, Omn = mindenevő, Nest = nektárfogyasztó, Gran = magevő, Ins = rovarevő, Frug = gyümölcsevő) tartozó madárfajok száma a három különböző területen vizsgált vasútállomásokon (SU – elővárosi, U – városi, R – vidéki)

Discussion

The assessment of the bird diversity in the railway stations provided imperative information about the species assemblage patterns, variations in species composition, and species-specific abundance and richness in the station areas, much in support of the positive effects of railways on bird assemblages (Li *et al*. 2010, Morelli *et al*. 2014, Wiącek *et al*. 2015, 2019, 2020, Kaiser-Bonk *et al.* 2019). Variations in the bird species composition along the rural-urban gradient context remained similar to the observations made from Kolkata (Sengupta *et al.* 2014, Pal *et al.* 2019) and Amravati (Kale *et al.* 2018a, 2018b), India. During the entire study period, a total of 43 bird species belonging to 12 orders and 26 families were recorded in the railway stations irrespective of the urban-rural gradient, with the dominance of representatives from Passeriformes. The dominance of birds from Sturnidae, Corvidae, Columbidae, and Ardeidae families was observed in each area. While, the relative abundance of Sturnidae and Columbidae were higher in rural railway stations, the abundance of Corvidae was higher in suburban railway station areas. The House Crow *(Corvus splendens)* and the Common Myna *(Acridotheres tristis)* were the predominant species in all railway stations. Considering global population trend of birds, 4 species of urban areas, 6 species in suburban areas and 8 species from rural areas exhibited a decreasing trend in abundance. However, further monitoring is required to confirm the reasons for the decline in the abundance of these bird species. The species richness and the diversity indices of the bird assemblages were highest for the rural railway stations followed by the railway stations of suburban and urban areas. The Jaccard and Sorensen similarity coefficients revealed that the railway stations from the suburban and rural landscapes were the regions with the most similar species composition. In contrast, the rural and urban rail stations were the least similar in terms of species composition. Such patterns appear to be similar to the observations made from Kolkata (Sengupta *et al.* 2014, Pal *et al.* 2019) and Amravati (Kale *et al.* 2018a, 2018b), where the bird species richness were higher in rural areas contrast to the urban areas. In all these studies, a nestedness (Sengupta *et al.* 2014, Kale *et al.* 2018a, Pal *et al.* 2019) pattern were observed where the majority of the species of the urban areas were part of bigger species-rich assemblages of rural areas. Likewise, in the present instance, the species commonness between the rural and urban areas was observed, reflected through the indices of community similarity. Changes in the relative abundance of feeding guild of one bird may influence the abundance of others and thus, affects the community composition of the ecosystem (Barik *et al*. 2019). In this study, we found relatively higher abundance of omnivores in each selected railway stations irrespective of the urban-rural gradient followed by insectivores, while the abundance of other four guilds were the least. In the railway tracks near the forest areas, the insectivores dominate owing to the abundance of the macroinvertebrates like insects, more likely due to the edge effect (Wiącek *et al.* 2020). The granivorous bird species were the most abundant in rural railway stations as compared to urban and suburban station regions. A possible reason might be the presence of the agricultural landscapes along the railway tracks in the rural regions (Hossian & Aditya 2016). The nectarivorous species were recorded only from the suburban and rural railway station areas and were completely missing in the urban railway stations. Positive effects of manmade infrastructures in course of urbanization on the reproductive success of some wildlife population were reported previously (Cardilini *et al.* 2013). The animals usually preferred to use the roadside constructions and associated structures have the physical and cognitive abilities to endure the possible risk (Fahrig & Rytwinski 2009). Utilization of small territory size, ability to avoid conflict with human activities, high productiveness could provide those animals the adaptability to survive with the anthropogenic interferences. Reduction of predation pressure, occurrence of roadside agriculture practices (Sundar & Kittur 2013, Hossain & Aditya 2016) as well as abundance of vegetation (Morelli *et al.* 2014, Wiącek *et al.* 2015, 2019, 2020, Kaiser-Bonk *et al.* 2019) provide foraging and nesting habitats to make a unique ecological corridor. The power lines, over bridge pillars, station railing borders, lamp posts possibly provide the suitable sites for chasing the prey by carnivores and insectivores (Morelli *et al.* 2014). The anthropogenic constructions somehow attract a large number of opportunist bird species by offering environmental heterogeneity (Morelli *et al.* 2014, Kaiser-Bonk *et al.* 2019, Wiącek *et al.* 2019, 2020). In this study, it was evident that the anthropogenic structures can be utilized to attract species too effectively to increase diversity irrespective to urban-rural gradient. The vegetation near railway station areas acting as ecological corridors for many insects, made these areas suitable for foraging habitat for many insectivorous bird species. It was reported that the passerine species used artificial light along the railway station areas, which increase their activity period. The passerines also used warm surface of station grounds, which could conserve their metabolic energy. Besides, the shrubs, lamp posts, bridges in station areas provide better place to construct nests for these species (Morelli *et al.* 2014). Construction along the railway tract, mainly the electric wires and poles provide suitable place for displaying and singing for the passerines. For granivorous bird species the availability of small stones near railway track could be a source for gastroliths and surface sand on station ground could help the passerine species to accomplish their sand-bathing, helpful for cleaning their feathers (Morelli *et al.* 2014). It was observed that the railway station areas are most suitable territory for rodents as they found it better ground for availability of food and safest hiding place. The availability of rodents and their traffic mortality turns the railway station area as a better foraging ground for carnivorous birds. During the study, it was reported that near the railway tracks, the relative abundance of omnivorous bird species were maximum irrespective of urban-rural gradient. It may be due to the fondness of bird species always to share ecotone environment. In addition to the open agricultural landscape along the railway track, which could provide excellent foraging ground due to the better insulation, higher temperature in station areas reinforce the growth and availability of rodents and invertebrates (Delgado *et al*. 2007). The abundance of various kinds of food along the railway station areas due to the existence of special microclimatic conditions might be qualified as an anthropogenic construction suitable for various bird species occupying different feeding guilds along with the dominance of omnivores due to their inclination towards the marginal habitats, which could provide them an ecotone environment (Delgado *et al*. 2007, Barbaro *et al*. 2014). Diverse and more affluent vegetation near the railway tracks provide most favourable habitat for a large number of invertebrate populations (Vermeulen 1994), which attracted various insectivorous birds species towards that ecotone environment. Though the noise from busy roadside traffic provides negative impact on many bird species (Rheindt 2003, Summers *et al.* 2011), in our study, we did not observe any negative interactions with the train movements to their surroundings. Such bird species frequently observed in station areas did not react much in response to the noise made by the movement of trains through the station (Wiącek *et al*. 2015, 2019, 2020).

In the present observations, the railway stations across urban-rural gradient appear to bear a positive impact on the bird species assemblages. Considerable extent of taxonomic and functional diversity of birds was observed across the urban-rural gradient with prominent differences in the rural against the urban areas. Such observations tally with the characteristic bird species assemblages in urban areas (Pollack *et al.* 2017, Rodriguez *et al.* 2018, Filloy *et al.* 2019) and the differences in the urban and rural context (Sengupta *et al.* 2014, Kale *et al.* 2018a, 2018b, Pal *et al.* 2019). In the present study, higher diversity and species richness were observed in thesuburban and rural station areas than that of urban areas. Higher species richness and diversity index in periurban and suburban landscape as well as railway construction suggests human constructions are attractive to numerous bird species (Sandilyan & Sudha 2013). On the basis of the habitat requirements, species can be divided into two groups. Some species that are highly accustomed to human activities and those with special habitat requirements (Fernández-Juricic 2000). Birds accustomed to stay with the human activities are not usually afraid of human activities rather they usually preferred such constructions like railway stations, bridges, light posts, which potentially have positive effects on their population to provide nesting sites, alternative feeding habitat increase habitat heterogeneity to support more species. Perhaps, these factors contributed to the abundance of the birds in the railway stations observed in the present instance, where, densely populated areas or agricultural landscapes in the adjacent regions were a redundant feature. As an extension to the present observation, the biotic homogenization (Pal *et al.* 2019) and the nestedness pattern (Sengupta *et al.* 2014) of the bird species assemblages in the railway associated landscapes can be explored to promote sustenance of the birds in the concerned spaces. Nonetheless, the present study substantiates the observations made on the railways associated bird species assemblages in different geographical locations (Morelli *et al.* 2014, Kaiser-Bonk *et al.* 2019, Wiącek *et al.* 2015, 2019, 2020), justifying that railway transportation infrastructures may play more positive role in organizing the bird species assemblages than their negative impacts. However, a gradient of the urban-rural context was also prominent in the assemblage structure and the guild features of the birds occurring in different railway stations considered in the study. Observations of the present study provide a foundation to consider the railway infrastructure of West Bengal and similar regions of India to be a prospective organizer of the bird species assemblages and thus, suitable for conservation initiatives.

Acknowledgement

The authors acknowledge the constructive comments of two anonymous reviewers in enhancement of the quality of the manuscript to its present form. The authors express thanks and gratitude to Dr. Tibor Csörgő, Editor-in-Chief, for his kind cooperation and helpful suggestions in formatting the manuscript to the present form. The authors acknowledge the respective Heads, Department of Zoology, University of Calcutta and The University of Burdwan for the facilities provided, including DST-FIST, and UGC-UPE II, Government of India.

References

Addinsoft, S. A. R. L. 2010. XLSTAT software, version 9.0. – Addinsoft, Paris, France

Aich, A. & Mukhopadhyay, S. 2008. Comparison of avifauna at the edges of contrasting forest 475 patches in Western Ghat Hills of India. – The Ring 30: 71–79. DOI: 10.2478/v10050-008-0001-6

Ali, S. & Ripley, S. D. 1980. Handbook of the birds of India and Pakistan, together with those of Bangladesh, Nepal, Bhutan, and Sri Lanka. – Oxford University Press, Delhi, India

Ali, S. 1996. The book of Indian birds. – Oxford University Press, USA

Barbaro, L., Giffard, B., Charbonnier, Y., van Halder, I. & Brockerhoff, E. G. 2014. Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. – Diversity and Distributions 20(2): 149–159. DOI: 10.1111/ddi.12132

Barik, S., Mazumder, S. & Saha, G. K. 2019. Composition and richness of avifauna in a suburban landscape of mid West Bengal, India. – In: Sanyal, A. K. (eds.) Wings of Life, Seminar & Public Lecture Series, pp. 178–207. The Asiatic Society, Kolkata, India

Basavarajappa, S. 2006. Avifauna of agro-ecosystems of Maidan area of Karnataka. – Zoos' Print Journal 21(4): 2217–2219. DOI: 10.11609/JoTT.ZPJ.1277.2217-9

Beissinger, S. R. & Osborne, D. R. 1982. Effects of urbanization on avian community organization. – The Condor 84(1): 75–83. DOI: 10.2307/1367825

Benítez-López, A., Alkemade, R. & Verwij, P. A. 2010. The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. – Biological Conservation 143(6): 1307–1316. DOI: 10.1016/j.biocon.2010.02.009

Bibby, C. J. 1999.Making the most of birds as environmental indicators. – Ostrich 70(1): 81–88. DOI: 10.1080/00306525.1999.9639752

Bibby, C. J., Burgess, N. D., Hill, D. A. & Mustoe, S. 2000. Bird census techniques. 2nd ed. – Elsevier, Academic Press, UK., pp. 302.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. – Ecological Applications 6(2): 506–519. DOI: 10.2307/2269387

Borad, C., Mukherjee, A. & Parasharya, B. 2001. Damage potential of Indian SarusCrane in paddy crop agroecosystem in Kheda district Gujarat, India. – Agriculture, Ecosystems & Environment 86(2): 211–215. DOI: 10.1016/S0167-8809(00)00275-9

Borda-de-Água, L., Barrientos, R., Beja, P. & Pereira, H. M. 2017. Railway ecology. – In: Borda-de-Água, L., Barrientos, R., Beja, P. & Pereira, H. M. (eds.) Railway Ecology. – Springer, Cham, pp. 3–7.

Bradford, D. F., Franson, S. E., Neale, A. C., Heggem, D. T., Miller, G. R. & Canterbury, G. E. 1998. Bird species assemblages as indicators of biological integrity in Great Basin rangeland. – Environmental Monitoring and Assessment 49(1): 1–22. DOI: 10.1023/A:1005712405487

Browder, S. F., Johnson, D. H. & Ball, I. 2002. Assemblages of breeding birds as indicators of grassland condition. – Ecological Indicators 2(3): 257–270. DOI: 10.1016/S1470-160X(02)00060-2

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. 1993. Distance sampling: estimating abundance of biological populations. – Chapman and Hall, London

Buzas, M. A. & Hayek, L. A. 1998. SHE analysis for biofacies identification. – The Journal of Foraminiferal Research 28(3): 233–239.

Canterbury, G. E., Martin, T. E., Petit, D. R., Petit, L. J. & Bradford, D. F. 2000. Bird communities and habitat as ecological indicators of forest condition in regional monitoring. – Conservation Biology 14(2): 544–558. DOI: 10.1046/j.1523-1739.2000.98235.x

Cardilini, A. P., Weston, M. A., Nimmo, D. G., Dann, P. & Sherman, C. D. H. 2013. Surviving in sprawling suburbs: suburban environments represent high quality breeding habitat for a widespread shorebird. – Landscape Urban Planning 115: 72–80. DOI: 10.1016/j.landurbplan.2013.04.001

Chace, J. F. & Walsh, J. J. 2006.Urban effects on native avifauna: a review. – Landscape and Urban Planning 74(1): 46–69. DOI: 10.1016/j.landurbplan.2004.08.007

Chamberlain, D. E., Cannon, A. R., Toms, M., Leech, D. I., Hatchwell, B. & Gaston, K. 2009. Avian productivity in urban landscapes: a review and meta-analysis. – Ibis 151(1): 1–18. DOI: 10.1111/j.1474-919X.2008.00899.x

Chatterjee, A., Adhikari, S., Barik, A. & Mukhopadhyay, S. K. 2014. The mid-winter assemblage and diversity of bird populations at Patlakhawa Protected Forest, Coochbehar, West Bengal, India. – The Ring 35(1): 31–53. DOI: 10.2478/ring-2013-0002

DeGregorio, B. A., Weatherhead, P. J. & Sperry, J. H. 2014. Power lines, roads, and avian nest survival: effects on predator identity and predation intensity. – Ecology and Evolution 49(9): 1589–1600. DOI: 10.1002/ece3.1049

del Hoyo, J., Elliott, A. & Sargatal, J. 1996. Handbook of the Birds of the World, Vol. 3. Hoatzin to Auks. – Lynx Edicions, Barcelona

Delgado, J. D., Arroyo, N. L., Arevalo, J. R. & Fernandez-Palacios, J. 2007. Edge effect of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests. – Landscape and Urban Planning 81(4): 328–340. DOI: 10.1016/j.landurbplan.2007.01.005

Dhindsa, M. S. & Saini, H. K. 1994. Agricultural ornithology: an Indian perspective. – Journal of Biosciences 19(4): 391–402. DOI: 10.1007/BF02703176

Eeva, T., Tanhuanpää, S., Råbergh, C., Airaksinen, S., Nikinmaa, M. & Lehikoinen, E. 2000. Biomarkers and fluctuating asymmetry as indicators of pollution-induced stress in two hole-nesting passerines. – Functional Ecology 14(2): 235–243. DOI: 10.1046/j.1365-2435.2000.00406.x

Fahrig, L. & Rytwinski, T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. – Ecology and Society 14(1): 1–20.

Fernández-Juricic, E. 2000. Avifaunal use of wooded streets in an urban landscape. – Conservation Biology 14(2): 513–521. DOI: 10.1046/j.1523-1739.2000.98600.x

Filloy, F., Zurita, G. A. & Bellocq, M. I. 2019. Bird diversity in urban ecosystems: the role of the biome and land use along urbanization gradients. – Ecosystems 22(1): 213–227. DOI: 10.1007/s10021-018-0264-y

Fraixedas, S., Lindén, A., Piha, M., Cabeza, M. & Gregory, R. 2020. A state-of-the-art review on birds as indicators of biodiversity: advances, challenges and future directions. – Ecological Indicators 118: 106728. DOI: 10.1016/j.ecolind.2020.106728

Gering, J. C. & Blair, R. B. 1999.Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? – Ecography 22(5): 532–541. DOI: 10.1111/j.1600-0587.1999.tb01283.x

Gilbert, O. 2012. The Ecology of Urban Habitats. – Springer Science & Business Media

Gregory, R. D., Noble, D., Field, R., Marchant, J., Raven, M. & Gibbons, D. W. 2003.Using birds as indicators of biodiversity. – Ornis Hungarica 12–13: 11–24.

Grimmett, R., Inskipp, C. & Inskipp, T. 2016. Birds of the Indian Subcontinent: India, Pakistan, Sri Lanka, Nepal, Bhutan, Bangladesh and the Maldives. – Bloomsbury India, pp. 448.

Haggard, W. H. 1990. Urban weather. – International Journal of Environmental Studies 36(1–2): 73–82. DOI: 10.1080/00207239008710584

Haskell, D. G., Knupp, A. & Schneider, M. 2001. Nest predator abundance and urbanization. – In: Marzluff, J. M., Bowman, R. & Donnelly, R. (eds.) Avian Ecology and Conservation in an Urbanizing World. – Springer, New York, pp. 243–258.

Hossain, A. & Aditya, G. 2016. Avian diversity in agricultural landscape: records from Burdwan, West Bengal, India. – Proceedings of the Zoological Society 69(1): 38–51. DOI: 10.1007/s12595-014-0118-3

Hutto, R. L., Pletschet, S. M. & Hendricks, P. 1986. A fixed-radius point count method for nonbreeding and breeding season use. – The Auk 103(3): 593–602. DOI: 10.1093/auk/103.3.593

Issa, M. A. 2019. Diversity and abundance of wild birds species' in two different habitats at Sharkia Governorate, Egypt. – The Journal of Basic and Applied Zoology 80(1): 1–7. DOI: 10.1186/s41936-019-0103-5

Kaiser-Bonk, J., Skórka, P., Bonk, M., Lenda, M., Rożej-Pabijan, E., Wantuch, M. & Moroń, D. 2019. The effect of railways on bird diversity in farmland. – Environmental Science and Pollution Research 26(30): 31086–31098. DOI: 10.1007/s11356-019-06245-0

Kale, M., Ferrante, M., Dudhe, N., Kasambe, R., Trukhanova, I. S., Ivanova, T., Bhattacharya, P. & Lövei, G. I. 2018a Nestedness of bird assemblages along an urbanisation gradient in Central India. – Journal of Urban Ecology 4(1): 1–8. DOI: 10.1093/jue/juy017

Kale, M., Dudhe, N., Ferrante, M., Ivanova, T., Kasambe, R., Trukhanova, I. S., Bhattacharya, P. & Lövei, G. I. 2018b The effect of urbanization on the functional and scale-sensitive diversity of bird assemblages in Central India. – Journal of Tropical Ecology 34(6): 341–350. DOI: 10.1017/S0266467418000317

Khan, S. & Naher, H. 2009. Birds in Kurigram district of Bangladesh. – Journal of Threatened Taxa 1(4): 245–250. DOI: 10.11609/JoTT.o1698.245-50

Koskimies, P. 1989. Birds as a tool in environmental monitoring. – Annales Zoologici Fennici 26: 153–166.

Krebs, C. J. 1999. Ecological methodology, 2nd ed. – Addison Wesley Longman, Menlo Park, CA.

Kumar, A., Tak, P. C. & Sati, J. P. 2006. Residential, population and conservation status of Indian wetland birds. – In: Boere, G. C., Galbraith, C. A. & Stroud, D. A. (eds.) Waterbirds Around the World. – The Stationery Office, Edinburgh, UK., pp. 308–309.

Kumar, P. & Gupta, S. 2013. Status of wetland birds of Chhilchhila Wildlife Sanctuary, Haryana, India. – Journal of Threatened Taxa 5(5): 3969–3976. DOI: 10.11609/JoTT.o3158.3969-76

Lee, P. F., Ding, T. S., Hsu, F. H. & Geng, S. 2004. Breeding bird species richness in Taiwan: distribution on gradients of elevation, primary productivity and urbanization. – Journal of Biogeography 31(2): 307–314. DOI: 10.1046/j.0305-0270.2003.00988.x

Li, Z., Ge, C., Li, J., Li, Y., Xu, A., Zhou, K. & Xue, D. 2010. Ground-dwelling birds near the Qinghai-Tibet highway and railway. – Transportation Research Part D: Transport and Environment 15(8): 525–528. DOI: 10.1016/j.trd.2010.07.004

Ludwig, J. A., Quartet, L., Reynolds, J. F. & Reynolds, J. F. 1988. Statistical ecology: a primer in methods and computing, Vol. 1. – Wiley-Interscience Pub., New York

Magurran, A. E. 1988. Ecological diversity and its measurement. – Chapman and Hall, London

Margalef, R. 1958. Information theory in biology. – General Systems Yearbook 3: 36–71.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. – In: Marzluff, J. M., Bowman, R. & Donnelly, R. (eds.) Avian Ecology and Conservation in an Urbanizing World. – Springer, Boston, MA, USA. DOI: 10.1007/978-1-4615-1531-9_2

McAleece, N., Gage, J. D. & Lambshead, J. 1997. Biodiversity Professional. – The Natural History Museum & The Scottish Association for Marine Science, UK.

Melles, S., Glenn, S. & Martin, K. 2003. Urban bird diversity and landscape complexity: species-environment associations along a multiscale habitat gradient. – Conservation Ecology 7(1): 5. DOI: 10.5751/ES-00478-070105

Morelli, F., Beim, M., Jerzak, L., Jones, D. & Tryjanowski, P. 2014. Can roads, railways and related structures have positive effects on birds? – A review. – Transportation Research Part D: Transport and Environment 30: 21–31. DOI: 10.1016/j.trd.2014.05.006

Mukherjee, S., Banerjee, S., Saha, G. K., Basu, P. & Aditya, G. 2015. Butterfly diversity in Kolkata, India: An appraisal for conservation management. – Journal of Asia-Pacific Biodiversity 8(3): 210–221. DOI: 10.1016/j.japb.2015.08.001

Pain, D. J., Gargi, R., Cunningham, A. A., Jones, A. & Prakash, V. 2004.Mortality of globally threatened Sarus Cranes *Grus antigon* from monocrotophos poisoning in India. – Science of the Total Environment 326(1–3): 55–61. DOI: 10.1016/j.scitotenv.2003.12.004

Pal, M., Pop, P., Mahapatra, A., Bhagat, R. & Hore, U. 2019. Diversity and structure of bird assemblages along urban-rural gradient in Kolkata, India. – Urban Forestry & Urban Greening 38(1): 84–96. DOI: 10.1016/j.ufug.2018.11.005

Pereira, H. M., Navarro, L. M. & Martins, I. S. 2012. Global biodiversity change: the bad, the good, and the unknown. – Annual Review of Environment and Resources 37: 25–50. DOI: 10.1146/annurev-environ-042911-093511

Pollack, L., Ondrasek, N. R. & Calisi, R. 2017. Urban health and ecology: the promise of an avian biomonitoring tool. – Current Zoology 63(2): 205–212. DOI: 10.1093/cz/zox011

Praveen, J., Jayapal, R. & Pittie, A. 2016. A checklist of the birds of India. – Indian Birds 11(5–6): 113–172.

Profillidis, V. A. 2006. Railway Management and Engineering. – Ashgate Publishing Company

Rheindt, F. E. 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? – Journal für Ornithologie 144(3): 295–306. DOI: 10.1007/BF02465629

Rodrigues, A. G., Borges-Martins, M. & Zilio, F. 2018. Bird diversity in an urban ecosystem: the role of local habitats in understanding the effects of urbanization. – Iheringia Série Zoologia 108(11): e2018017. DOI: 10.1590/1678-4766e2018017

Sandilyan, S. & Sudha, M. 2013. Check list of avifauna in between Kutralam and Narasingampattai Railway Track, Tamilnadu, India. – International Journal of Pure and Applied Zoology 1(1): 7–14.

Şekercioğlu, C. H. 2012a Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. – Journal of Ornithology 153(1): 153–161. DOI: 10.1007/s10336-012-0869-4

Şekercioğlu, C. H. 2012b Promoting community-based bird monitoring in the tropics: Conservation, research, environmental education, capacity-building, and local incomes. – Biological Conservation 151(1): 69–73. DOI: 10.1016/j.biocon.2011.10.024

Sengupta, S., Mondal, M. & Basu, P. 2014. Bird species assemblages across a rural urban gradient around Kolkata, India. – Urban Ecosystems 17(2): 585–596.

Sorace, A. 2002. High density of bird and pest species in urban habitats and the role of predator abundance. – Ornis Fennica 79(2): 60–71.

Summers, P. D., Cunnington, G. M. & Fahrig, L. 2011. Are the negative effects of roads on breeding birds caused by traffic noise? – Journal of Applied Ecology 48(6): 1527–1534. DOI: 10.1111/j.1365-2664.2011.02041.x

Sundar, K. G. & Kittur, S. 2013. Can wetlands maintained for human use also help conserve biodiversity? Landscape-scale patterns of bird use of wetlands in an agricultural landscape in north India. – Biological Conservation 168: 49–56. DOI: 10.1016/j.biocon.2013.09.016

Vallecilo, S., Maes, J., Polce, C. & Lavalle, C. 2016. A habitat quality indicator for common birds in Europe based on species distribution models. – Ecological Indicators 69: 488–499. DOI: 10.1016/j.ecolind.2016.05.008

van der Ree, R., Jaeger, J. A., van der Grift, E. A. & Clevenger, A. P. 2011. Effects of roads and traffic on wildlife populations and landscape function: road ecology is moving toward larger scales. – Ecology and Society 16(1): 48. URL: http://www.ecologyandsociety.org/vol16/iss1/art48/

Venier, L. A. & Pearce, J. L. 2004.Birds as indicators of sustainable forest management. – The Forestry Chronicle 80(1): 61–66. DOI: 10.5558/tfc80061-1

Veríssimo, D., Fraser, I., Groombridge, J., Bristol, R. & MacMillan, D. C. 2009. Birds as tourism flagship species: a case study of tropical islands. – Animal Conservation 12(6): 549–558. DOI: 10.1111/j.1469-1795.2009.00282.x

Vermeulen, H. J. 1994. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles Carabidae. – Biological Conservation 69(3): 339–349. DOI: 10.1016/0006-3207(94)90433-2

Whelan, C. J., Wenny, D. G. & Marquis, R. J. 2008. Ecosystem services provided by birds. – Annals of the New York Academy of Sciences 1134(1): 25–60. DOI: 10.1196/annals.1439.003

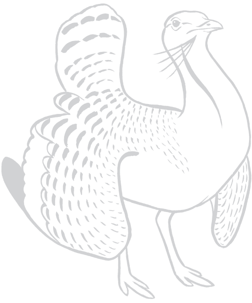
Wiącek, J., Polak, M., Filipiuk, M., Kucharczyk, M. & Bohatkiewicz, J. 2015. Do birds avoid railroads as has been found for roads? – Environmental Management 56(3): 643–652. DOI: 10.1007/s00267-015-0528-7

Wiącek, J., Polak, M., Filipiuk, M. & Kucharczyk, M. 2019. Does railway noise affect forest birds during the winter? – European Journal of Forest Research 138(5): 907–915. DOI: 10.1007/s10342-019-01212-3

Wiącek, J., Polak, M., Filipiuk, M., Kucharczyk, M. & Dawidowicz, Ł. 2020. Do railway lines affect the distribution of woodland birds during autumn? – PLoS ONE 15(4): e0231301. DOI: 10.1371/journal.pone.0231301

Williams, P. H., Burgess, N. D. & Rahbek, C. 2000. Flagship species, ecological complementarity and conserving the diversity of mammals and birds in sub-Saharan Africa. – Animal Conservation 3(3): 249–260. DOI: 10.1111/j.1469-1795.2000.tb00110.x

Zar, J. H. 1999. Biostatistical analysis, 4th ed. – Pearson Education Singapore Pte. Ltd., Indian Branch, New Delhi, India



Ornis Hungarica 2020. 28(2): 111–119.
DOI: 10.2478/orhu-2020-0020

Population status and habitat assessment of Cheer Pheasant *(Catreus wallichii)* in Western Nepal

Keshab Chokhal[1*], Tilak Thapamagar[2] & Tej Bahadur Thapa[1]

Received: August 21, 2020 – Revised: September 22, 2020 – Accepted: September 28, 2020

Chokhal, K., Thapamagar, T. & Thapa, T. B. Population status and habitat assessment of Cheer Pheasant *(Catreus wallichii)* in Western Nepal. – Ornis Hungarica 28(2): 111–119. DOI: 10.2478/orhu-2020-0020

Abstract The Cheer Pheasant *(Catreus wallichii)* is a protected species found abundantly to the west of Kaligandaki River. This study was conducted in the Myagdi district located in the western part of Kaligandaki River from October 2016 to June 2017. Our aim was to assess the habitat and population status of Cheer Pheasant, using acoustic survey and quadrate methods. A total of 38 breeding individuals were estimated in 7 bird/km^2 density. The study also revealed that Cheer Pheasants showed a preference for exposure components of the habitat. They preferred moderately steep eastern slopes (10–35°) and steep southern slopes (35–67°) between 1800–2400 m elevations. Additionally low tree density and high herbs density showed a significant effect on the habitat choice of the species. Poaching and habitat destruction are the major threats in the study site, calling upon a strategic management plan for the long-term conservation of the Cheer Pheasant.

Keyword: acoustic survey, quadrate, aspect, slope, elevation

Összefoglalás A bóbitás fácán *(Catreus wallichii)* védett faj, legnagyobb számban a Kaligandaki folyótól nyugatra fordul elő. A Myagdi nevű területen, a folyótól nyugatra végeztünk kutatást a faj élőhelyének és populációja helyzetének felmérésére 2016 október és 2017 június között akusztikus és kvadrát felmérési módszer alkalmazásával. A területen összesen 38 költő egyedet becsültünk, 7 madár/km^2 sűrűségben. A vizsgálatból az is kiderült, hogy a faj a kitett élőhelyeket preferálja, így a közepesen meredek keleti lejtőket (10–35°) és a meredek déli lejtőket (35–67°) részesíti előnyben, továbbá az alacsony faborítottság és a magas lágyszárú borítás is jelentős szerepet játszik élőhelyválasztásában. A fajra a vizsgálati területen az orvvadászat és az élőhelyek pusztítása jelenti a legnagyobb veszélyt, ezért a bóbitás fácán hosszú távú megőrzésére stratégiai kezelési tervet szükséges kidolgozni.

Kulcsszavak: akusztikus felmérés, kvadrát, tájolás, lejtő, tengerszintfeletti magasság

[1] *Central Department of Zoology, Tribhuvan University, Kirtipur, Kathmandu, Nepal*
[2] *Himalayan Biodiversity Network Nepal, Bharatpur-11, Chitwan, Nepal*
** corresponding author, e-mail: keshabchokhal@gmail.com*

Introduction

Cheer Pheasant *(Catreus wallichii)* belongs to the order Galliformes and family Phasianidae. It is one of the native birds of the western Himalaya foothills distributed in Nepal, India and Pakistan (Garson *et al.* 1992, Grimmett *et al*. 1998, Birdlife International 2014). The species is negatively influenced by human disturbance (Kaul 1989), while the reversibly successional vegetation is a positive impact factor (Garson *et al.* 1992). It has been facing substantial threats due to habitat degradation such as forest fire, deforestation and agricultural land expansion (Inskipp & Inskipp 2003, Aacharya 2006). Changes in land-use patterns and human settlements have also resulted in a decline of the Cheer Pheasant population across its distribution range (Kalsi 1999, Ramesh 2003). Moreover, the poaching of the species is excessive, which has brought the species to the verge of extinction (Birdlife International 2018). Therefore, Cheer Pheasant has been classified as "Vulnerable" in the IUCN Redlist category and Appendix I of CITES. In Nepal, the distribution of this species extended from the west of Kaligandaki River to western Nepal, particularly associated with tall grass steppes, large mountain meadows, pastures, stunted tree and rocky cliffs with sub-tropical coniferous forest (Inskipp & Inskipp 2003, Aacharya *et al.* 2004, Budha 2006, Bishta *et al*. 2007). A key distribution area was reported from Annapurna Conservation Area and Rara National Park (Lelloit 1981, Inskipp & Inskipp 2003, Aacharya 2006, Singh & K. C. 2008) of an elevation of 900–4500 m. It has been also distributed throughout Dhorpatan Hunting Reserve and western Nepal; however, many of these breeding populations are amounted to 35 individuals (Subedi 2003) with less than a total of 1,000 isolated individuals in Nepal (Inskipp & Inskipp 2003). In this paper, we aimed to describe the abundance and distribution of Cheer Pheasant in the Myagdi district of western Nepal.

Materials and method

Study area

This study was conducted in a Myagdi District of western Nepal (83.46860 E to 28.63330 N). It had been confirmed as a breeding area in previous studies (Singh *et al.* 2011). The study site comprises ecosystems ranging from temperate to sub-alpine habitats with steep slopes consisting of mixed broadleaved and coniferous forests. The land use category of the area includes forest (36.76%), shrub (1.85%), barren land (21.27%) and rock cover (2.61%) (DFO 2016). The forest of Myagdi consists of conifer forests (13.99%), broadleaf forests (49.30%), mixed forest (31.375%) and scrubs (5.32%) (DFO 2016). Temperate and sub-alpine forests, sometimes with an extensive bamboo understory and often on steep slopes are also found in the region. These comprise mixed broadleaves and conifers forests. Kali Gandaki, Myagdi Khola and Raguganga khola are the main river systems of Myagdi district *(Figure 1)*. The altitude varies from 900 m to 3200 m (above sea level/asl.) The commonest plants include *Schima wallichi, Abis pindrow, Alnus nepalensis, Ficus auriculata, Leucoseptrum canum, Saurauia napaulensis, Cryptomeria japonica, Alangium alpinum* and *Quercus glauca* in the study area. Some important mammalian species recorded from Myagdi *e.g. Uncia uncia, Macca assamensis, Panthera pardus, Felis chaus, Muntiacus vaginalis, Ailurus fulgens*. The avifauna includes keystone species such as *Sarcogyps calvus, Lophophorus impejanus, Tragopan satyra, Gyps himalayensis, Gypaetus barbatus.*

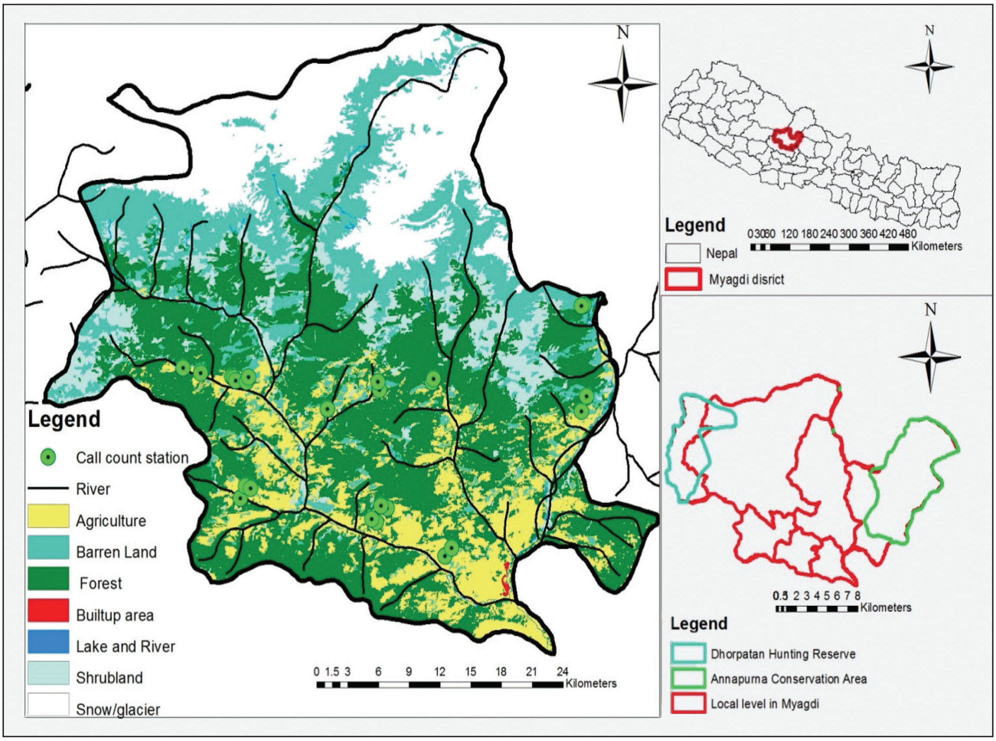


Figure 1. Study area (land cover patterns and sampling stations)
1. ábra Vizsgálati terület (felszínborítások és mintavételi helyek)

Field design

The study area was divided into three potential sites where the presence or absence of Cheer Pheasant was assessed. Those sites were divided into a 5×5 km^2 grid, providing 16 grids in total, applying Arc GIS 10.1. For field surveys, five grids were randomly selected from each site on the basis of potential area and literature review. A call counting station of 300 m radius was set up in each grid cell and the potential area was divided into three parts.

Surrounding areas of Kaligandaki (28.49987 N, 83.656266 E) are located in the vicinity of Annapurna Conservation areas, 12 km from Beni, the capital of Myagdi. The altitude varies between 900 m to 2500 m asl. This locality was divided into two study sites*:* i.e. Tatopani and Dana. Four acoustic survey stations were established in the vicinity of the study site. Lower Kali Gandaki is the only known area in Nepal where all six Himalayan Pheasant species are found. Surrounding areas of Raguganga (28.5106 N, 83.45335 E) are located 30 km in the north of Beni in southern sites of Dhaulagiri Himal. The elevation varies between 1400 m to 3500 m. It was also divided into four call counting stations. Study sites in the surroundings of Myagdi Khola (28.42772 N, 83.296377 E) are located about 5 to 40 km far from Myagdi headquarters. The elevation range is 1000 to 3500 m. This study area was also divided into 17 acoustic counting stations.

Methodology

A total of 25 surveys were conducted in the study area from October 2016 to June 2017. We applied down and dusk **acoustic survey** techniques to collect the presence data during the breeding season. Call counting started at 30 minutes before sunrise and continued 60 minutes after sunset. The distance between the two call counting stations was 200 m. The call of the species has been identified by the help of an expert and duplication of calls was removed from the datasheet for the identification of unique call numbers.

$$\text{Encounter rate } (\Sigma\overline{X}) = \frac{\text{Replication days of total survey times}}{\text{number of birds estimated by call counting station}}$$

BPE ($\Sigma\overline{X}$) = 0.75, where $\Sigma\overline{X}$= Total mean of the individual, populations were estimated by pool mean and pool variance

$$\text{Mean population density} = \frac{\text{(mean number of calling birds in an area)}}{\text{(the total area covered in each station)}}$$

In order to analyze the potential habitat used by Cheer Pheasant, the vegetation density was determined by quadrates methods at all calling and non-calling sites. Trees, shrubs, herbs were sampled by quadrates of 10×10 m, 5×5 m, 1×1 m respectively. Phytosociological parameters were also measured i.e. slope, aspect, elevation ground cover and distance to human settlement. All parameters were noted for each station. The population was the dependent variable and others (groundcover, vegetation density and distance of human settlement) were predictors. The R version 2.15.2 (R Development Core Team 2012) was used for correlation analysis. Digital Elevation Model was used to digitize i.e. slope, aspect and elevation.

Results and discussions

Population status

In total, 38 breeding individuals have been estimated from 25 call counting stations, whereas Cheer Pheasant calls were recorded from 17 sites. In total, 48.97 mean call and 63 maximum calls were recorded from each different call counting station with a detection rate of 1.50 bird/station *(Figure 2)*. A total of 7 bird/km^2 mean population density of the Cheer Pheasant has been estimated from the study area, where 4 and 10 bird/km^2 was a non-acoustic range of calling sites. It is based on the mean of 2.94 in 300 m radius of call counting stations. Similarly, 7.5 bird/km^2 densities were estimated by Singh *et al.* (2011) in the uniform habitats of Muri Myagdi. Relatively lower population densities of 2.65 bird/km^2 and 1.98 birds/km^2 have been reported by Aacharya (2006), in Lower Kali Gandaki Valley and Young *et al.* (1987) at Ghasa Mustang might be a different elevation range from the present study area. Relatively stable population densities such as 8 birds/km^2 (Subedi 2003) and 7.08 bird/

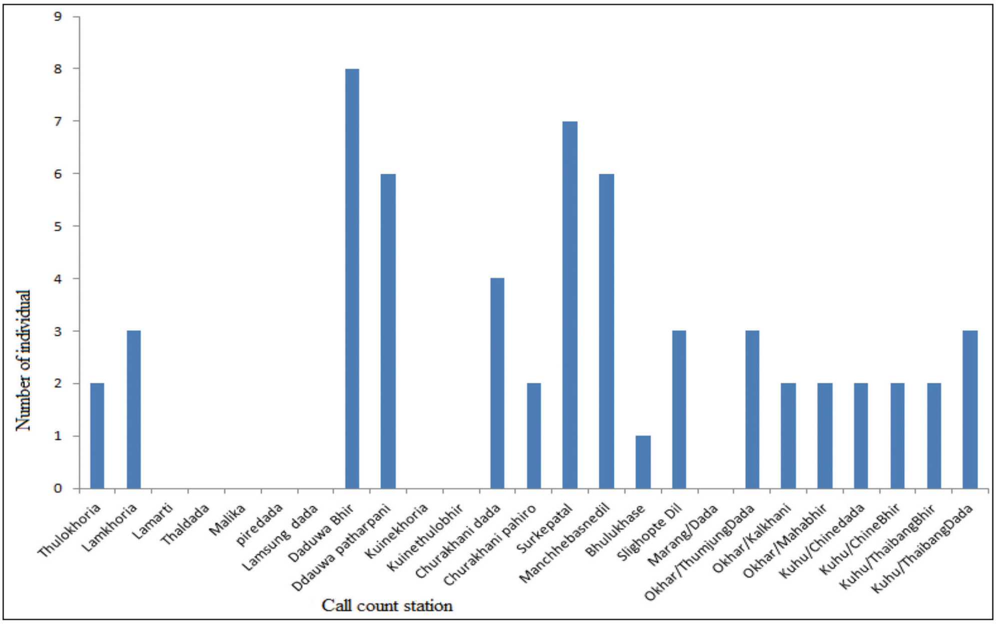


Figure 2. Number of calling pheasants for each survey station
2. ábra Az egyes megfigyelő helyeken hallott fácánok egyedszáma

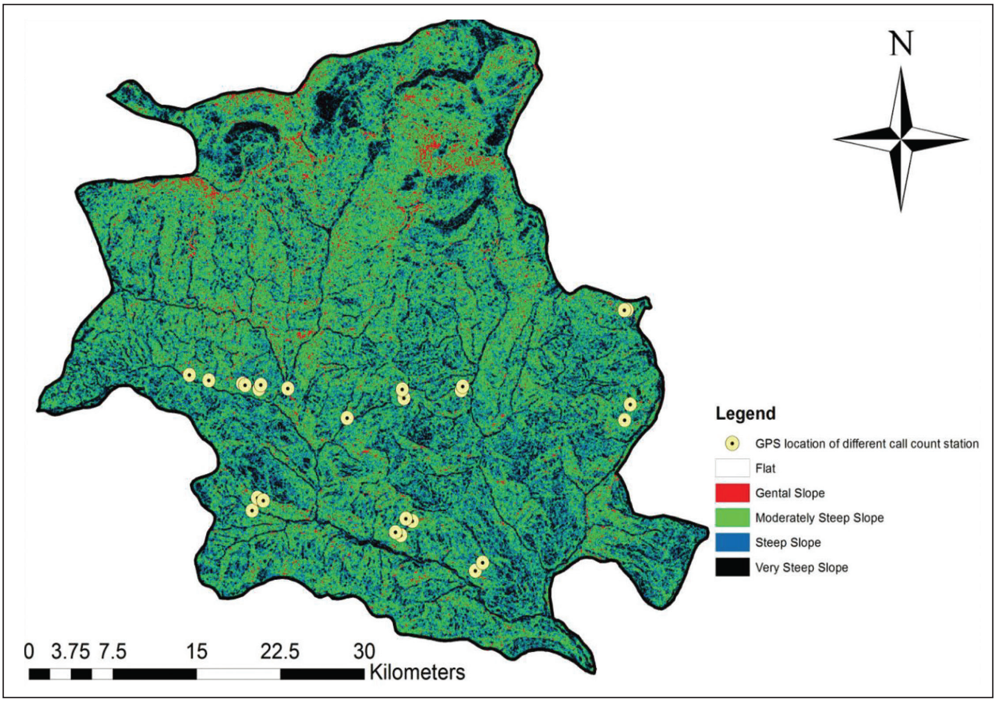


Figure 3. Number of call counting stations in various slope classes
3. ábra Az egyes megfigyelő helyek száma különböző meredekségű lejtő osztályokban

km^2 (Basnet 2014) have been recorded in Dhorpatan hunting reserve which also supports higher density (7.75 birds/km^2) of Cheer Pheasant (Basnet 2016) than Bajura district Nepal. Further, a total of 579 individuals have been reported from Azad Jammu Kashmir, while the largest population (n = 434) was noted at Qazi Nag Game Reserve (Iftikhar *et al.* 2017).

Habitat Assessment Survey of Cheer Pheasant

To provide environmental data for the distribution and habitat analysis of Cheer Pheasant, the study area was digitized covering an elevation gradient from 900 m to above 3000 m. Based on slope angles, slopes were also categorized into flat, gentle steep and very steep *(Figure 3)*. The area was digitized at South, North, East and West facing aspects *(Figure 4)* at the basis of 600–1200 m, 1200–1600 m, 1600–2400 m, 2400–3000 m and above 3000 m elevation ranges *(Figure 5)*. This rare species were densely distributed in the 1800 to 2400 m elevation range with east and south facing slopes while the majority of the individuals were also distributed in moderately steep slope (10–35°) in this study area. Lelloit (1981), Singh *et al*. (2011) reported that the species prefers elevation ranges between 1400–3200 m with South and North facing aspects in Muri and Khibang Myagdi. Similarly, it was reported from a wide elevation range of 701–2400 m in Chail Wildlife Sanctuary India (Gaston & Singh 1980, Akthar *et al*. 2004). Correlations were detected between Cheers population with ground cover ($r = 0.012$, $P>0.05$) and herbs density ($r = 0.64$, $P < 0.01$), however only herbs density showed significantly positive correlation. The breeding and feeding ecology were significant correlated to dense ground cover (Lelloit 1981, Singh *et al*. 2011). Among the correlations between Cheers population with shrubs ($r = –0.023$, $P > 0.05$), tree density ($r = –0.57$, $P < 0.01$) and distance of human settlement ($r = –0.18$, $P > 0.05$), only tree density showed significantly negative correlations with the population. It indicates that scattered tree and open rocky terrain are the favored habitat of this pheasant species (Baker *et al.* 1918, Ali & Ripely 1968, King 1981, Johnsgard 1986, Roberts 1991, Garson *et al.* 1992, Bisht *et al.* 2007, Awan *et al.* 2014) whereas Singh and K. C. (2008) reported that most of the Cheer Pheasant distribution was closely associated with around the human settlement area in Rara National Park. In comparison with different habitat variables, dense herbs vegetation and scattered tree have been preferred habitat of this species in this study area.

Conclusions

A total of 38 breeding Cheer Pheasant were recorded at 25 call counting stations with 7 bird/km^2 density. In conclusion, moderately steep slopes (10–35°), steep slope (35–67°), east and south face aspects at 1800–2400 m an elevation range were the most suitable geographical features of the Cheer Pheasant. The scattered tree and dense herb vegetation have played more significant role than other factors in governing the distribution of Cheer Pheasant. Habitat deteriorating, agricultural activities, poaching and livestock grazing were noticeable threats to the species. Hence, a long term sustainable conservation strategic plan is necessary for the protection of this species in the study area.

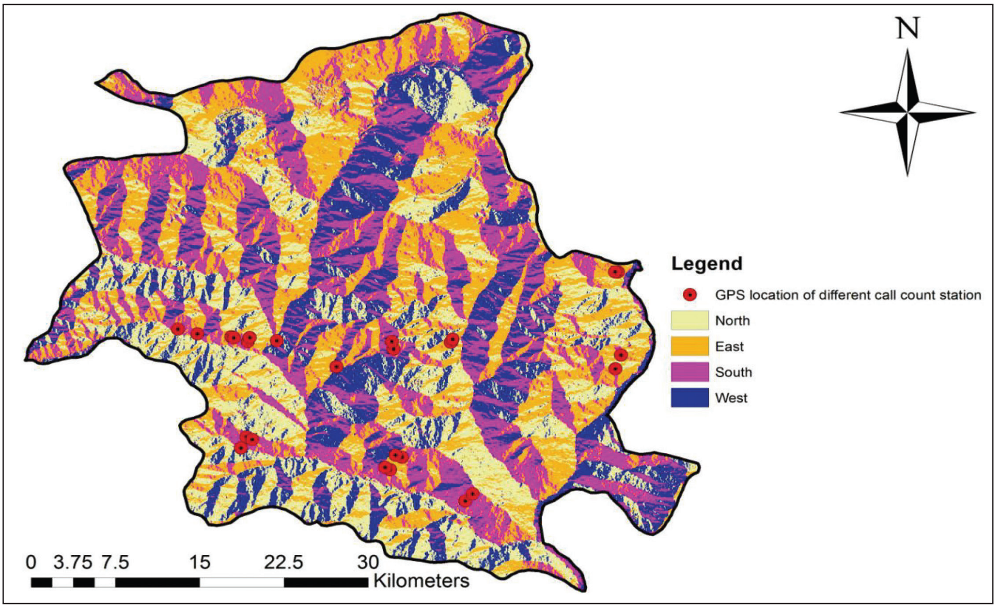


Figure 4. Number of call counting stations in various aspect class
4. ábra Az egyes megfigyelő helyek száma különböző tájolású lejtők szerinti besorolásban

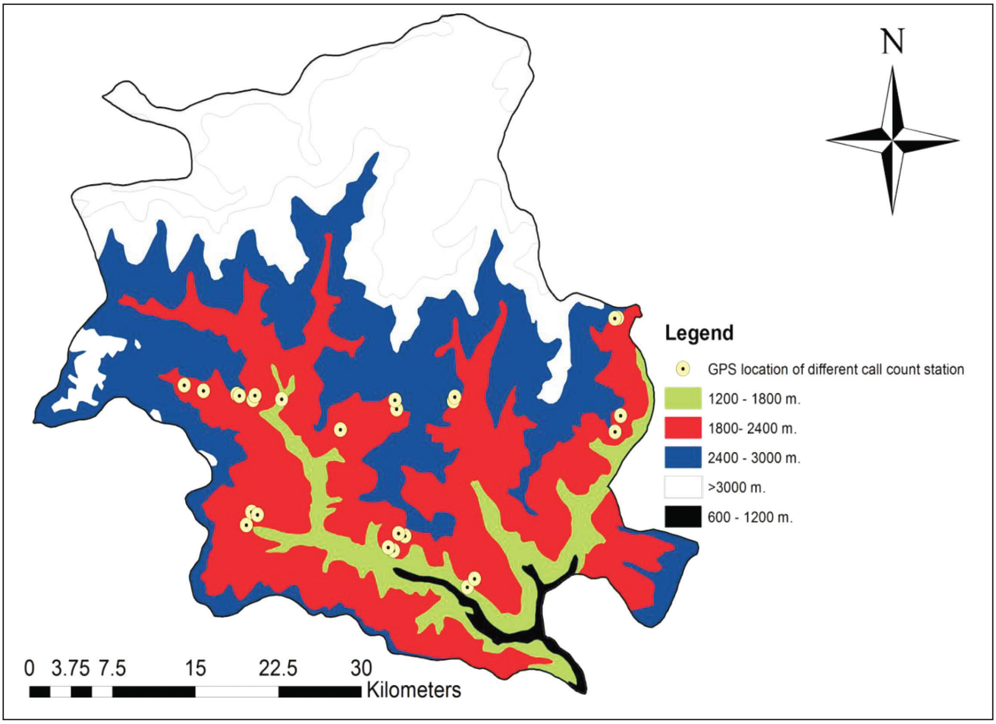


Figure 5. Number of call counting stations in various elevation classes
5. ábra Az egyes megfigyelő helyek száma különböző tengerszintfeletti magassági osztályokban

Acknowledgements

This research was funded by the National Trust for Nature Conservation (NTNC). We would like to thank IDEA WILD for equipment support. We thank Ian Clark World Pheasant Association. We also thank the Department of National Park and Wildlife Conservation (DNPWC) for permission letters.

References

Aacharya, R., Thapa, S. & Ghimirey, Y. 2004. Monitoring of Cheer Pheasant in Lower Kali Gandaki Valley, Mustang Nepal. – Report Submitted to King Mahendra Trust for Nature Conservation Annapurna Conservation Area, Nepal

Aacharya, R. 2006. Cheer Pheasant exist east of Kali Gandaki Valley, Nepal. – Danphe 15(10): 7–8.

Akthar, N., Narang, M. L. & Kumar, M. 2004. Status and distribution of Cheer Pheasant in Chail Wildlife Sanctuary, India. – Proceedings of the 3rd International Galliformes Symposium. World Pheasant Association, Fordingbridge, UK, pp. 102–108.

Awan, M. N., Ali, H. & Lee, D. C. 2014. Population survey and Conservation assessment of the globally threatened Cheer Pheasant in Jhelum Valley, Azad Kashmir, Pakistan. – Chinese Journal of Zoological Research 35(4): 1–8. DOI: 10.13918/j.issn.2095-8137.2014.4.338.

Baker, E. C. S. & Ellison, C. M. Z. S. 1918. The game birds of India, Burma and Ceylon. – Journal of the Bombay Natural History 25(3): 1–325.

Basnet, H. 2014. Population status, occupancy and distribution modeling of Cheer Pheasant in Dhorpatan Hunting Reserve, Nepal. – MSc Thesis, Central Department of Zoology, T. U. Kirtipur, Kathmandu

Basnet, H. 2016. Survey of Cheer Pheasant in Bajura District, Nepal. – Report submitted to Oriental Bird Club, U.K.

Bisht, M. S., Phurailatpam, S., Kathait, B. S., Dobriyal, A. K., Chandola, A. & Kaul, R. 2007. Survey of threatened Cheer Pheasant in Garhwal Himalaya. – Journal of the Bombay Natural History Society 104(2): 134–139.

BirdLife International 2014. Species fact sheet of Cheer Pheasant. – Downloaded from http//www.birdlife.org on 11/06/2017

BirdLife International 2018. Cheer Pheasant. The IUCN Red List of Threatened Species. – Downloaded from www.iucnredlist.org on 2/02/2018

Budha, P. B. 2006. The Cheer Pheasant *Catreus wallichii* (Hardwicke, 1827) and indigenous hunting techniques in mid and far west Nepal. – Danphe 15(3): 2–3.

District Forest Office 2016. Annual improvement report, Vol. 1. – District Forest Office Beni Myagdi

Gaston, A. J. & Singh, J. 1980. The Status of the Cheer Pheasant in the Chail Wildlife Sanctuary, Himachal Pradesh. – World Pheasant Association, U.K. 5: 68–73.

Garson, P. J., Young, L. & Kaul, R. 1992. Ecology and conservation of the Cheer Pheasant: Studies in the wild and the progress of a reintroduction project. – Biological Conservation 59: 25–35. DOI: 10.1016/0006-3207(92)90710-5.

Grimmett, R., Inskipp, C. & Inskipp, T. 1998. Birds of Indian Subcontinent 2nd ed. – Oxford University Press, London

Iftikhar, N., Qamar, Q. Z., Ali, U., Awan, M. S., Bibi, S. S. & Minshas, R. A. 2017. Population status of Cheer Pheasant in Azad Jammu and Kashmir. – Pakistan. Punjab University of Journal Zoology 32(1): 101–109.

Inskipp, C. & Inskipp, T. 2003. Bird conservation priorities of the Annapurna Conservation Area. – Report submitted to King Mahendra Trust for Nature Conservation Annapurna Conservation Area Project Nepal

Johnsgard, P. A. 1986. The Pheasants of the world: biology and natural history 1st ed. – Oxford University Press, New York, USA

Kaul, R. 1989. Ecology of Cheer Pheasant *Caterus wallichii* in Kumuan Himalaya. – PhD Thesis, University of Kashmir Shreenagar

Kalsi, R. S. 1999. Status and habitat of the Cheer Pheasant in Himachal Pradesh. – Tragopan 13–14: 19–25.

King, W. B. 1981. Endangered birds of the world: red data book 1st ed. – Smithsonian Institute Press and International Council for Bird Preservation, Washington, D.C., USA

Lelliot, A. D. 1981. Studies of Himalayan pheasants in Nepal with reference to their conservation. – BSc Thesis, Durham University, U.K.

Ramesh, K. 2003. An ecological study on the pheasants of Great Himalayan National Park, Western Himalaya. – PhD Thesis, Forest Research Institute, Dehradun, India

R Development Core Team 2012. A Language and Environment for Statistical computing version 2.15.2. – R Foundation for Statistical Computing, Viena, Austria (http://www.R-project.org). Assessed on 2017/5/6.

Roberts, T. J. 1991. A Supplementary note in Khair Pakistan. – Oriental Birds Club Bulletin 14: 35–37.

Singh, P. B. & K. C. S. 2008. Study on Cheer Pheasant in Botamalik grassland, Rara National Park and Buffer Zone, Mid-Western Nepal. – Report submitted to Pheasant Specialist Group, World Pheasant Association and Oriental Bird Club, U.K. Unpublished, 35.

Singh, P. B., Subedi, P., Garson, P. J. & Poudyal, L. 2011. Status, habitat use and threats of Cheer Pheasant in and around Dhorpatan Hunting Reserve, Nepal. – International Journal of Galliformes Conservation 2: 22–30.

Subedi, P. 2003. Status and Distribution of Cheer Pheasant in Dhorpatan hunting Reserve. – BSc Thesis, Instituted of Forestry Pokhara, Nepal

Young, L., Garson, P. J. & Kaul, R. 1987. Calling behavior and social organization in the Cheer Pheasant. Implications for survey technique. – Journal of World Pheasant Association 12: 30–43.

Ornis Hungarica 2020. 28(2): 120–134.
DOI: 10.2478/orhu-2020-0021

Main mortality factors for the Eastern Imperial Eagle (*Aquila heliaca* Savigny, 1809) in Bulgaria

Ivanka Lazarova[1*], Dobromir Dobrev[3], Gradimir Gradev[4], Rusko Petrov[2], Stoycho Stoychev[3], Ivaylo Klisurov[2] & Dimitar Demerdzhiev[3]

Received: September 02, 2020 – Revised: November 22, 2020 – November 24, 2020

Lazarova, I., Dobrev, D., Gradev, G., Petrov, R., Stoychev, S., Klisurov, I. & Demerdzhiev, D. 2020. Main mortality factors for the Eastern Imperial Eagle (*Aquila heliaca* Savigny, 1809) in Bulgaria. – Ornis Hungarica 28(2): 120–134. DOI: 10.2478/orhu-2020-0021

Abstract The Eastern Imperial Eagle is a globally threatened species, represented with not more than 35–40 pairs in Bulgaria. As a facultative scavenger feeding on carcasses and parts of dead domestic and wild animals, this species is extremely vulnerable to poisonous baits and toxic agents, intentionally or accidentally set up in its food. The present study identified electrocution and poisoning as the main mortality factors for the eagles in Bulgaria. We analysed a total of 56 cases among which 44 cases were related to the mortality of non-territorial eagles in different age classes, and we found 12 dead or distressed territorial birds recorded between 1992–2019. The main mortality factor was electrocution, accounted for 30.4% of fatalities. The poisoning was the cause of mortality in 12.5% of the non-territorial and 10.7% of the breeding birds. Some of the cases were laboratory confirmed as intoxication, while the others, based on the history, clinical symptoms and field evidence, indicated poisoning. The most commonly used toxic agents were anticholinesterase's inhibitors. As a result of a timely therapy applied to the live birds found in distress with symptoms of poisoning, six eagles were successfully treated and released back in the wild. We found that mortality of eagles depended on the age of birds, breeding or dispersal grounds, while season had no significant effect.

Keywords: mortality factors, raptors, population, poisonous baits, electrocution, floaters

Összefoglalás A parlagi sas egy világszerte veszélyeztetett madárfaj, amelynek bulgáriai állománya nem haladja meg a 35–40 párat. A faj részlegesen dögöt is fogyaszt, így a szándékos vagy véletlen mérgezések jelentősen veszélyeztetik. Jelenlegi vizsgálatunk alapján az áramütés és a mérgezés bizonyult a legjelentősebb halálozási oknak a parlagi sasok között Bulgáriában. Összesen 44 különböző korú, nem költő madarat és 12 territoriális madarat találtunk elpusztulva vagy legyengülve 1992–2019 között. A legfontosabb megkerülési ok az áramütés volt, amely az esetek 30,4%-át tette ki. Mérgezés következtében a nem költő madarak 12,5%-a, míg a territoriális madarak 10,7%-a került meg. A mérgezéses esetek egy részét laboratóriumi vizsgálatok igazolták, míg más esetekben a terepi körülmények alapján lehetett arra következtetni. A leggyakoribb méreganyagok a kolinészteráz-gátló vegyületek voltak. Az életben talált madarak közül hat példányt sikerült gyógyultan szabadon engedni a gyors állatorvosi beavatkozásoknak köszönhetően. Eredményeink azt mutatták, hogy a sasok halálozását a madarak kora, valamint költő vagy diszperziós területen való előfordulásuk befolyásolta. Az évszakoknak nem volt szignifikáns hatása.

Kulcsszavak: halálozási ok, ragadozómadár, populáció, mérgezett csalétek, áramütés, nem költő madarak

[1] *Faculty of Veterinary Medicine, Trakia University, Stara Zagora 6000, Bulgaria*
[2] *Wildlife Rehabilitation and Breeding Center – Green Balkans – Stara Zagora NGO, 6006 P. Box: 27 Stara Zagora, Bulgaria*
[3] *Bulgarian Society for the Protection of Birds, Yavorov complex, bl. 71, ent. 4, app. 1, Sofia 1111 Bulgaria*
[4] *Green Balkans – Stara Zagora NGO, 9 Stara Planina Str., 6000 Stara Zagora, Bulgaria*
* *corresponding author, e-mail: i_asenova_lazarova@abv.bg*

Introduction

Human activities are severely affecting raptor populations, bringing some of them to the brink of extinction (Donàzar *et al.* 2016, McClure *et al.* 2018). Electrocution and poisoning were identified as main mortality factors for many threatened species (Gonzalez *et al.* 2007, Smart *et al.* 2010, Demerdzhiev 2014, Dwyer *et al.* 2015, Demeter *et al*. 2018).

The Eastern Imperial Eagle *(Aquila heliaca)*, hereafter EIE, is a long-lived, large-size territorial raptor whose distribution range spans throughout the forest steppe zone of Eurasia (Thiollay 1994). It extends to Austria to the west, through Ukraine, Kazakhstan, and Russia to the east, and the Balkans and Asia Minor to the south (Ferguson-Lees & Christie 2001). The adult birds of the Pannonian population and the Balkans are resident, while the immatures disperse at different distances (Gradev *et al.* 2011, Horváth *et al.* 2011, Vili *et al.* 2013, Stoychev *et al.* 2014). The last population estimates show that the global population of the species might exceed 10,000 mature individuals (BirdLife International 2020), whereas the European population of the EIE is estimated at 1800–2200 pairs during the period of 2000–2010 (Demerdzhiev *et al.* 2011a). The EIE is classified as vulnerable by IUCN (with decreasing population) (BirdLife International 2019). Currently, the species is legally protected under the terms of Directive 2009/147/EC on the conservation of wild birds (Anonymous 2009), Appendix 1 of CITES, (Anonymous 2019) and Appendix 2 of the Bonn and Bern Conventions (Anonymous 1979). The main reasons for the decreasing population included: habitat loss and degradation along with high adult mortality due to persecution and hazardous powerlines, nest robbing, and prey depletion (BirdLife International 2020).

In Bulgaria, the EIE was widespread by the end of the 19th century and considered a sacred bird among the native folk (Hristovich 1890). However, in the mid of the 20th century, the EIE population decreased significantly, becoming one of the rarest Bulgarian birds (Patev 1950). During the next decades, the number of breeding pairs declined due to the rapid changes in land use pattern and the agricultural landscape system, together with the massive use of poisonous agents (Petrov *et al.* 1996). As the species reached near extinction till the‘90s, the combined efforts of NGOs, supported by the local institutions were intensified (Nikolova 2010), thus resulting in slowly restoration of the population in Bulgaria. Since 2000, the population of the species gradually increased reaching 25–30 pairs in the first decade (Demerdzhiev *et al.* 2011b) and 35–40 pairs nowadays (authors’ data). The EIE is distributed mainly in the south-eastern part of Bulgaria (Demerdzhiev *et al.* 2014a).

Recent studies on the species diet showed that it mainly foraged with medium size mammals, birds and reptiles (Marin *et al.* 2004, Katzner *et al.* 2006, Horváth *et al.* 2010, Demerdzhiev *et al.* 2014b, Horváth *et al.* 2018a). However, the EIE is an opportunistic species, therefore taking advantage of the most abundant prey in the occupied territory (Kovács e*t al.* 2005). Because of their prey species, eagles became subject to hunting and poaching (Horváth *et al.* 2018b). Similarly, because the eagles are hunting farm animals (Meyburg & Kirwan 2020) conflicts between human and nature may arise (Duriez *et al.* 2019).

At Balkans level, the most common threats to the species population include electrocution (Stoychev *et al.* 2014), the use of poisonous baits (used mainly to fight livestock predators) (Pantović & Andevski 2018).

Any action against the species welfare is treated as environmental or wildlife crime according to the Bulgarian jurisdiction, as EIE appeared to be protected species under the terms of the Biodiversity Act (Anonymous 2002). Furthermore, specific provisions by the national legislation are foreseen whenever cruelty towards vertebrate animals occurs (Kirov *et al.* 2019), resulting in fine or imprisonment.

The study aimed to summarize and analyse the main causes of incidents among the EIE in Bulgaria: non-human related and human-related causes. Based on the obtained results, we also proposed specific conservation measures to be undertaken to mitigate the identified threats.

Material and methods

Study area

The survey was primarily accomplished in Bulgaria, although the dataset of some birds, which were marked in Bulgaria, but found dead outside the territory of the country, was also included.

Study period and data procedures

Fifty-six cases of injured or dead EIEs were investigated in the period 1992–2019, retrieved by the Green Balkans Wildlife Rehabilitation and Breeding Center (WRBC) and Bulgarian Society for the Protection of Birds (BSPB) species database. The database information included (1) the regular species monitoring scheme within the breeding territories to record the EIE's breeding rates, (2) the surveys of hazardous electric power lines within species home range and (3) intensive monitoring of satellite- or radio-tagged birds. The study covered only incidents with fledged birds and nest mortality cases were excluded from the analysis. The identified factors were compared with the age of birds, season and period. Regarding EIE distribution in age groups, floaters were initially defined as birds prevented from breeding by territoriality or other spacing behaviours (Brown 1969, Newton 1992). If resource availability limits the number of breeders, and territory competition makes some individuals become floaters when all suitable breeding habitats are occupied. Floaters are individuals able to enter the reproductive population as breeders when a breeding site or potential mate becomes available (Penteriani *et al.* 2005, 2006, 2008).

The cases of birds found alive or distressed were analysed by the database of WRBC, where the birds were sent for therapy and rehabilitation. Dead birds were processed according to the status of the corpses. The corpses suitable for analysis (not decomposed) were sent either to WRBC for X-ray and necropsy, or directly to laboratory for toxicological analysis. Several laboratories were chosen with regards to location proximity or capacity for certain analytical methods. Laboratory findings indicated presence of substances - anticholinesterase's inhibitors. Particular pesticides were not determined as the methodology was able to detect only the group mechanism of action. In cases where the birds' corpses did not allow further analysis due to high rate of decomposition, the cause of death was estimated based on evidence found around the bird in the field. We checked each location in the field to verify the condition of the GPS-tagged eagles.

The causes of incidents were classified in two main groups: non-human related reasons, such as intraspecific aggression or windstorm, and human-related activities, such as poisoning, electrocution, shooting and collision with power lines or traffic.

Statistical procedures

To examine the correlation of the incidents due to the age, individuals were categorized as juveniles (the period from fledging to the end of the first winter), immatures (from their second to fifth plumage) and adults (after their fifth plumage) (Forsman 2005). The fluctuation in the number of incidents was investigated in relation to the eagle's reproductive cycle: (1) breeding, i.e. laying and incubation (during spring), (2) chick-rearing period (in summer), (3) post-fledgling period (autumn), and (4) pre-laying period (during winter season) (Kovács *et al.* 2005). Analysis of the temporal variation in the incident cases was divided into three periods: (1) till 2006, the period before the acquisition of Bulgaria in the European Union; 2) 2007–2013, Bulgaria being accepted as a member state in the EU, implementation of the EU legislation and period of active conservation measures for the species with increase in the population numbers, (3) 2014–2019, the period of population stagnation and increase in the threats for the species.

The data were processed with IBM SPSS Statistics (SPSS-Inc., 2019, SPSS Reference Guide 26 SPSS, Chicago, USA) using descriptive statistics with frequency distribution tables. The correlation between different variables was investigated with the Pearson correlation coefficient. All categorical data were organized in 2×2 contingency table. As within the table there were cells with expected count less than 5, the Fisher exact test was applied. Significance of results was presented with the exact P-value (2-tail), known in SPSS as Exact Sig (2-sided).

Results

Main mortality factors

We registered 56 cases of incidents with EIE in Bulgaria within the study period. The majority of all analysed birds were found dead (n = 45, 80.40%) and the rest of the eagles were found alive (n = 11, 19.60%). It was possible to determine the cause of death for 76.90% (n = 43) of the individuals (those found dead at discovery and those that died during therapy at WRBC). Electrocution (30.40%, n = 17 cases) and poisoning (19.60%, n = 11 cases) were the most frequent causes of mortality. Of the remaining causes, only shooting (n = 7 cases, 12.50%), collision with power lines (n = 3 cases, 5.40%) and mortality due to collision with vehicle (n = 2 cases, 3.60%) were particularly frequent.

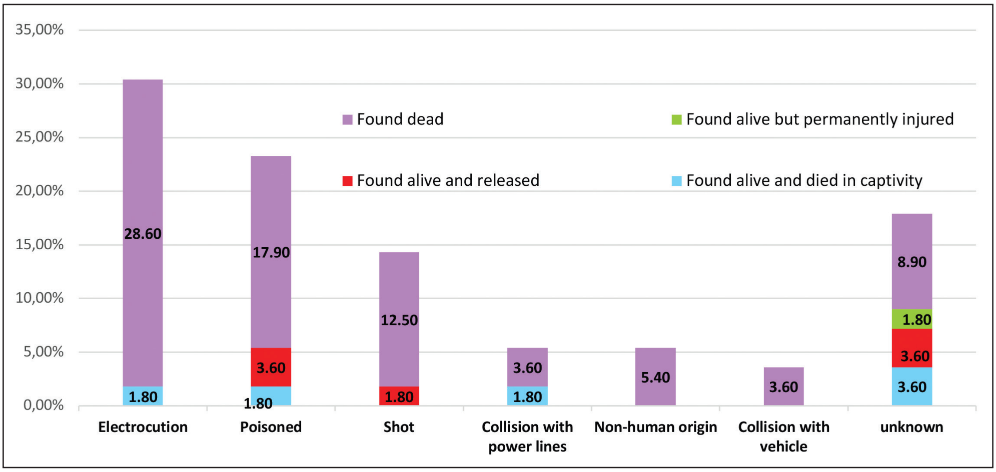


Figure 1. Causes of mortality or injury among Eastern Imperial Eagles in Bulgaria according to the status at discovery and outcome of the injury

1. ábra Parlagi sasok pusztulási vagy sérülési okai Bulgáriában a megtalálási állapot és a sérülés kimenetele alapján

The eagles found alive after the incidents were sent to the WRBC for therapy. Results showed that 10.70% (n = 6) of the birds survived the therapy and were consequently released (only one bird was left for aviary keeping due to its permanent disabilities). There were no significant differences between the cause of the incident and the final outcome from the injury (exact P = 0.26). The subject for the traumatic injury in all of the cases was analysed and for the most of the incidents was associated with human-related activities (n = 43, 76.80%), and only small share of the birds (n = 3, 5.40%) had suffered from non-human related reasons (intraspecific aggression and windstorm). In 17.90% of the cases (n = 10) the cause of injury remained unknown (for both alive and dead specimens) *(Figure 1)*. No significant differences were found between the cause of incident and the health status of the bird at discovery (exact P = 0.14).

Age related mortality

There were significant differences in the cause of death between age classes (exact P = 0.01). Incidents at different age stages appeared to be significantly influenced by the cause for the mortality.

The main factor for casualties in juvenile EIE was electrocution (n = 7, 12.50%), followed by poisoning (n = 3, 5.40%). However, unknown causes accounted for seven birds (n = 7, 12.50%). Immature eagles were mainly affected by electrocution, followed by shooting and poisoning. The main cause for incidents in adult birds was poisoning, followed by electrocution and causes from non-human origin.

We found that 46.2% (n = 6) of all registered poisoning incidents were diagnosed as such based on the case history and clinical symptoms of the birds. The rest 53.8% (n = 7) of the poison samples were confirmed to contain anticholinesterase's inhibitors, suggesting the use of pesticides.

Table 1. Causes of mortality or injury among Eastern Imperial Eagles in Bulgaria according to the different variables studied

1. táblázat Parlagi sasok pusztulási vagy sérülési okai Bulgáriában az egyes vizsgált változók alapján

	Electrocution	**Poisoned**	**Shot**	**Collision with power lines**	**Non-human origin**	**Collision with vehicle**	**Unknown**	**Total**
Age								
juvenile	7	3	0	1	1	0	7	**19**
immature	8	5	7	2	0	1	3	**26**
adult	2	5	1	0	2	1	0	**11**
Season								
spring	1	3	2	2	1	1	1	**11**
summer	8	4	0	0	0	1	3	**16**
autumn	4	2	1	0	0	0	4	**11**
winter	4	4	5	1	2	0	2	**18**
Period								
until 2006	0	4	2	1	1	0	4	**12**
2007–2013	8	3	4	0	0	0	5	**20**
2014–2019	9	6	2	2	2	2	1	**24**
Territorial/Floaters								
Floaters	15	7	5	3	2	2	10	**44**
Territorial	2	6	3	0	1	0	0	**12**
Tagged/Non-tagged								
Transmitter-tagged	8	7	3	0	0	2	3	**23**
Non tagged	9	6	5	3	3	0	7	**33**
Country								
Bulgaria	13	12	8	3	3	2	7	**48**
Turkey	3	1	0	0	0	0	2	**6**
Syria	1	0	0	0	0	0	0	**1**
Sudan	0	0	0	0	0	0	1	1
Total	17	13	8	3	3	2	10	56

Season-related mortality

The maximum number of incidents occurred during winter and summer *(Table 1)*. No significant differences were found between the cause of death and seasonality (exact P = 0.18). The majority of the traumas (detected in live and dead birds at discovery) in juveniles and immatures were recorded in the autumn season. On the contrary, we registered the majority of incidents with adult birds in the summer.

Temporal changes in mortality

The study found a relationship between the period of the registered casualties and the main causes identified as factors for the incidents (exact P = 0.04) *(Table 2)*. A statistically significant difference was determined between the period 2007–2013 and the increase of electrocution traumas in EIE.

Mortality in breeding and dispersal areas

The territorial dependence appeared to be an important factor related to circumstances for fatal incidents for the EIE (exact P = 0.07). Floaters were affected with a significantly higher rate by electrocution injuries than territorial ones.

Tagging-devices were found to play no important role in the traumatic injuries (exact P = 0.25). However, a slight increase in the number of electrocution casualties was found for the group of the non-tagged EIE.

Table 2. Ratio of Eastern Imperial Eagle specimens found dead or injured in Bulgaria in relation to the Bulgarian breeding population. Data till 2014 were retrieved from Demerdzhiev, 2015. After 2015 we used unpublished authors data and field observations

2. táblázat Az elpusztultan vagy sérülten megtalált parlagi sasok száma Bulgáriában az országos költő állomány nagyságához viszonyítva

Year	Population size (n) (Number of nesting pairs x 2)	Number of specimens found (n)	Ratio of incidents vs. population size (%)
1992	4	1	25.00
1993	4	1	25.00
1998	12	1	8.33
2001	20	1	5.00
2004	30	7	23.33
2005	28	1	3.57
2008	38	2	5.26
2009	40	3	7.50
2010	36	4	11.11
2011	44	5	11.36
2012	46	5	10.87
2013	50	1	2.00
2014	52	10	19.23
2015	56	5	8.93
2016	56	2	3.57
2017	56	5	8.93
2018	58	1	1.72
2019	62	1	1.61

Discussion

The sustainability of the ecological food systems is highly dependent on the sustainability of the scavenger and raptor populations for maintaining the environmental balance. Unfortunately, growing evidence shows a negative change in the apex scavenger populations worldwide (O'Bryan *et al.* 2019), which become vulnerable with other predatory species due to violent human activities (Santangeli *et al.* 2019). Human disturbance, bad weather or a combination of both were identified as factors causing chick mortality in the threatened EIE in Austria (Wichmann 2011). Although our study did not include mortality at this early stage (chick growing) in the estimations, we found that 71.5% of the mortality cases of the EIE from Bulgaria were also result from human interventions, with the other 5.4% caused by intraspecific aggression and extreme weather. Similar results were found for the threatened

Spanish Imperial Eagle *(Aquila adalberti)*, as well, with the illegal use of poisonous baits and veterinary drugs as main causes for mortality (Ferrer *et al.* 2013, Margalida *et al.* 2017).

The protection of EIE in Bulgaria was directly addressed for the first time in the 1990s (Petrov & Stoychev 2002). The systematic conservation activities, implemented since 2000, have led to increase in the number of pairs and occupied territories. This positive trend appeared to be a consequence as well from both better protection of breeding grounds and some immigration of eagles from adjacent regions (Demerdzhiev *et al.* 2015). The observations on the status of the Bulgarian populations of EIE improved till 2014 (Demerdzhiev *et al.* 2011b, Demerdzhiev *et al.* 2014a, Demerdzhiev *et al.* 2015).

Despite the success of the conservation efforts and the implementation of the European legislation on wildlife protection and regulation on pesticide use in Bulgaria since 2007 (Anonymous 2009, Nikolova *et al.* 2015), our results indicated non-significant decrease in the number of incidents and total mortality rates in eagles. Our data confirmed the previous findings that the most important factor causing the mortality of immature eagles was electrocution (Stoychev *et al.* 2014), accompanied by shooting and poisoning too (Demerdzhiev *et al.* 2014a).

The natal dispersal of EIEs was found to be the most threatened period, as high mortality rates were revealed for the first calendar year birds (Demerdzhiev *et al.* 2015), that increased further for the second and third calendar years (Stoychev *et al.* 2014), while we found significant decrease mortality rates in adults. The main factor for fatal casualties in juvenile eagles was electrocution, followed by unknown causes and poisoning. For the immatures key mortality factor was electrocution, accompanied by shooting and poisoning. Likewise, the main causes for trauma injuries in juvenile and immature eagles from the Bulgarian population were identified by other studies as well (Stoychev *et al.* 2014).

We speculate that adult eagles appeared to be less likely to die from electrocution due to their life experience. By occupying a certain area, they learned to avoid electric poles and landed on trees instead. At the same time, we rarely registered shot adult EIE in their breeding territories as a result of successful long-term awareness raising work. Immature birds that visited different areas within their dispersal period (very often outside Bulgaria) could be shot due to misunderstanding or intentionally, so the work with hunters at these places should be intensified. Poisoning appeared as a threat of equal intensity for all age groups, with the juveniles and immatures being poisoned in the dispersal areas and the adults in the nesting areas. We could assume also that most of the unknown causes of death were probably due to poisoning, however, the late discovery of the body or its remains, prevented us to confirm the cause of dead.

Regarding the Spanish Imperial Eagle, data suggested that electrocution occurred more frequently in autumn and winter (Gonzalez *et al.* 2007). In contrary to these findings, we registered high mortality due to electrocution in summer. Considering the EIE mortality by seasons, it could be pointed out that electrocution was more common in summer for floaters, which used to concentrate in Temporal Settlement Areas such as Sliven field, appeared to be attracted by abundant prey in this season, mostly European Souslik *(Spermophilus citellus),* and due to lack of tall trees they often perched on the poles where got injured. Winter and spring were suggested as the seasons with more frequent poisoning cases of Spanish Imperial Eagles (Thirgood *et al.* 2000), related to the illegal control on other predator species

(Gonzalez *et al.* 2007). For EIE, we found that the highest number of registered poisoning incidents occurred in winter and summer, when EIE become attracted by poisonous baits, which we hypothesized to be intended for wolves and jackals (winter), or when baits for rodents were dispersed (summer). This hypothesis was based only on field observations as we lacked sufficient evidence from toxicological analyses. The shooting incidents were mainly detected in winter, due to the permitted active hunting in this season, which imposed the necessity for more intensive conservation work with hunters during winter. To summarize, the winter period was generally associated with the highest mortality rates among EIE, due to the difficulties in finding food and deteriorating weather conditions and other mortality factors with anthropogenic character occurring then.

Despite the numerous conservation activities undertaken during the second and third periods of the study, the number of EIE found dead increased. In consistence with previous studies, our results showed that till 2006 the fatal cases due to electrocution were 0%, in the period 2007–2013 they increased to 14.30% and in 2014–2019 they reached 16.10%. This contradiction is due to the lack of systematic studies until 2004 on bird mortality caused by the hazardous power grid (Demerdzhiev *et al.* 2009), as well as to more precise method for determining mortality factors by marking eagles with transmitters (Stoychev *et al.* 2014). At the same time, more than 3000 hazardous electric poles in the territories of the Bulgarian population of the species were modified to bird-friendly design to prevent the casualties (Demerdzhiev *et al.* 2014a, authors' data). Explanation of increased mortality due to electrocution in the third period could be found in expansion of the population and colonization of new breeding territories mainly by unexperienced immature birds and also by probably increased number of the floaters, which made the risk of incidents by unsecured poles higher. As a measure for reducing the hazard, the modification of risky electric poles in the new nesting areas and new dispersal sites should be continued. Regarding the poisoning incidents, we found no differences till 2014. During the next few years from 2014–2019, an increase in the number of registered poisoning cases was documented. The role of anthropogenic factors as shooting and human disturbance, which pose a threat for the EIE populations was confirmed as well (Schmidt & Horal 2018), despite the intensive conservative measures in the period 1998–2014 (Demerdzhiev *et al.* 2015).

When compared with the population size, the noted increase in the total number of incidents in the second and third periods was accompanied by a significant increase in the number of the EIE population during the same time. Thus, registered EIE casualties per year represented a small share compared to the total population size *(Table 2)*.

Data for the mortality rates estimations were obtained from both transmitter-tagged and non-tagged birds, as Gonzalez *et al.* (2007) suggested that records of individuals from both groups provided similar information on the frequency of the causes of mortality.

Mortality due to electrocution had been estimated through specific methodology of studying this factor based on regular inspections of hazardous electric poles when the injured eagles were easily found. Data from the 27 satellite-tracked EIE unambiguously proved electrocution as a major factor in floater mortality (Stoychev *et al.* 2014).

It should be noted that certain difference in mortality between territorial birds and floaters existed. The study found that nesting birds died more often from poisoning and less often from electrocution, while in floaters mortality due to electrocution was more frequent than poisoning. The last fact could be explained by the lack of experience of the floaters and probably their wider distribution. Together with young birds, in their dispersal areas, they used to land often on electric poles and become casualties of electrocution. At the same time, the breeding EIE used to stay within the familiar nesting territories, while the floaters explored many different places, thus, increasing the risk to get injured or die from any of the anthropogenic factors.

Understanding on the nature of poisoning in wildlife is provided by a number of studies on the human-wildlife conflict (Margalida *et al.* 2014, Schmidt & Horal 2018). The unstable coexistence of carnivores and birds of prey with game and livestock, resulting in damages in human property and safety, was stated to be a motive for a hostile attitude towards raptors (Brochet *et al.* 2019, BirdLife International 2020), scavengers (Plaza *et al.* 2019), and use of poisonous baits to control livestock predators like wolves (Petrov *et al.* 1996, Peterson *et al.* 2010). Thus, secondary or malicious animal poisoning was recorded to pose an enormous threat for the stability of the Spanish Imperial Eagle populations with estimation of 54% mortality cases in adult birds since 1990, due to increased use of poison in hunting areas (Ferrer & Penteriani 2008), and illegal practices related to use of poisonous baits in EIE (Horváth *et al.* 2016, Chiaria *et al.* 2017). The fatal incidents with the EIEs in Bulgaria were associated also with the use of poisonous baits against the Grey Wolf *(Canis lupus)* population, but affecting also raptors and scavengers. In fact, data reported no presence of the grey wolf in territories, co-inhabited by the eagle pairs, till 2014 (Anonymous 2013). On the other side, evidences for the presence of several wolf packs were received through field observations (authors' data) after 2014. Indirectly, the role of poisonous baits for wolves as a mortality factor for the eagles was confirmed due to the change in the land use in agriculture (Lazarova & Balieva 2020) and signals from farmers for wolf attacks on their herds.

Reasons behind poisoning in wildlife were investigated in a range of European countries like Belgium, France, Greece, Italy and Spain. Data over a ten-year period reported that deliberate primary or secondary poisonings, mainly in birds, including raptors, were of a concern to all countries. Analysis showed that in poisoning incidents with fatal consequences among the frequently identified agents were metals (particularly lead arising from sporting/hunting activities) and pesticides (mainly anticholinesterases and anticoagulants) (Guitart *et al.* 2010). Poisoning was the most significant mortality factor for EIE in Hungary (Deák *et al.* 2020b). Regarding scavenger species, like vultures, it was found that secondary poisoning due to human-wildlife conflict exposed the birds to the toxic effect of pesticides (Plaza *et al.* 2019) and in long-term resulted in 60% of all registered vulture poisoning events in the southern Balkan Peninsula during the last 36 years. Most frequently used substances in poisonous baits were strychnine, carbamate, and organophosphorus compounds (Parvanov *et al.* 2018). Moreover, highly toxic pesticides were detected in intentional poisoning of domestic animals and wildlife in Spain (aldicarb, carbofuran and strychnine) (Martínez-Haro *et al.* 2008), Italy (insecticides – anticholinesterases, rodenticides, molluscicides and herbicides) (Chiaria *et al.* 2017), Tunisia (carbamates, organophosphates and rodenticides-anticoagulants) (Lahmar *et al.* 2019) and Hungary (carbofuran, brodifacoum, terbufos and diazinon) (Deák *et al.* 2020a). In correspondence with these findings, our results showed that laboratory confirmed intoxications in EIEs from the study were caused by anticholinesterase's inhibitors such as organophosphate and carbamate insecticides.

The extremely high number of poisoning incidents in raptors and scavengers registered worldwide in the last decades redirected the conservation efforts towards improvement of the detection efficiency of poisonous baits. In Europe, poison-and carcass searching dog units were established and joint forces of NGOs, governmental officers, wildlife veterinarians, police and prosecutors were set to improve detection, reporting, investigation and persecution of illegal poisoning in vulnerable species like the EIE (Petrov *et al.* 1996, Horváth *et al.* 2018b).

Conclusion

EIEs are using a larger range and visiting diverse areas during their wanderings, while territorial birds are attached to a specific area, therefore different mortality factors are affecting these two groups, which require different conservation approaches. Among the main mortality causes for the eagles appeared to be electrocution and poisoning, despite the continuous joint efforts of conservation organisations in the last two decades.

Modification of the hazardous electric poles should be considered the main conservation priority in both natal and species dispersal areas. Anti-poisoning actions should be considered at a first priority step in EIE breeding territories and as a second priority in dispersal areas outside Bulgaria. Moreover, international pressure and support on these threats can result in better conservation applicability, especially outside Bulgaria. Least, but importantly not last, it is necessary to intensify the work with local institutions and stakeholders such as hunters, farmers, etc., who have a crucial role in the long-term survival of the EIE in Bulgaria.

Acknowledgements

These results were achieved with the support of a foundation EuroNatur – Germany, Enterprise for Management of Environment Protection Activities – MOEW, Bulgaria, LIFE14NAT/BG/001119, LIFE12NAT/BG/000572, LIFE07 NAT/BG/000068, LIFE14NAT/BG/001119, LIFE12NAT/BG/000572, LIFE07 NAT/BG/000068. The authors express their gratitude to all those who co-operated and contributed to field data observations, conservation activities, treatment and rehabilitation of injured EIE: Svetoslav Spasov, Ivaylo Angelov, Nikolai Terziev, Tzeno Petrov, Petar Iankov, Vladimir Trifonov, Nedko Nedyalkov, Georgi Georgiev, Dimitar Plachiysky, Georgi Popgeorgiev, Georgi Gerdzhikov, Vera Dyulgerska, Vladimir Dobrev, Vanyo Angelov, Alexander Georgiev, Vasilena Georgieva, Valentin Velev, Volen Arkumarev, Konstantin Dichev, Dimitar Popov, Iliyan Stoev, Dimitar Marinov, Konstantin Popov, Hristina Klisurova, Ivelin Ivanov, Simeon Marin, Petya Karpuzova, Dobromir Dobrinov, Stefka Dimitrova, Galina Simeonova, Tsvetan Chaprazov.

References

Anonymous 1979. Council of Europe, Convention on the Conservation of European Wildlife and Natural Habitats, Appendix II – strictly protected fauna species, European Treaty Series – No. 104. – Bern Convention, https://rm.coe.int/1680078af f

Anonymous 2002. Biodiversity Act. State Gazette 77/09.08.2002. – last amended State Gazette 98/27.11.2018 (BG)

Anonymous 2009. Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds. 26.1.2010. – Official Journal of the European Union L 20/7

Anonymous 2013. Information systems for protected areas from the ecological network NATURA 2000. Ministry of Environment and Water. (BG) – http://natura2000.moew.government.bg/

Anonymous 2019. Convention On International Trade In Endangered Species Of Wild Fauna And Flora, Appendices I, II and III valid from 26 November 2019 Interpretation. – https://cites.org/sites/default/files/eng/app/2019/E-Appendices-2019-11-26.pdf

BirdLife International 2020. *Aquila heliaca* (amended version of 2017 assessment). – The IUCN Red List of Threatened Species DOI: 10.2305/IUCN.UK.2019-3.RLTS.T22696048A155464885.en

BirdLife International Species factsheet 2020. *Aquila heliaca*. – http://www.birdlife.org on 20/01/2020

Brochet, A., Van Den Bossche, W., Jones, V. R., Arnardottir, H., Damoc, D., Demko, M., Driessens, G., Flensted, K., Gerber, M., Ghasabyan, M., Gradinarov, D., Hansen, J., Horváth, H., Karlonas, M., Krogulec, J., Kuzmenko, T., Lachman, L., Lehtiniemi, T., Lorgé, P., Lötberg, U., Lusby, J., Ottens, G., Paquet, J., Rukhaia, A., Schmidt, M., Shimmings, P., Stipnieks, A., Sultanov, E., Vermouzek, Z., Vintchevski, A., Volke, V., Willi, G. & Butchart, S. H. M. 2019. Illegal killing and taking of birds in Europe outside the Mediterranean: assessing the scope and scale of a complex issue. – Bird Conservation International 29(1): 10–40. DOI: 10.1017/S0959270917000533

Brown, J. L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. – Wilson Bulletin 81(3): 293–329.

Chiaria, M., Cortinovis, C., Vitale, N., Zanoni, M., Faggionato, E., Biancardi, A. & Caloni, F. 2017. Pesticide incidence in poisoned baits: A 10-year report. – Science of the Total Environment 601–602: 285–292. DOI: 10.1016/j.scitotenv.2017.05.158

Deák, G., Juhász, T., Árvay, M. & Horváth, M. 2020a Vadon élő állatokat érintő mérgezéses esetek alakulása Magyarországon 2017 és 2019 között [The situation of wild animal poisoning in Hungary between 2017 and 2019.]. – Heliaca 16: 60–64. DOI: 10.13140/RG.2.2.22228.14726 (in Hungarian with English Summary)

Deák, G., Fatér, I., Juhász, T. & Horváth, M. 2020b Parlagi sasok *(Aquila heliaca)* pusztulási és kézre kerülési okainak alakulása Magyarországon 2010 és 2019 között [Causes of death, injuries and diseases of Eastern Imperial Eagles *(Aquila heliaca)* in Hungary between 2010 and 2019]. – Heliaca 16: 114–117. DOI: 10.13140/RG.2.2.14678.40006 (in Hungarian with English Summary)

Demerdzhiev, D. Stoychev, S., Petrov, Tz., Angelov, I. & Nedyalkov, N. 2009. Impact of power lines on bird mortality in Southern Bulgaria. – Acta Zoologica Bulgarica 61(2): 175–183.

Demerdzhiev, D., Horváth, M., Kovács, A., Stoychev, S. & Karyakin, I. 2011a Status and population trend of the Eastern Imperial Eagle *(Aquila heliaca)* in Europe in the period 2000–2010. – Acta Zoologica Bulgarica Suppl. 3: 5–14.

Demerdzhiev, D. A., Gradev, G. Zh., Stoychev, S. A., Ivanov, I., Petrov, Tz. & Marin, S. A. 2011b Increase of the population of the Eastern Imperial Eagle *(Aquila heliaca)* in Bulgaria. – Acta Zoologica Bulgarica Suppl. 3: 41–54.

Demerdzhiev, D. 2014. Factors influencing bird mortality caused by power lines within Special Protected Areas and undertaken conservation efforts. – Acta Zoologica Bulgarica 66(2): 411–423.

Demerdzhiev, D., Stoychev, S., Dobrev, D., Spasov, S. & Terziev, N. 2014a Conservation measures undertaken to improve the population status of Eastern Imperial Eagle *(Aquila heliaca)* in Bulgaria. – Slovak Raptor Journal 8(1): 27–39. DOI: 10.2478/srj-2014-0007.

Demerdzhiev, D., Dobrev, D., Isfendiyaroğlu, S., Boev, Z., Stoychev, S., Terziev, N. & Spasov, S. 2014b Distribution, abundance, breeding parameters, threats and prey preferences ofthe Eastern Imperial Eagle *(Aquila heliaca)* in European Turkey. – Slovak Raptor Journal 8(1): 17–25. DOI: 10.2478/srj-2014-0004.

Demerdzhiev, D., Stoychev, S., Dobrev, D., Spasov, S. & Oppel, St. 2015. Studying the demographic drivers of an increasing Imperial Eagle population to inform conservation management. – Biodiversity and Conservation 24(3): 627–639. DOI: 10.1007/s10531-014-0841-0

Demeter, I., Horváth, M., Nagy, K., Görögh, Z., Tóth, P., Bagyura, J., Solt, S., Kovács, A., Dwyer, J. & Harness, R. 2018. Documenting and reducing avian electrocutions in Hungary: a conservation contribution from citizen scientists. – The Wilson Journal of Ornithology 130(3): 600–614. DOI: 10.1676/17-031.1

Donàzar, J. A., Cortés-Avizanda, A., Fargallo, J. A., Margalida, A., Moleón, M., Morales-Reyes, Z., Moreno-Opo, R., Pérez-García, J. M., Sánchez-Zapata, J. A., Zuberogoitia, I. & Serrano, D. 2016. Roles of raptors in a changing world: from flagships to providers of key ecosystem services. – Ardeola 63(1): 181–234. DOI: 10.13157/arla.63.1.2016.rp8

Duriez, O., Descaves, S., Gallais, R., Neouze, R., Fluhr, J. & Decante, F. 2019. Vultures attacking livestock: a problem of vulture behavioural change or farmers' perception? – Bird Conservation International 29(3): 437–453. DOI: 10.1017/S0959270918000345

Dwyer, J. F., Kratz, G. E., Harness, R. E. & Little, S. S. 2015. Critical dimensions of raptors on electric utility poles. – Journal of Raptor Research 49(2): 210–216. DOI: 10.3356/0892-1016-49.2.210

Ferguson-Lees, J. & Christie, D. A. 2001. Raptors of the World. – Houghton Mifflin Company, New York

Ferrer, M. & Penteriani, V. 2008. Non-independence of demographic parameters: positive density-dependent fecundity in eagles. – Journal of Applied Ecology 45(5): 1453–1459. DOI: 10.1111/j.1365-2664.2008.01497.x

Ferrer, M., Newton, I. & Muriel, R. 2013. Rescue of a small declining population of Spanish Imperial Eagles. – Biological Conservation 159: 32–36. DOI: 10.1016/j.biocon.2012.10.011

Forsman, D. 2005. Eastern Imperial Eagle plumages. – Alula 4: 147–152.

Gonzalez, L. M., Margalida, A., Manosa, S., Sanchez, R., Oria, J., Molina, J.´ I., Caldera, J., Aranda, A. & Prad, L. 2007. Causes and spatio-temporal variations of non-natural mortality in the Vulnerable Spanish Imperial Eagle *Aquila adalberti* during a recovery period. – Oryx 41(4): 495–502. DOI: 10.1017/S0030605307414119

Gradev, G., Matarranz, V., Dobreva, E., Popov, D., Ivanov, I., Klisurov, I., Kmetova, E. & Vasilakis, D. 2011. First results of the tracking of an Eastern Imperial Eagle *(Aquila heliaca)* tagged with a GPS/ GSM Transmitter in Bulgaria. – Acta Zoologica Bulgarica Suppl. 3: 15–20.

Guitart, R., Sachana, M., Caloni, F., Croubels, S., Vandenbroucke, V. & Berny, P. 2010. Animal poisoning in Europe. Part 3. Wildlife. – The Veterinary Journal 183(3): 260–265. DOI: 10.1016/j.tvjl.2009.03.033

Horváth, M., Szitta, T., Firmánszky, G., Solti, B., Kovács, A. & Moskát, C. 2010. Spatial variation in prey composition and its possible effect on reproductive success in an expanding Eastern Imperial Eagle *(Aquila heliaca)* population. – Acta Zoologica Academiae Scientiarum Hungaricae 56(2): 187–200.

Horváth, M., Demeter, I., Fatér, I., Firmánszky, G., Kleszó, A., Kovács, A., Szitta, T., Tóth, I., Zalai, T. & Bagyura, J. 2011. Population dynamics of the Imperial Eagle *(Aquila heliaca)* in Hungary between 2001 and 2009. – Acta Zoologica Bulgarica Suppl. 3: 61–70.

Horváth, M., Bagyura, J., Deák, G., Fatér, I., Firmánszky, G., Horváth, Á., Juhász, T., Klébert, A., Lóránt, M., Németh, T., Pongrácz, Á., Prommer, M., Serfőző, J., Tóth, I. & Váczi, M. 2016. A parlagisas-védelmi és mérgezés-megelőzési munkacsoportok 2014. évi beszámolója [Annual Report of the Hungarian Imperial Eagle and Anti-poisoning Working Groups – 2014]. – Heliaca 12: 6–11. DOI: 10.13140/RG.2.2.31092.37768 (in Hungarian with English Summary)

Horváth, M., Solti, B., Fatér, I., Juhász, T., Haraszthy, L., Szitta, T., Ballók, Zs. & Pásztory-Kovács, Sz. 2018a Temporal changes in the diet composition of the Eastern Imperial Eagle *(Aquila heliaca)* in Hungary. – Ornis Hungarica 26(1): 1–26. DOI: 10.1515/orhu-2018-0001

Horváth, M., Deák, G., Fatér, I., Juhász, T., Bánfi, P., Horváth, Á., Kiss, Á., Kovács, G., Pongrácz, Á. & Sós, E. 2018b A HELICON LIFE projekt eredményei a mérgezésmegelőzés és a parlagisas-védelem területén 2012 és 2016 között [The results of the HELICON LIFE project in the prevention of poisoning and in the conservation of Eastern Imperial Eagle between 2012 and 2016]. – Heliaca 13: 100–105. DOI: 10.13140/RG.2.2.23314.89286 (in Hungarian with English Summary)

Hristovich, G. 1890. Materials for studying the Fauna of Bulgaria. – Collection of Folklore 2: 185–225.

Katzner, T., Bragin, E., Knick, S. & Smith, A. 2006. Spatial structure in the diet of Imperial Eagles *Aquila heliaca* in Kazakhstan. – Journal of Avian Biology 37(6): 594–600. DOI: 10.1111/j.2006.0908-8857.03617.x

Kirov, V., Kostov, I., Kirova, S. & Balieva, G. 2019. Contemporary development of legislation on criminalization of animal cruelty. – International Journal Scientific Papers 32(1): 201–206.

Kovács, A., Demeter, I., Horváth, M., Fülöp, Gy., Frank, T. & Szilvácsku, Zs. 2005. Imperial Eagle Management Guidelines. – MME / BirdLife Hungary, Budapest

Lahmar, R., Berny, P., Mahjoub, T. & Ben Youssef, S. 2019. Animal pesticide poisoning in Tunisia. – Frontiers in Veterinary Science 6: 369. DOI: 10.3389/fvets.2019.00369.

Lazarova, I. & Balieva, G. 2020. Pesticide agents as factors for wild animals poisoning. – Scientific reports from the 12th scientific conference "Climate changes – a global threat for the food chain". Edited by the Risk Assessment Centre on Food Chain, Bulgarian Focal Point of EFSA, pp. 18–40. DOI: 10.5281/zenodo.3647855 (BG)

Margalida, A., Campión, D. & Donázar, J. A. 2014. Vultures vs livestock: conservation relationships in an emerging conflict between humans and wildlife. – Oryx 48(2): 172–176. DOI: 10.1017/S0030605312000889

Margalida, A., Colomer, M. À., Sánchez, R., Sánchez, F. J., Oria, J. & González, L. M. 2017. Behavioral evidence of hunting and foraging techniques by a top predator suggests the importance of scavenging for preadults. – Ecology and Evolution 7(12): 4192–4199. DOI: 10.1002/ece3.2944

Marin, S., Ivanov, I., Georgiev, D. & Boev, Z. 2004. On the food of the Imperial Eagle *Aquila heliaca* on Sakar Mountain and Dervent Heights, Bulgaria. – In: Chancellor, R. & Meyburg, B-U. (eds.) Raptors Worldwide, WWGBP/MME, pp. 589–592.

Martínez-Haro, M., Mateo, R., Guitart, R., Soler-Rodríguez, F., Pérez-López, M., María-Mojica, P. & García-Fernández, A. J. 2008. Relationship of the toxicity of pesticide formulations and their commercial restrictions with the frequency of animal poisonings. – Ecotoxicology and Environmental Safety 69(3): 396–402. DOI: 10.1016/j.ecoenv.2007.05.006

McClure, Ch. J. W., Westrip, J. R. S., Johnson, J. A., Schulwitz, S. E., Virani, M. Z., Davies, R., Symes, A., Wheatley, H., Thorstrom, R., Amar, A., Buij, R., Jones, V. R., Williams, N. P., Buechley, E. R. & Butchart, S. H. M. 2018. State of the world's raptors: Distributions, threats, and conservation recommendations. – Biological Conservation 227: 390–402. DOI: 10.1016/j.biocon.2018.08.012

Meyburg, B-U. & Kirwan, G. M. 2020. Imperial Eagle *(Aquila heliaca),* version 1.0. – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds.) Birds of the World – Cornell Lab of Ornithology, Ithaca, NY, USA DOI: 10.2173/bow.impeag1.01

Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behaviour. – Biological Reviews 67(2): 129–173. DOI: 10.1111/j.1469-185X.1992.tb01017.x

Nikolova, G. 2010. Bulgarian contribution for saving the wildlife biodiversity – legislative basis and organizational structures. – 17th Scientific Conference with International Participation "Animal Protection and Welfare", Conference Proceedings, edited by the Conference Scientific Committee, University of Veterinary and Pharmaceutical Sciences, Brno, Czech Republic, pp. 178–183.

Nikolova, G., Kostov, I. & Baliev, S. 2015. Legislative regulatory mechanisms for reducing the negative effects of pesticides on public health. – Reports from the 8th Scientific conference of the Bulgarian Focal Point of European Food Safety Authority (EFSA). Edited by the Risk Assessment Center, Sofia, Bulgaria (BG) DOI: 10.5281/zenodo.4061734

O'Bryan, Ch. J., Holden, M. H. & Watson, J. E. M. 2019. The mesoscavenger release hypothesis and implications for ecosystem and human well-being. – Ecology Letters 22(9): 1340–1348. DOI: 10.1111/ele.13288

Pantović, U. & Andevski, J. 2018. Review of the problem of poison use and vulture poisoning in the Balkan Peninsula. – Vulture Conservation Foundation, Netherlands

Parvanov, D., Stoynov, E., Vangelova, N., Peshev, H., Grozdanov, A., Delov, V. & Iliev, Y. 2018. Vulture mortality resulting from illegal poisoning in the southern Balkan Peninsula. – Environmental Science and Pollution Research 25: 1706–1712. DOI: 10.1007/s11356-017-0594-x

Patev, P. 1950. Birds of Bulgaria. – BAS, Sofia (in Bulgarian)

Penteriani, V., Otalora, F. & Ferrer, M. 2005. Floater survival affects population persistence. The role of prey availability and environmental stochasticity. – Oikos 108(3): 523–534. DOI: 10.1111/j.0030-1299.2005.13514.x

Penteriani, V., Otalora, F. & Ferrer, M. 2006. Floater dynamics can explain positive patterns of density dependence fecundity in animal populations. – American Naturalist 168(5): 697–703. DOI: 10.2307/3873463

Penteriani, V., Otalora, F. & Ferrer, M. 2008. Floater mortality within settlement areas can explain the Allee effect in breeding populations. – Ecological Modelling 213(1): 98–104. DOI: 10.1016/j.ecolmodel.2007.11.009

Peterson, M. N., Birckhead, J. L., Leong, K., Peterson, M. J. & Peterson, T. R. 2010. Rearticulating the myth of human-wildlife conflict. – Conservation Letters 3(2): 74–82. DOI: 10.1111/j.1755-263X.2010.00099.x

Petrov, Tz., Iankov, P., Darakchiev, A., Nikolov, H., Michev, T., Profirov, L. & Milchev, B. 1996. Status of the Imperial Eagle *Aquila heliaca* in Bulgaria in the period between 1890 and 1993. – In: Meyburg, B-U. & Chancellor, R. D. (eds.) Eagle Studies. – World Working Group on Birds of Prey (WWGBP), Berlin, London & Paris, pp. 429–434.

Petrov, T. & Stoychev, S. 2002. National action plan for the Imperial Eagle *(A. heliaca)*. – In: Bulgarian Society for Protection of Birds, Ministry of Environment and Water (eds.) Globally threatened birds in Bulgaria: national action plans for conservation Part 1. – BSPB-MOSV, Sofia, pp. 132–161.

Plaza, P. I., Martínez-López, E. &. Lambertucci, S. A. 2019. The perfect threat: Pesticides and vultures. – Science of the Total Environment 687: 1207–1218. DOI: 10.1016/j.scitotenv.2019.06.160

Santangeli, A., Girardello, M., Buechley, E. R., Eklund, J. & Phipps, L. W. 2019. Navigating spaces for implementing raptor research and conservation under varying levels of violence and governance in the Global South. – Biological Conservation 239: 108212, 1–9. DOI:10.1016/j.biocon.2019.108212

Schmidt, M. & Horal, D. 2018. Eastern Imperial Eagle *(Aquila heliaca)* on its most north-west distribution edge. – Raptors Conservation Suppl. 1: 102–103. DOI: 10.19074/1814-8654

Smart, J., Amar, A., Sim, I. M. W., Etheridge, B., Cameron, D., Christie, G. & Wilson, J. D. 2010. Illegal killing slows population recovery of a re-introduced raptor of high conservation concern – The Red Kite *Milvus milvus*. – Biological Conservation 143: 1278–1286. DOI: 10.1016/j.biocon.2010.03.002

Stoychev, S., Demerdzhiev, D., Spasov, S., Meyburg, B-U. & Dobrev, D. 2014. Survival rate and mortality of juvenile and immature Eastern Imperial Eagles *(Aquila heliaca)* from Bulgaria studied by satellite telemetry. – Slovak Raptor Journal 8(1): 53–60. DOI: 10.2478/srj-201 4-0008.

Thiollay, J. M. 1994. Family Accipitridae (Hawks and Eagles). – In: del Hoyo, J., Elliot, A. & Sargatal, J. (eds.) Handbook of the Birds of the World, Vol. 2. New World Vultures to Guineafowl. – Lynx Edicions, Barcelona

Thirgood, S. J., Redpath, S. M., Rothery, P. & Aebischer, N. J. 2000. Raptor predation and population limitation in red grouse. – Journal of Animal Ecology 69(3): 504–516. DOI: 10.1046/j.1365-2656.2000.00413.x

Vili, N., Szabó, K., Kovács, Sz., Kabai, P. Kalmár, L. & Horváth, M. 2013. High turnover rate revealed by non-invasive genetic analyses in an expanding Eastern Imperial Eagle population. – Acta Zoologica Academiae Scientiarum Hungaricae 59(3): 279–295.

Wichmann, G. 2011. The situation of the Eastern Imperial Eagle *Aquila heliaca* in Austria. – Acta Zoologica Bulgarica Suppl. 3: 37–40.

Ornis Hungarica 2020. 28(2): 135–145.
DOI: 10.2478/orhu-2020-0022

Does human hair attract or deter potential ground nest predators?

Jenő J. Purger[1,2*], Zsófia Szegleti[1] & Dávid Szép[1]

Received: June 23, 2020 – Revised: August 06, 2020 – Accepted: August 08, 2020

Purger, J. J., Szegleti, Zs. & Szép, D. 2020. Does human hair attract or deter potential ground nest predators? – Ornis Hungarica 28(2): 135–145. DOI: 10.2478/orhu-2020-0022

Abstract The nests of rare and threatened bird and reptile species that breed on the ground are often attempted to be protected from predators with fences, grids, and various repellent materials. Results of some experiments refer to the repellent function of human scent, whereas others suggest that it has an attractive role. We aimed to investigate how effectively ground nests can be protected from predators if human hair is placed around nests. We performed the experiment in a riverine oak-elm-ash forest using 90 artificial nests, each with 1 quail and 1 plasticine egg: 30 nests were protected with a game fence, 30 nests were surrounded with human hair and 30 nests were unprotected (control). During the 24 days, predators damaged 23% of the nests protected by a game fence, 40% of unprotected nests and 47% of the nests surrounded with hair. The daily survival rate of quail eggs in nests protected with a game fence was significantly higher than the ones in the nests surrounded with human hair. Only 18% of the quail eggs and 36% of plasticine eggs were damaged. Such difference can be explained by the fact that small-bodied birds and mammals could pass through the game fence and left traces on plasticine eggs but they were unable to crack the shell of quail eggs. Within the game fence, denser vegetation can provide better nesting conditions and result in greater breeding success. The repellent role of human hair has not been proved, on the contrary, in some cases we have observed signs of its attractant role, such as small-bodied birds took hair away for nest building.

Keywords: birds, game fence, human scent, predation, repellent

Összefoglalás A talajon költő ritka és veszélyeztetett madár- és hüllőfajok fészkeit gyakran kerítésekkel, rácsokkal és különböző repellens anyagokkal próbálják megvédeni a predátoroktól. Egyes kísérletek eredményei az emberszag repellens, mások attraktáns funkciójára utalnak. Célunk az volt, hogy megvizsgáljuk, a talajfészkek mennyire hatékonyan védhetők a predátoroktól, ha emberi hajjal szórjuk körbe őket. A kísérletet egy keményfás tölgy-kőris-szil ligeterdőben hajtottuk végre. A vizsgálathoz összesen 90 mesterséges fészket használtunk 1 fürj- és 1 gyurmatojással: 30 fészket vadkerítéssel védtünk, 30 fészket emberi hajjal szórtunk körbe, és 30 fészket nem védtünk (kontroll). A predátorok 24 nap alatt a vadkerítéssel védett fészkek 23%-át, a nem védett fészkek 40%-át és a hajjal körbeszórt fészkek 47%-át fedezték fel és károsították a tojásokat. A vadkerítéssel védett fészkekben a fürjtojások napi túlélési rátája szignifikánsan magasabb volt, mint a hajjal körbeszórt fészkekben lévőké. A fürjtojások csak 18%-a, míg a gyurmatojások 36%-a sérült. Ez a különbség azzal magyarázható, hogy a kis testű madarak és emlősök átjuthattak a vadkerítésen és nyomokat hagytak a gyurmatojásokon, de nem tudták feltörni a fürjtojások héját. A vadkerítésen belül a sűrűbb növényzet jobb fészkelési feltételeket biztosíthat és nagyobb költési sikert eredményezhet. Az emberi haj reppellens szerepét nem bizonyítottuk, inkább bizonyos esetekben attraktáns szerepére utaló jeleket tapasztaltunk, például a kis testű madarak elhordták a kihelyezett hajat és fészeképítéshez használták.

Kulcsszavak: madarak, vadkerítés, emberszag, ragadozás, repellens

[1] *Department of Ecology, Institute of Biology, University of Pécs, 7624 Pécs, Ifjúság útja 6., Hungary*
[2] *BioRes Limited Partnership, 7624 Pécs, Barackvirág utca 27., Hungary*
* *corresponding author, e-mail: purgerjj@gmail.com*

Introduction

Breeding success and population dynamics of birds are strongly influenced by the predation of their nests (eggs, nestlings) (e.g. Ricklefs 1969, Martin 1993, 1995). Predation is a selective pressure on species coexistence, habitat selection, and life strategies (Ibáñez-Álamo *et al.* 2015). To maximize their reproductive success, birds have adequate strategies for site selection to protect themselves more effectively against potential nest predators (Fontaine & Martin 2006, LaManna *et al.* 2015). The type of nests can vary considerably because birds can breed in cavities and holes, can make open or closed nests, while some species use nests of other species or just lay their eggs on the ground (e.g. Collias & Collias 1984, Mainwaring *et al.* 2014). Bird species that do not build a nest with such behaviour do not attract the attention of potential predators to themselves or the nest (Moreno 2012). The identification of nest predators and environmental factors associated with predation is essential to understand the reproductive ecology of birds, conservation of endangered bird species and the management of habitats (Lyons *et al.* 2015, Bu *et al.* 2019).

Ground nesting bird species hide their nests well, their eggs and the plumage of female camouflage into the environment (Haskell 1996, Albrecht & Klvaňa 2004). However, they are also sensitive to nest predation, as their nests are easily accessible for both terrestrial and aerial predators (Ricklefs 1969, Collias & Collias 1984). Birds are visually oriented predators, which can rob ground nests and also nests in bushes and trees (Rangen *et al.* 2000). Unlike birds, mammals rely not only on their visual sense but also on their sense of smell (Wyatt 2014). Many of them are also active at night and, as a result, respond more strongly to scent (Storaas 1988).

The populations of ground-nesting bird species have a declining trend worldwide, partly due to nest predation (Isaksson *et al*. 2007). This negative trend can be mitigated by predator control or by protecting the nests. The regulation of the number of predators by lethal methods is objectionable from the aspects of ethics and conservation impact (e.g. Macdonald & Baker 2004, Latham *et al.* 2019). Therefore, several non-lethal techniques have been developed to increase the breeding success of birds and to mitigate the damage caused by potential nest predators (Harriman *et al.* 2007). For example, fences (e.g. Fitzwater 1972, Hayward & Kerley 2009), electric fences (e.g. Hygnstrom & Craven 1988, Curtis *et al.* 1994), and various alarm substances so-called repellents (e.g. Andelt *et al.* 1994, Milunas *et al.* 1994, Belant *et al.* 1998, Macdonald & Baker 2004, Ward & Williams 2010, Miller *et al.* 2014) have long been used to prevent damage. These methods can be used to protect ground-nesting birds and also turtle nests (e.g. Cox *et al.* 2004, Düttmann *et al.* 2007, Harriman *et al.* 2007, Vilardell *et al.* 2008, Kurz *et al.* 2011).

Artificial nests and clutches have long been used to understand predation events (e.g. Major & Kendal 1996, Bateman *et al.* 2017). Apart from its weaknesses, the method has many advantages, such as its ability to test the effectiveness of certain treatments (Báldi 1999, Moore & Robinson 2004). The effectiveness of methods used to protect birds' nests can also be tested without disturbing the birds. Indeed, in experiments with real nests it is a question how often we should check nests to avoid exposing birds to disturbance or to draw the attention of predators that rely on their vision or their smell in searching for prey (Whelan *et* *al.* 1994, Harriman *et al.* 2007, Kurucz *et al.* 2015). Some studies prove that frequent check attracts potential nest predators (e.g. Vacca & Handel 1988, Hockin *et al.* 1992, Bolduc & Guillemette 2003, Beale & Monaghan 2004, Medeiros *et al.* 2007), but some results suggest that certain scents can also keep unwanted visitors away (Götmark 1992, Ibáñez-Álamo *et al.* 2015). Some studies suggest that human odour (sweat, urine and hair) can also provide effective protection against predators (Rosell & Czech 2000, Harriman *et al.* 2007). The methods used to control wildlife damage can also be used to protect the nests of ground-nesting bird species, but under certain conditions their effectiveness should be tested by using artificial nests.

Our study aimed to explore how effectively the nests of ground-nesting bird species can be protected by a game fence and by surrounding them by human hair. We wanted to analyse separately the predation of quail eggs, which model the clutch of medium-bodied birds, and plasticine eggs, which may only be suitable for studying the nest predation of small-bodied birds.

Material and methods

Study area

The study was carried out in Duna-Drava National Park (DDNP), 8 km west from the city Barcs, in a riverine oak-elm-ash forest next to the Old-Drava oxbow (Csete & Purger 2019) *(Figure 1)*.

To increase shrub layer diversity and to protect plants from grazing by game, DDNP staff designated 15 plots (20×20-meter squares) in the forest patch in the fall of 2015, and fenced them with a game fence *(Figure 1)*. The shrub layer of the fenced areas consisted almost exclusively of red dogwood *(Cornus sanguinea)*, therefore some clearings were made and then tatarian maple *(Acer tataricum)*, European spindle *(Euonymus europaeus)*, European crab apple *(Malus sylvestris)*, wild pear *(Pyrus pyraster)* and European hornbeam *(Carpinus betulus)* were planted instead. This treatment was repeated in the summer of 2016, in the spring of 2017 when tatarian maple and hornbeam were planted. The fences were made primarily to exclude games, since in this game-rich area Red Deer *(Cervus elaphus)*, Fallow Deer *(Dama dama)* and Roe Deer *(Capreolus capreolus)* can cause severe damage by chewing or biting plants, while Wild Boar *(Sus scrofa)* can cause harm by digging holes. The nests of ground-nesting bird species are threatened by Wild Boar and Red Fox *(Vulpes vulpes)*, Golden Jackal *(Canis aureus)* and Badger *(Meles meles)*, as well as by Otter *(Lutra lutra)* appearing in the nearby oxbow. These larger mammals can be excluded by game fencing. In the forests surrounding the oxbow, Beech Marten *(Martes martes)*, Pine Marten *(Martes foina)* and Wildcat *(Felis silvestis)* occur (Purger 2019) and destroy not only the nests on the ground but also those in the shrub layer or the canopy level.

So far, 127 bird species are known to occur in and around the Old-Drava oxbow near Barcs, of which 68 species have been proven to breed here (Purger & Fenyősi 2019). From these, only 11 species breed on the ground or in shrubs close to the ground. Among the

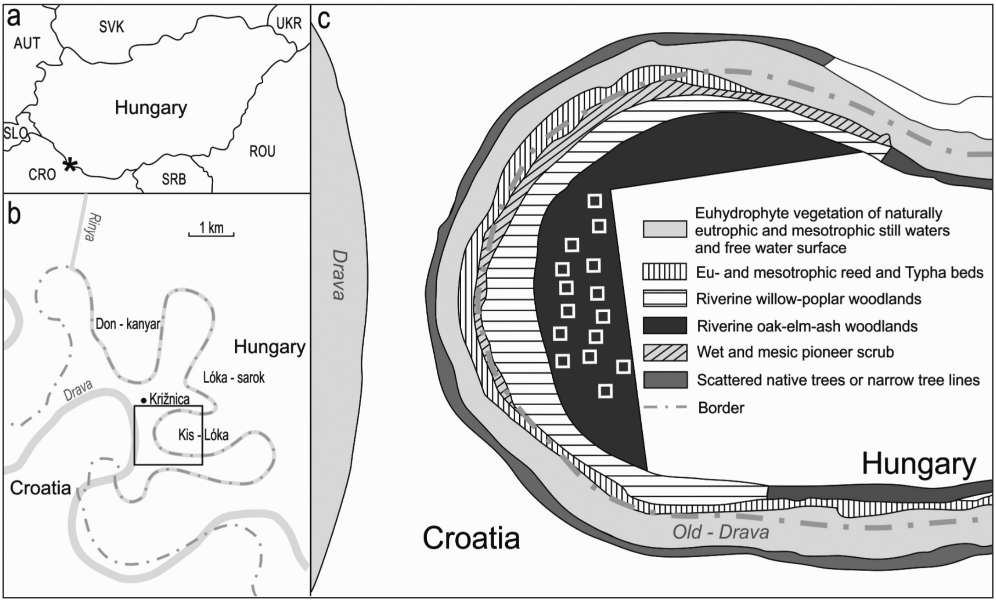


Figure 1. The study was carried out in the south-western part of Hungary (black asterix) in close proximity to the Hungarian-Croatian state border (a), in a patch of hardwood riverine oak-elm-ash forest on the left bank of the Old-Drava oxbow near Barcs (b) (c), where the 15 white squares show the location of the game fences

1. ábra A vizsgálat Magyarország délnyugati részén (fekete csillag) a magyar-horvát országhatár közvetlen közelében (a), a Barcsi Ó-Dráva holtág (b) bal partján lévő keményfás tölgy-kőris-szil ligeterdő foltban (c) folyt, ahol a 15 fehér négyzet a vadkerítések elhelyezkedését mutatja

larger species, the Pheasant *(Phasianus colchicus)* and Mallard *(Anas platyrhynchos)*, while among the smaller songbirds, the Eurasian Sylark *(Alauda arvensis)*, the Wood Warbler *(Phylloscopus sibilatrix)*, the Common Chiffchaff *(Phylloscopus collybita)*, the Eurasian Wren *(Troglodytes troglodytes)*, the European Robin *(Erithacus rubecula)*, the Tree Pipit *(Anthus trivialis)*, the White Wagtail *(Motacilla alba)*, the Yellowhammer *(Emberiza citrinella)* and the Corn Bunting *(Emberiza calandra)*, nest in small numbers in the study area or on its edge (Purger & Fenyősi 2019).

Following the preliminary fieldwork, our experiment started on 19 May 2017 and lasted for 24 days. The 90 artificial nests were made in the hardwood riverine oak-elm-ash forest, of which 30 were set within the fenced areas of the forest (originally set to protect plants from grazing by game), 30 nests were surrounded with human hair (repellent) and 30 nests were placed without any protection (control). No nest material was used for the nests, only a quail egg and a plasticine egg of similar size were placed on the leaf-litter, forming the clutch.

Quail eggs along with plasticine eggs coated with liquid rubber (PlastiDip) were stored in a cool, ventilated place for two weeks before use (Purger *et al.* 2012). Before the experiment with the eggs, the people carrying out the work wore sterile rubber gloves and rubbed their hands with leaf-litter at the site. Two nests were randomly placed in two of the four corners of the square in each fenced area *(Figure 1)*. Outside the fence, 2 nests surrounded with human hair and 2 unprotected nests (control) were formed in random order at least 15 meters from the corners. The location of the nests was recorded with a GPS, and it was marked with a yellow 5 cm long tape attached to a nearby branch for easier finding. Checkings were carried out on the third (May 22), sixth (May 25), twelfth (May 31), eighteenth (June 6), and twenty-fourth (June 12) days after launching of the experiment. During the last checking, the remaining eggs and marker strips were collected and removed from the area.

To determine and compare the predation rates of the three nest types, nests were considered predated if either of the egg types were missing or damaged in some way (e.g. Bayne *et al.* 1997, Clark & Wobeser 1997, Purger *et al.* 2012, Bocz *et al.* 2017). The daily survival rates of quail and plasticine eggs were analysed separately: quail eggs were used to estimate the survival chances of a clutch of medium-bodied birds, while plasticine eggs were used to estimate the survival chances of a clutch of small-bodied ground-nesting birds. Daily survival rates of eggs were calculated with the Mayfield (1975) method and compared using the test proposed by Johnson (1979). For comparisons, the freeware "J-test" developed by K. Halupka (2009) was used. To determine the difference between the number of predated plasticine and quail eggs, Chi-Square goodness of fit for two categories was used (Zar 2010). The minimum probability level of $P < 0.05$ was accepted for all the statistics.

Results

During the 24 days, predators damaged 23.3% (n = 7) of the nests protected by a game fence, 40% (n = 12) of unprotected nests and 46.6% (n = 14) of the nests surrounded with human hair. From the total number of quail eggs (n = 90) used in the experiment, 82.2% (n = 74) remained intact, 12.2% (n = 11) disappeared, and 5.6% (n = 5) were damaged, i.e. the predators managed to break them. Two eggs in nests protected by a game fence, 4 in unprotected nests, and 10 quail eggs in nests surrounded by human hair were damaged, respectively. The daily survival rate of quail eggs in nests protected by the game fence was significantly higher than that of nests surrounded by human hair *(Table 1).*

Table 1. Comparison of daily survival rates (DSR) of quail eggs, in nests protected by a game fence, surrounded by human hair, and in unprotected (control) nests
1. táblázat A vadkerítéssel védett, hajjal körbeszórt, valamint a védelem nélküli (kontroll) fészkekben lévő fürjtojások napi túlélési rátáinak (DSR) összehasonlítása

		Fenced	**Hair scent**	**Control**
	DSR	**0.997**	**0.985**	**0.994**
Control	Z	0.862	-1.638	
	P	0.389	0.101	
Hair scent	Z	2.378		
	P	0.017*		

*P<0.05

Table 2. Comparison of daily survival rates (DSR) of plasticine eggs in nests protected by a game fence, surrounded by human hair, and in unprotected (control) nests

2. táblázat A vadkerítéssel védett, hajjal körbeszórt, valamint a védelem nélküli (kontroll) fészkekben lévő gyurmatojások napi túlélési rátáinak (DSR) összehasonlítása

		Fenced	**Hair scent**	**Control**
	DSR	**0.989**	**0.977**	**0.981**
Control	Z	1.151	-0.466	
	P	0.249	0.642	
Hair scent	Z	1.632		
	P	0.103		

Significantly more ($\chi^2 = 8.225$, df= 2, P = 0.0164) plasticine eggs (n = 32) than quail eggs (n=16) were damaged. From the total number of plasticine eggs (n = 90) used in the experiment 64.4% (n = 58) remained intact, 18.9% (n = 17) disappeared and 16.7% (n = 15) were damaged (in 12 cases teeth marks of small mammals, in 3 cases small bird's beak marks were preserved). Seven plasticine eggs in nests protected by a game fence, 11 in unprotected nests, and 14 plasticine eggs in nests surrounded by human hair were damaged, respectively. The comparison of daily survival rates (DSR) of plasticine eggs in nests protected by a game fence, surrounded by human hair, and in unprotected (control) nests showed no significant difference *(Table 2).*

Discussion

Nests protected by a game fence were less predated than unprotected (control) as well as nests surrounded by human hair. This result is expected and is not surprising, as the effectiveness of the game fence has been supported by several experiments and has therefore long been used to protect nests of ground-nesting bird species (e.g. Smith *et al.* 2011, Homberger *et al.* 2017, Roos *et al.* 2018, Berger-Geiger *et al.* 2019). Since fencing does not exclude bird predators, its use is recommended only in areas where terrestrial nest predators, primarily mammals, predominate (Sargeant *et al.* 1993). It should be stressed that in our study area the vegetation was more diverse and dense in the fenced plots, due to the shrub planting carried out in previous years, while the other parts of the forest were dominated by dogwood. Dense vegetation plays an important role in hiding nests and thus, can contribute to breeding success (e.g. Rangen *et al.* 1999, Seibold *et al.* 2013, Bu *et al*. 2019). Although the fence does not provide protection against all types of predators, it significantly increases the daily survival rate of eggs (Homberger *et al.* 2017, Cocquelet *et al.* 2018), even more effectively than repellents (Santangeli *et al.* 2015).

In our experiment, nests surrounded by hair were slightly more attractive to predators than unprotected (control) nests, but this was not significant. Our results are in line with uncertainty of earlier studies that the role of human hair is not only questionable as a repellent but on the contrary, it may attract even more predators to the nests (e.g. Whelan *et al.* 1994, Skagen *et al.* 1999, Harriman *et al.* 2007). Human scent has no alarming effect on predators accustomed to human settlements, neither does on birds (Düttman *et al.* 2007).

Hardly 18% of the total number of quail eggs suffered some damage. The daily survival rate of quail eggs protected by the game fence was significantly higher than that of eggs surrounded by human hair. Based on our results, the predators of quail eggs may have been primarily larger mammals moving on the ground, excluded by the fence, but which may have been attracted by hair or human odour. However, we could not prove this with our experiment, as some of the eggs disappeared and there were no marks on the broken eggs that could have allowed the identification of predators. Quail eggs may also have been taken away by Common Jays *(Garrulus glandarius)* frequently occurring in the area (Purger & Fenyősi 2019), but we have no evidence for this, and nor did we find any marks on plasticine eggs that could have confirmed this assumption. These results also suggest that the experiments with quail eggs should not be used to infer the predation rate of real nests, but rather to compare habitats and nesting sites (Roper 1992).

During the experiment, significantly more plasticine eggs than quail eggs were damaged, which can be explained by the fact that plasticine can also preserve beak marks of small-bodied birds and the tooth prints of small mammalian predators, which cannot damage quail eggs (e.g. Roper 1992). Partly for this reason, in many cases, artificial nests are considered predated only if the real eggs (in this case quail eggs) disappear or are damaged in some way (Bayne & Hobson 1999), while plasticine eggs are used only to identify predators (Major 1991, Niehaus *et al.* 2003). Nest predation experiments have been widely criticized in the past for the use of plasticine eggs particularly because their odour has attracted predators with a good sense of smell (Rangen *et al.* 2000, Maier & DeGraaf 2001). In a previous study, we found that if small mammals find the nest and leave a mark on plasticine eggs, with their presence or urine and faeces, they could attract larger predators to the nest, which can break the real eggs (Purger *et al.* 2008). To hide the characteristic odour of the plasticine, eggs were coated with liquid rubber in this experiment, so this confounding factor was excluded (Purger *et al.* 2012). However, in the course of our study, instead of the odour of plasticine, the human odour appeared in some nests, which was achieved by the appearance of human hair placed around the nest. We did not anticipate that hair could be attractive not only to typical nest predators. On the very first days, we noticed that hair almost completely disappeared from 3 nests. In one case, we observed a Great Tit *(Parus major)* that flew up from the nest, with hair in its beak, which was probably used as nest-building material. The beak prints of the small-bodied birds found on the plasticine eggs suggested that the hair tended to attract them to the nests. While a fence can keep large-bodied mammals moving on the ground away from nests, they can be easily approached by birds or small mammals, and if they leave marks only on plasticine, erroneous conclusions can be drawn. The listed facts also confirmed that the predation events for the two egg types should be separate, as quail eggs model the clutch of medium-sized ground-nesting species, while plasticine eggs are used as a model of the clutch of small-bodied birds.

Conclusion

Based on the results of our study, we can conclude that the nests of medium-sized birds that breed on the ground can be protected from predators more effectively by game fence, rather than by repellents, e.g. human hair. Game fences are used primarily to protect plants from grazing by game, though this additional role showed in our study should be explored more thoroughly. However, human hair has an attractive effect rather than a repellent. The nests surrounded by human hair were more frequently visited by small mammals and small-bodied birds and with their increased presence they could draw the attention of other larger nest predators to the nests. In several cases, human hair was even removed from the site by birds and used as nest-building material.

Acknowledgements

Mobility for the research was facilitated by Duna-Drava National Park Directorate (project: LIFE 13/Nat/HU000388 Life Old-Drava).

References

Albrecht, T. & Klvaňa, P. 2004. Nest crypsis, reproductive value of a clutch and escape decisions in incubating female Mallards *Anas platyrhynchos*. – Ethology 110(8): 603–613. DOI: 10.1111/j.1439-0310.2004.00992.x

Andelt, W. F., Burnham, K. P. & Baker, D. L. 1994. Effectiveness of capsaicin and bitrex repellents for deterring browsing by captive Mule Deer. – Journal of Wildlife Management 58(2): 330–334. DOI: 10.2307/3809398

Báldi, A. 1999. A fészekaljpredáció jelentősége, valamint kísérletes vizsgálatának előnyei, hátrányai és módszertana [The use of artificial nests for estimating rates of nest survival]. – Ornis Hungarica 8–9: 39–55. (in Hungarian)

Bateman, P. W., Fleming, P. A. & Wolfe, A. K. 2017. A different kind of ecological modelling: the use of clay model organisms to explore predator-prey interactions in vertebrates. – Journal of Zoology 301(4): 251–262. DOI: 10.1111/jzo.12415

Bayne, E. M. & Hobson, K. A. 1999. Do clay eggs attract predators to artificial nests? – Journal of Field Ornithology 70(1): 1–7.

Bayne, E. M., Hobson, K. A. & Fargey, P. 1997. Predation on artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. – Ecography 20(3): 233–239. DOI: 10.1111/j.1600-0587.1997.tb00366.x

Belant, J. L., Seamans, T. W. & Tyson, L. A. 1998. Predator urines as chemical barriers to White-tailed Deer. – Proceedings of the Eighteenth Vertebrate Pest Conference 4. https://digitalcommons.unl.edu/vpc18/4

Berger-Geiger, B., Galizia, C. G. & Arroyo, B. 2019. Montagu's Harrier breeding parameters in relation to weather, colony size and nest protection schemes: a long-term study in Extremadura, Spain. – Journal of Ornithology 160: 429–441. DOI: 10.1007/s10336-018-1618-0

Bocz, R., Szép, D., Witz, D., Ronczyk, L., Kurucz, K. & Purger, J. J. 2017. Human disturbances and predation on artificial ground nests across an urban gradient. – Animal Biodiversity and Conservation 40(2): 153–157. DOI: 10.32800/abc.2017.40.0153

Bolduc, F. & Guillemette, M. 2003. Human disturbance and nesting success of Common Eiders: interaction between visitors and gulls. – Biological Conservation 110(1): 77–83. DOI: 10.1016/S0006-3207(02)00178-7

Bu, H., Shen, X. & Li, S. 2019. Predation patterns on artificial nests of ground nesting pheasants in the montane forest, Southwest China. – Acta Ornithologica 54(1): 35–43. DOI: 10.3161/00016454AO2019.54.1.003

Clark, R. G. & Wobeser, B. K. 1997. Making sense of scents: effects of odour on survival of simulated duck nests. – Journal of Avian Biology 28(1): 31–37. DOI: 10.2307/3677091

Collias, N. E. & Collias, E. C. 1984. Nest building and bird behavior. – Princeton University Press, Princeton, New Jersey

Cox, R., Baker, S. E., Macdonald, D. W. & Berdoy, M. 2004. Protecting egg prey from Carrion Crows: the potential of aversive conditioning. – Applied Animal Behaviour Science 87(3–4): 325–342. DOI: 10.1016/j.applanim.2004.01.008

Csete, S. & Purger, D. 2019. Élőhelyek és növényzet a Barcsi Ó-Dráva holtág területén [Habitats and vegetation in the area of Old-Drava oxbow near Barcs]. – In: Purger, D. & Purger, J. J. (eds.) A Barcsi Ó-Dráva holtág élőhelyei és élővilága [Habitats and wildlife of the Old-Drava oxbow near Barcs]. – BioRes, Pécs, pp. 23–46. (in Hungarian with English Summary)

Curtis, P. D., Fargione, M. J. & Richmond, M. E. 1994. Preventing deer damage with barrier, electrical, and behavioral fencing systems. – Proceedings of the Sixteenth Vertebrate Pest Conference 15. https://digitalcommons.unl.edu/vpc16/15

Düttmann, H., Lettau, K. & Barkow, A. 2007. Can noxious odours effectively protect clutches of ground-nesting birds? – Ardea 95(2): 267–274. DOI: 10.5253/078.095.0209

Fitzwater, W. D. 1972. Barrier fencing in wildlife management. – Proceedings of the Vertebrate Pest Control Conference 5: 49–55.

Fontaine, J. J. & Martin, T. E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. – Ecology Letters 9(4): 428–434. DOI: 10.1111/j.1461-0248.2006.00892.x

Götmark, F. 1992. The effects of investigator disturbance on nesting birds. – Current Ornithology 9: 63–104. DOI: 10.1007/978-1-4757-9921-7_3

Halupka, K. 2009. J-test. – http://zeb.uni.wroc.pl/halupka/

Harriman, V. B., Pitt, J. A. & Larivière, S. 2007. Do repugnant scents increase survival of ground nests? A test with artificial and natural duck nests. – Canadian Field Naturalist 121(2): 150–154. DOI: 10.22621/cfn.v121i2.439

Haskell, D. G. 1996. Do bright colors at nests incur a cost due to predation? – Evolutionary Ecology 10(3): 285–288. DOI: 10.1007/BF01237685

Hayward, M. W. & Kerley, G. I. H. 2009. Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? – Biological Conservation 142(1): 1–13. DOI: 10.1016/j.biocon.2008.09.022

Hockin, D., Ounsted, M., Gormant, M., Hillt, D., Kellert, V. & Barker, M. A. 1992. Examination of the effects of disturbance on birds with reference to its importance in ecological assessments. – Journal of Environmental Management 36(4): 253–286. DOI: 10.1016/S0301-4797(08)80002-3

Homberger, B., Duplain, J., Jenny, M. & Jenni, L. 2017. Agri-evironmental schemes and active nest protection can increase hatching success of a reintroduced farmland bird species. – Landscape and Urban Planning 161: 44–51. DOI: 10.1016/j.landurbplan.2017.01.001

Hygnstrom, S. E. & Craven, S. R. 1988. Electric fences and commercial repellents for reducing deer damage in cornfields. – Wildlife Society Bulletin 16(3): 291–296.

Ibáñez-Álamo, J. D., Magrath, R. D., Oteyza, J. C., Chalfoun, A. D., Haff, T. M., Schmidt, K. A., Thomson, R. L. & Martin, T. E. 2015. Nest predation research: recent findings and future perspectives. – Journal of Ornithology 156(Suppl.1): 247–262. DOI: 10.1007/s10336-015-1207-4

Isaksson, D., Wallander, J. & Larsson, M. 2007. Managing predation on ground-nesting birds: The effectiveness of nest exclosures. – Biological Conservation 136(1): 136–142. DOI: 10.1016/j.biocon.2006.11.015

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. – Auk 96(4): 651–661. DOI: 10.1093/auk/96.4.651

Kurucz, K., Batáry, P., Frank, K. & Purger, J. J. 2015. Effects of daily nest monitoring on predation rate - an artificial nest experiment. – North-Western Journal of Zoology 11(2): 219–224. http://biozoojournals.ro/nwjz/content/v11n2/nwjz_141605_Kurucz.pdf

Kurz, D. J., Straley, K. M. & DeGregorio, B. A. 2011. Out-foxing the Red Fox: how to best protect the nests of the endangered loggerhead Marine Turtle *Caretta caretta* from mammalian predation? – Oryx 46(2): 223–228. DOI: 10.1017/S0030605311000147

LaManna, J. A., Hemenway, A. B., Boccadori, V. & Martin, T. E. 2015. Bird species turnover is related to changing predation risk along a vegetation gradient. – Ecology 96(6): 1670–1680. DOI: 10.1890/14-1333.1

Latham, M. C., Anderson, D. P., Norbury, G., Price, C. J., Banks, P. B. & Latham, A. D. M. 2019. Modeling habituation of introduced predators to unrewarding bird odors for conservation of ground-nesting shorebirds. – Ecological Applications 29(1): e01814. DOI: 10.1002/eap.1814

Lyons, T. P., Miller, J. R., Debinski, D. M. & Engle, D. M. 2015. Predator identity influences the effect of habitat management on nest predation. – Ecological Applications 25(6): 1596–1605. DOI: 10.1890/14-1641.1

Macdonald, D. & Baker, S. E. 2004. Non-lethal control of fox predation: the potential of generalised aversion. – Animal Welfare 13(1): 77–85.

Maier, T. J. & DeGraaf, R. M. 2001. Differences in depredation by small predators limit the use of plasticine and zebra finch eggs in artificial-nest studies. – The Condor 103: 180–183. DOI: 10.1093/condor/103.1.180

Mainwaring, M. C., Hartley, I. R., Lambrechts, M. M. & Deeming, D. C. 2014. The design and function of birds' nests. – Ecology and Evolution 4(20): 3909–3928. DOI: 10.1002/ece3.1054

Major, R. E. 1991. Identification of nest predators by photography, dummy eggs, and adhesive tape. – The Auk 108(1): 190–195. DOI: 10.1093/auk/108.1.190

Major, R. E. & Kendal, C. E. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. – Ibis 138(2): 298–307. DOI: 10.1111/j.1474-919X.1996.tb04342.x

Martin, T. E. 1993 Nest predation and nest sites: new perspectives on old patterns. – BioScience 43(8): 523–532. DOI: 10.2307/1311947

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. – Ecological Monographs 65(1): 101–127. DOI: 10.2307/2937160

Mayfield, H. F. 1975. Suggestions for calculating nest success. – Wilson Bulletin 87: 456–466.

Medeiros, R., Ramos, J. A., Paiva, V. H., Almeida, A., Pedro, P. & Antunes, S. 2007. Signage reduces the impact of human disturbance on little tern nesting success in Portugal. – Biological Conservation 135(1): 99–106. DOI: 10.1016/j.biocon.2006.10.001

Miller, E. A., Young, J. K., Stelting, S. & Kimball, B. A. 2014. Efficacy of Ropel® as a Coyote repellent. – Human-Wildlife Interactions 8(2): 271–278. DOI: 10.26077/vgqg-f189

Milunas, M. C., Rhoads, A. F. & Mason, J. R. 1994. Effectiveness of odour repellents for protecting ornamental shrubs from browsing by White-tailed Deer. – Crop Protection 13(5): 393–397. DOI: 10.1080/00063657.2012.684550

Moore, R. P. & Robinson, W. D. 2004. Artificial bird nests, external validity, and bias in ecological field studies. – Ecology 85(6): 1562–1567. DOI: 10.1890/03-0088

Moreno, J. 2012. Avian nests and nest-building as signals. – Avian Biology Research 5(4): 238–251. DOI: 10.3184/175815512X13534385822786

Niehaus, A. C., Heard, S. B., Hendrix, S. D. & Hillis, S. L. 2003. Measuring edge effects on nest predation in forest fragments: do finch and quail eggs tell different stories? – The American Midland Naturalist 149(2): 335–343. DOI: 10.1674/0003-0031(2003)149[0335:MEEONP]2.0.CO;2

Purger, J. J. 2019. A Barcsi Ó-Dráva holtág és környékének emlősfaunája [Mammalian fauna of the Old-Drava oxbow near Barcs and its surroundings]. – In: Purger, D. & Purger, J. J. (eds.) A Barcsi Ó-Dráva holtág élőhelyei és élővilága [Habitats and wildlife of the Old-Drava oxbow near Barcs]. – BioRes, Pécs, pp. 189–202. (in Hungarian with English Summary)

Purger, J. J. & Fenyősi, L. 2019. Madarak monitorozása és állománybecslése a Barcsi Ó-Dráva holtágon [Monitoring and population estimation of the avian fauna along the Old-Drava oxbow near Barcs]. – In: Purger, D. & Purger, J. J. (eds.) A Barcsi Ó-Dráva holtág élőhelyei és élővilága [Habitats and wildlife of the Old-Drava oxbow near Barcs]. – BioRes, Pécs, pp. 155–188. (in Hungarian with English Summary)

Purger, J. J., Csuka, S. & Kurucz, K. 2008. Predation survival of ground nesting birds in grass and wheat fields: experiment with plasticine eggs and artificial nests. – Polish Journal of Ecology 56(3): 481–486.

Purger, J. J., Kurucz, K., Tóth, Á. & Batáry, P. 2012. Coating plasticine eggs can eliminate the overestimation of predation on artificial ground nests. – Bird Study 59(3): 350–352. DOI: 10.1080/00063657.2012.684550

Rangen, S. A., Clarc, R. G. & Hobson, K. A. 1999. Influence of nest-site vegetation and predator community on the success of artificial songbird nests. – Canadian Journal of Zoology 77(11): 1676–1681. DOI: 10.1139/z99-141

Rangen, S. A., Clarc, R. G. & Hobson, K. A. 2000. Visual and olfactory attributes of artificial nests. – The Auk 117(1): 136–146. DOI: 10.1642/0004-8038(2000)117[0136:VAOAOA]2.0.CO;2

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. – Smithsonian Contributions to Zoology 9: 1–48. DOI: 10.5479/si.00810282.9

Roos, S., Smart, J., Gibbons, D. W. & Wilson, J. D. 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. – Biological Reviews 93(4): 1915–1937. DOI: 10.1111/brv.12426

Roper, J. J. 1992. Nest predation experiments with quail eggs: too much to swallow? – Oikos 65(3): 528–530. DOI: 10.2307/3545570

Rosell, F. & Czech, A. 2000. Responses of foraging Eurasian Beavers *Castor fiber* to predator odours. – Wildlife Biology 6(4): 13–21. DOI: 10.2981/wlb.2000.033

Santangeli, A., Arroyo, B., Millon, A. & Bretagnolle, V. 2015. Identifying effective actions to guide volunteer-based and nationwide conservation efforts for a groundnesting farmland bird. – Journal of Applied Ecology 52(4): 1082–1091. DOI: 10.1111/1365-2664.12445

Sargeant, A. B., Greenwood, R. J. Sovada, M. A. & Shaffer, T. L. 1993. Distribution and abundance of predators that affect duck production - prairie pothole region. – U.S. Fish and Wildlife Service, Resource Publication 194: 1–96.

Seibold, S., Hempel, A., Piehl, S., Bassler, S., Brandl, R., Rosner, S. & Müller, J. 2013. Forest vegetation structure has more influence on predation risk of artificial ground nests than human activities. – Basic and Applied Ecology 14(8): 687–693. DOI: 10.1016/j.baae.2013.09.003

Skagen, S. K., Stanley, T. R. & Dillon, M. B. 1999. Do mammalian nest predators follow human scent trails in the shortgrass prairie? – Wilson Bulletin 111(3): 415–420.

Smith, R. K., Pullin, A. S., Stewart, G. B. & Sutherland, W. J. 2011. Is nest predator exclusion an effective strategy for enhancing bird populations? – Biological Conservation 144(1): 1–10. DOI: 10.1016/j.biocon.2010.05.008

Storaas, T. 1988. A comparison of losses in artificial and naturally occurring Capercaillie nests. – The Journal of Wildlife Management 52(1): 123–126. DOI: 10.2307/3801071

Vacca, M. M. & Handel, C. M. 1988. Factors influencing predation associated with visits to artificial goose nests. – Journal of Field Ornithology 59(3): 215–223.

Vilardell, A., Capalleras, X., Budó, J., Molist, F. & Pons, P. 2008. Test of the efficacy of two chemical repellents in the control of Hermann's Tortoise nest predation. – European Journal of Wildlife Research 54(4): 745–748. DOI: 10.1007/s10344-008-0176-9

Ward, J. S. & Williams, S. C. 2010. Effectiveness of deer repellents in Connecticut. – Human-Wildlife Interactions 4(1): 56–66. DOI: 10.26077/v0bn-9k23

Whelan, C. J., Dilger, M. L., Robson, D., Hallyn, N. & Dilger, S. 1994. Effects of olfactory cues on artificial-nest experiments. – The Auk 111(4): 945–952. DOI: 10.2307/4088826

Wyatt, T. D. 2014. Pheromones and animal behaviour: communication by smell and taste, 2nd ed. – Cambridge University Press, Cambridge DOI: 10.1017/CBO9781139030748

Zar, J. H. 2010. Biostatistical Analysis. 5th ed. – Pearson, Prentice-Hall, Harlow

Ornis Hungarica 2020. 28(2): 146–157.
DOI: 10.2478/orhu-2020-0023

Population dynamics and habitat preference of two urbanized Columbidae species and their nest predator in two settlement types

Sámuel Zsolt Varga* & Lajos Juhász

Received: July 10, 2020 – Revised: October 14, 2020 – Accepted: October 16, 2020

Varga, S. Zs. & Juhász, L. 2020. Population dynamics and habitat preference of two urbanized Columbidae species and their nest predator in two settlement types – Ornis Hungarica 28(2): 146–157. DOI: 10.2478/orhu-2020-0023

Abstract Since urbanization is a worldwide phenomenon, numerous species have gained the advantage of urban ecosystems. The Eurasian Collared Doves *(Streptopelia decaocto)* has become widespread all across Europe along with human-altered habitats. In general, population levels are stable but numbers have locally decreased in the past few decades. In parallel, a new wave of urbanization came forward, so Wood Pigeons *(Columba palumbus)* entered urban ecosystems alongside with other Columbidae species. In this paper, our primary goal was to find any connection between habitat availability factors such as coniferous tree density and the population dynamics of two urbanized species. A locally emerging corvid species, the Hooded Crow *(Corvus cornix)* was also taken into consideration in influencing tree-nesting doves and pigeons as a primary nest predator. During the research period, we aimed to express the differences in habitat structure of two urban ecotypes by nesting tree availability and structure and to prove the power of predator presence in sampling sites. Our results showed that residential areas have a higher proportion of coniferous trees, as well as the high preference of residential areas by Wood Pigeons and Eurasian Collared Doves.

Keywords: urbanization, Eurasian Collared Dove, Wood Pigeon, Hooded Crow, coniferous tree-availability

Összefoglalás Az urbanizáció egy világszerte zajló folyamat, mely során egyes fajok előnyt kovácsoltak a városi ökoszisztéma nyújtotta lehetőségekből. Így lett a balkáni gerle *(Streptopelia decaocto)* Európa-szerte széleskörűen elterjedt kultúrakövető faj, amelynek állománya összességében stabil, azonban vannak olyan kisebb régiók, ahol állományuk csökkenő tendenciát mutat. Ezzel párhuzamosan az örvös galamb *(Columba palumbus)* fokozatosan erősödő városi térnyerése is megfigyelhető. Jelen kutatás célja, hogy a városi élőhely nyújtotta adottságok, valamint a két galambfaj állománydinamikája közötti kapcsolatokat feltárja. A populációt befolyásoló tényezők közé bekerült a helyi szinten megerősödő dolmányos varjú *(Corvus cornix)* populációja is, mint elsődleges fészekpredátor. A kutatás során két különböző településtípus fenti fajokra gyakorolt hatását kívántuk megismerni, ezzel egyidejűleg a ragadozók állományszabályozó erejét is bizonyítani. A két városi élőhelytípus között jelentős különbségek voltak tapasztalhatók a fafajkínálat és a populációsűrűség értékei között egyaránt.

Kulcsszavak: városökológia, balkáni gerle, örvös galamb, dolmányos varjú, tűlevelű fafaj-készlet

Department of Nature Conservation Zoology and Game Management, University of Debrecen, Faculty of Agricultural and Food Sciences and Environmental Management, 4032 Debrecen, Böszörményi út 138., Hungary
** corresponding author, e-mail: varga.samuel@agr.unideb.hu*

Introduction

Urbanization is a common phenomenon that changed the overall identity of human-altered habitats. It describes the shift of human populations migrating from rural areas, filling up cities and their environment. In urban areas, natural flora and fauna have become a secondary factor. As a result, urban habitats are characterized by many extreme anthropogenic factors such as elevated chemical levels, transformed landscape elements, pollution patches, and disturbance sources from the enriched population (Marzluff *et al.* 2001, Devictor *et al.* 2007). The alteration of habitats offers different food-availability, and in most cases, a specialized predator presence. As a consequence, qualitative differences can be observed among urban and non-urban habitats in interspecific interactions such as predator-prey relationships (Chace & Walsh 2006). Most of the species disappeared from cities, but some genera were successfully adapted to the changes in habitats. Urbanization acts as an environmental filter: as urbanization increases, bird species with similar ecological needs come forward (Croci *et al.* 2008, Meffert & Dziock 2013, Sol *et al.* 2014). The urban fauna has a strictly narrowed spectrum, compared to a natural habitat. (Rosenberg *et al.* 1987, Mills *et al.* 1989, Jokimäki & Suhonen 1993, O'Connell *et al.* 2000, Ives *et al.* 2016, Morelli *et al.* 2016). Firstly, during urbanization, granivorous, insectivorous, and in air hunting insectivorous bird species were known to be more common (Emlen 1974, Allen & O'Conner 2000), but recent studies showed, that omnivorous and seed eater species are the most common in cities, because they gain the most profit in urban habitats. On the other hand, birds that usually feed on insects are the most vulnerable to the negative effects of urbanization, so they are more abundant in rural and suburban regions (Máthé & Batáry 2015). In nesting ecology, permanent nesting has an advantage against wandering birds (Allen & O'Conner 2000, Kluza *et al.* 2000, Poague *et al.* 2000). The studies coping deeper with the effect of urbanization revealed that the density and diversity of birds concentrate in the peak on less disturbed, mostly suburban, or boundary zones (Jokimäki & Suhonen 1993, Blair 1999). As the urbanization effect grows, the less adaptive birds disappear from urban ecosystems (Blair 2001). A very impressive example for successful colonization of urban areas in Hungary are the corvid species, such as Hooded Crows *Corvus cornix* (Kövér *et al.* 2015), Ravens *Corvus corax* (Bagyura *et al.* 2017) or Jackdaws *Corvus monedula*, which are either presented in urban and agricultural or natural habitats (Meyrier *et al.* 2017). As a spontaneous expansion of the Eurasian Collared Dove *Streptopelia decaocto* has led to following urban habitats and a strong connection to human presence, so the urbanizing predators are assumed as a high risk for this species. In parallel, the presence of Wood Pigeons *Columba palumbus* in urban areas has also increased in the past decades (Bankovics 2001). According to formerly presented publications, the main reasons for regressing trends of Eurasian Collared Doves in Hungary are the lack of food sources, the higher level of built-up areas in the city, the competition of other species (Feral Pigeon *Columba livia domestica*), and the increasing level of nest predators (Juhász 1990).

Bird communities in Debrecen are highly affected by the increasing population of Hooded Crows, which is the primary nest predator of urbanized bird species, such as Eurasian Collared Doves and Wood Pigeons. Other corvids, like Magpies *Pica pica*, can also destroy urban bird nests. This species has also increased in urban habitats (Jokimäki *et al.* 2016).

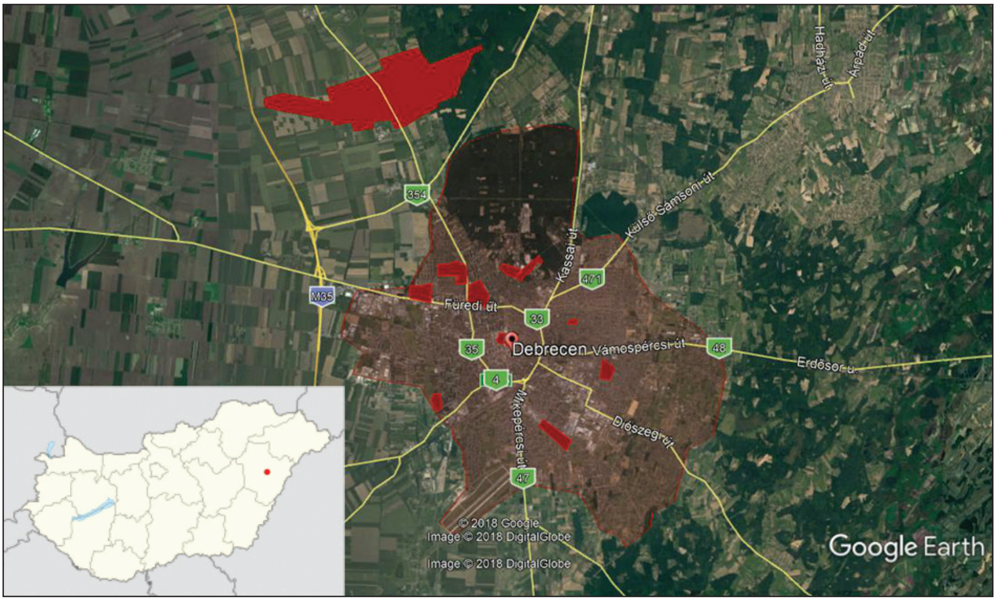


Figure 1. Map of sampling sites
1. ábra A vizsgált mintaterületek térképe

In this study, our main goals were to identify the possible connection between populations of two urbanized Columbidae species and their potential urban nest predator the Hooded Crow, which has been increased in numbers in the past ten years (Kövér *et al.* 2015). Since corvids prefer evergreen vegetation, the coniferous trees were also taken into consideration as an influential factor. In our opinion, Eurasian Collared Doves were migrated from disturbed areas to outskirts, since a higher abundance was discovered near Debrecen.

Materials and methods

Study areas

Our survey was carried out in Debrecen, Hungary, because the most data of population dynamics were presented from this city from the early '80s. We assigned 10 sampling sites (172.08 ha) in the city and 6 more sites in Józsa (458.1 ha), which was formerly an individual village *(Figure 1)*. The 10 sites were chosen to represent the diversity of habitat types in the whole city. The area of Józsa was entirely recorded. Observations were performed from 2016–2020 with a year of pause in 2017.

Data collection

In each year between 21–27 July, all sites were recorded. Daily observations were carried out from 7:00 am to 12:00 am. During data collection, all sites were covered by foot the following factors were recorded: the size of the study area (ha), density of Eurasian Collared Dove density of Wood Pigeon, density of Hooded Crows as the primary nest predator (densities were calculated to individual/10 ha). Tree densities were calculated from the observed individuals and the area of the sampling site. Records were summarized and the mean population density was calculated. In Józsa we used Pielowski's line estimation method (Pielowski 1969). The street network was used as stripes with a 50 metres width to both sides (100 m bandwidth) for bird density surveys in the entire village. Birds flying forwards and inside the line were not taken into the summary. The transect length was estimated from city maps, then during the field work a GPS based pedometer was used for exact values. Tree height was estimated with Christen's tree height measuring device, then data was validated by laser distance meter. Tree densities were calculated from observed trees and the area of each site. In Debrecen, the overall area of each site was observed, and all birds and trees were recorded within the area, then densities were calculated.

From the records, a standard density was calculated, the average tree height was also evaluated from field records. Control measurements by Pielowski (1969) revealed that the method usually overestimates brown hare populations, so during the evaluation of Pielowski's estimation, a 20% correction was used in our research.

Habitat preference was computed by Duncan's index of habitat preference: HPI=(Oh/Ot)/(Ah/At) with 'Oh' being observations in habitat 'h', 'Ot' is all observations in all habitats, 'Ah' is area covered by habitat 'h' and 'At' is the total area. This index uses a top-open scale in which 0 indicates avoidance, between 0 and 1 indicates preference, and above 1 it indicates overuse, e.g. a value of 2.00 represents 200% of habitat overuse.

Statistical analysis

After the data was organized, Mann-Whittney U and Kruskal-Wallis tests were used to determine any difference in population densities of the observed bird species between observation years and cities. Then, data was grouped by cities, and Pearson's correlation was computed to reveal if higher coniferous tree species density results higher population densities. Since the general appearance and branch structure of each species are different, these species were correlated to the three observed species individually. For evaluation, SPSS 25.0 software was used. Due to numerous correlations, False Discovery Rate was used to check significance values.

Results

Differences between populations

Since the Kolmogorov-Smirnov test revealed that none of the observation data have a normal distribution at 95% confidence interval, nonparametric tests were used.

Eurasian Collared Dove density was significantly higher (Mann-Whitney U: 2.457, P = 0.014, n = 16 sites) and Hooded Crow was significantly lower in Józsa (Mann-Whitney

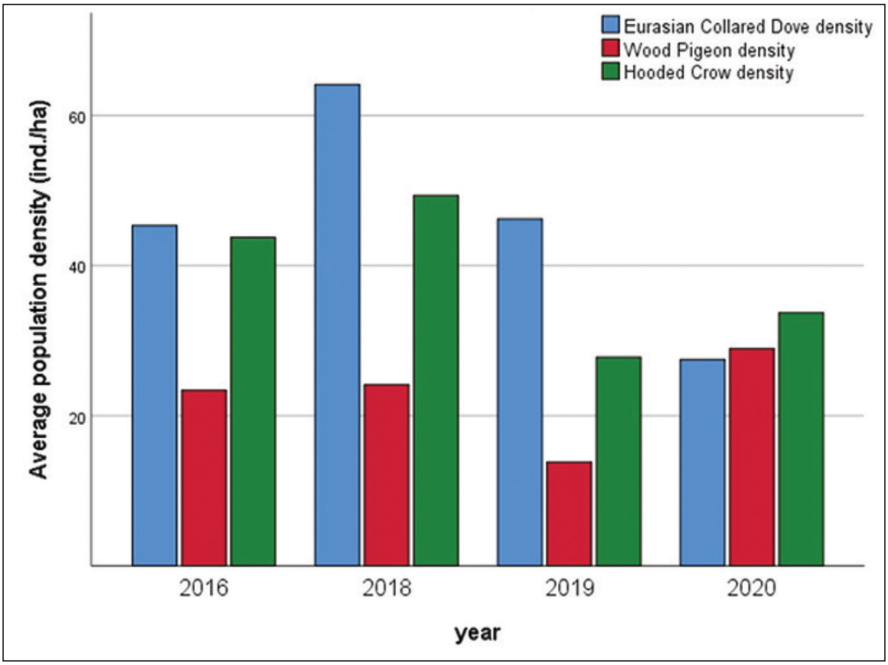


Figure 2. Population dynamics of the three observed species in Debrecen
2. ábra A három megfigyelt faj populációdinamikája Debrecenben

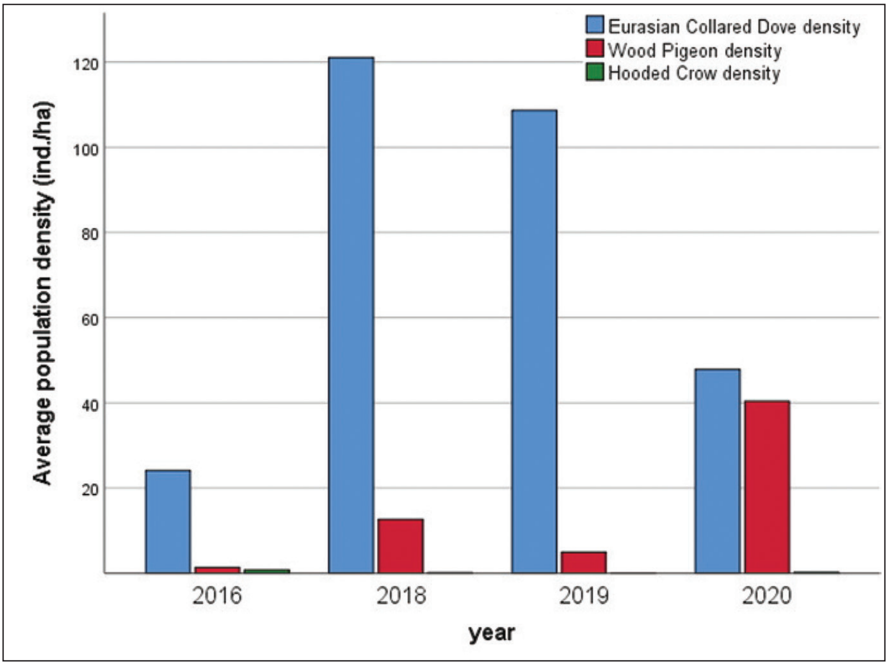


Figure 3. Population dynamics of the three observed species in Józsa
3. ábra A három megfigyelt faj populációdinamikája Józsán

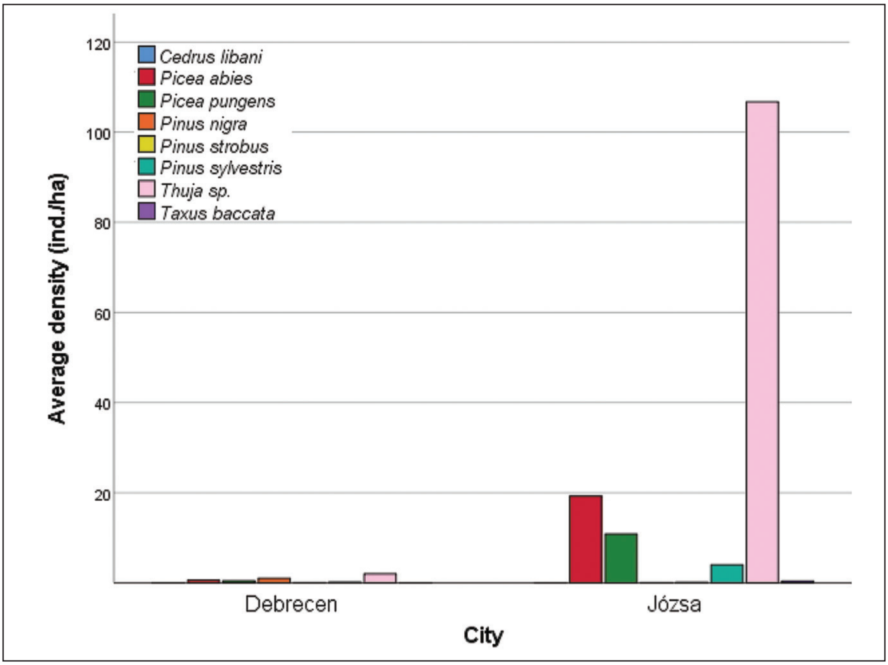


Figure 4. Coniferous tree densities in study areas
4. ábra Tűlevelű fák állománysűrűsége a vizsgált területeken

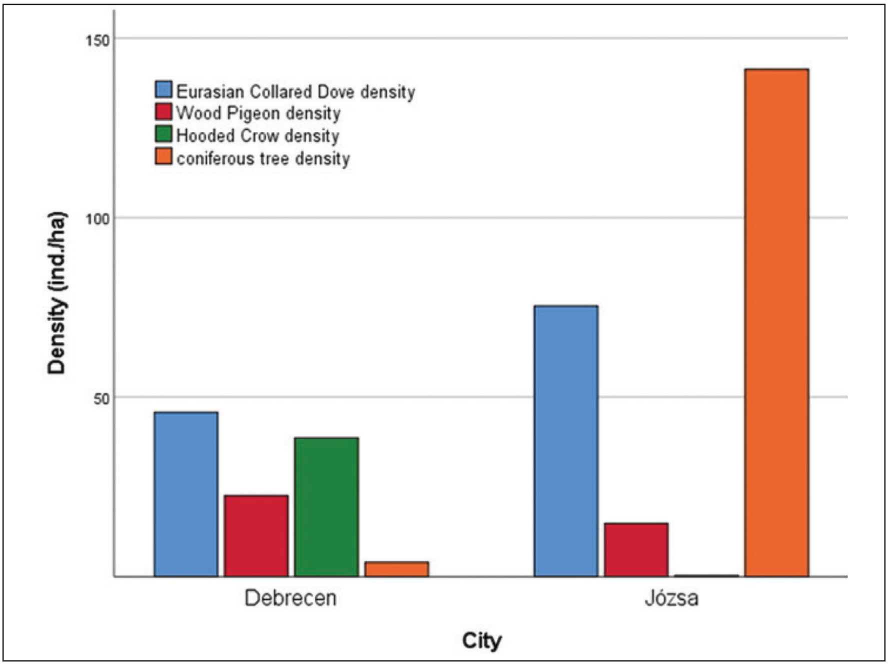


Figure 5. Population densities of the three species with overall coniferous tree density values
5. ábra A három vizsgált faj és az összes tűlevelű fa denzitásértékei

U: –5.585, P < 0.01, n = 16 sites) than Debrecen. During the evaluation of temporal trends, no significant differences were found in Debrecen, meanwhile in Józsa the Eurasian Collared Dove population was higher in 2018, then fell back continuously until 2020 (Kruskal-Wallis:12.604, P = 0.006, n = 24 counts at six sites in the four years). Simultaneously, Wood Pigeons have gained ground and began to rise in 2020 (Kruskal-Wallis: 16.049, P = 0.001, n = 24 counts at six sites in the four years) *(Figure 3)*.

Tree availability of sampling sites

The two settlements showed great difference in species abundance and species richness of coniferous trees. Since Józsa is an emerging suburban residential area, the proportion of green areas is higher. The preference of planting coniferous trees can be related to old traditions, because before the introduction of black locust *(Robinia pseudo-acacia)* pine tree species were used as building material. Since on plain lands wood availability was low, residents grew pine (mostly *Pinus sylvestris*) trees on their land to ensure their wood supply. Later, citizens of Debrecen moved out to this town, and a new suburban community grew out. The most common decorative tree species were *Picea abies, Picea pungens* and *Thuja* sp., which can be clearly seen on *Figure 4.* The overall density of coniferous tree species are significantly higher in Józsa (Mann-Whitney U: 6.674, P < 0.05, n = 16). In average tree height, there was no significant difference (Mann-Whitney U: 13.0, p = 0.073, n = 16).

Correlations

During the examination of possible correlations between species and coniferous tree species availability, numerous significant correlations were found. In Debrecen, Eurasian Collared Dove was correlated to Thuja sp. (cor.: 0.656, p = 0.04, n = 10), Hooded Crow was correlated with Pinus nigra (cor.: 0.760, p = 0.011, n=10) and Wood Pigeons (cor.: 0.681, p = 0,030, n = 10). In Józsa, Eurasian Collared Doves density correlated to Pinus strobus (cor.: 0.909, p = 0.012, n = 6), so did the Hooded Crows (cor.: 0,904, p = 0.013, n =6), and the two species also correlated with each other (cor.: 0.913, p = 0.011, n = 6). All p-values were calculated with FDR correction.

The dependence of Eurasian Collared Doves to coniferous trees is presumable from tree availability and correlations. In Debrecen, preferred tree species availability is lower, such as Collared Dove density in comparison to Józsa, where a greater amount of preferred tree individuals are available, letting the doves nest more freely. In addition, the lack of nest predator presence could increase hatching success *(Figure 5)*.

Habitat preference

From the values in *Table 1*, it can be assumed that Eurasian Collared Doves prefer various urban parks, suburban habitats and flats closer to the city limits in Debrecen. The abundant food provided by the Debrecen Zoo also showed higher preference values, however, it was the second most preferred habitat by the hooded crows. The habitat preference of the Wood Pigeon was outstanding in the examined habitats in Debrecen, in the habitats with higher wood cover, the closed, downtown area was the least preferred by the examined individuals. Hooded Crow preferred habitats sparsely overgrown with trees in the northern part of the city.

In Józsa, due to the continuous and abundant food base and the avoidance behaviour of Hooded Crows, the HPI value of the Eurasian Collared Doves showed multiple overuse. The good positioning of the settlement and the large proportion of the surrounding agricultural areas are able to serve the food needs of the species. Where the surrounding area was less favourable, the species preference index was lower. The known nesting sites of the Wood Pigeon in the open area, e.g. the gallery forests, are underrepresented in these sample areas, so they are characterized by lower, but more balanced, preference values due to solitary nesting.

Table 1. Summary of HPI values on research sites
1. táblázat A vizsgált fajok HPI értékei a mintaterületeken

No.	**City /Habitat type**	**Habitat Preference Index (HPI)**		
		Eurasian Collared Dove	**Wood Pigeon**	**Hooded Crow**
Debrecen				
1	Campus of the institution	0.490	0.512	0.445
2	Nagyerdő – Closed forest area	0.068	1.301	0.191
3	Debrecen Zoo – park area	1.118	1.118	0.266
4	Rural area with gallery forest	0.142	1.208	0.079
5	Flats in city centre	0.343	0.098	0.053
6	Downtown park and its environment	2.833	1.594	0.161
7	City park – with direct connection to residentials	3.606	0.314	0.044
8	Flats in rural area	6.326	1.265	0.088
9	Industrial area	0.435	0.338	0.020
10	Residential area	1.954	0.781	0.087
Józsa				
11	Residential area – linked with agricultural land	2.091	0.061	0.014
12	Residential area – linked with agricultural land	4.124	0.313	0.000
13	Residential area – central area	3.901	0.246	0.009
14	Residential area – linked with agricultural land	3.116	0.292	0.015
15	Residential area – linked with grasslands	1.777	0.211	0.000
16	Residential area – linked with closed forest area	2.032	0.296	0.000

Discussion

Changes in bird communities of Debrecen

Table 2. Comparison of former researches of Eurasian Collared Dove population in Debrecen with recent data

2. táblázat A korábban Debrecen balkáni gerle állományát vizsgáló kutatások és a jelenlegi adatok összehasonlítása

Year	Habitat type	pairs/10ha
1980	City center	94.50
	Flats	35.50
	Residential area	13.70
1982	City center	27.00
	Flats	28.00
	Residential area	16.50
1983	City center	29.00
	Flats	21.00
	Residential area	13.30
2016–2020 (mean)	City center	37.45
	Flats	4.54
	Residential area	25.82
	Józsa	37.72

During our research, we found that the spatial distribution Eurasian Collared Doves population of Debrecen has changed from highly-altered habitats to residential areas in comparison to formerly published data *(Table 2)*.

Columbidae and Corvidae are common species that are easy to identify and monitor, so they are an easy example to track down the changes in urban habitats and the response of urban bird communities. In our case, the expansive forthcoming of Hooded Crows in urban environment (Kövér *et al.* 2015) and the decreasing of food sources, such as the bankrupt of mills in the city led to the decrease of Eurasian Collared Doves. Debrecen's biggest mill facility was destroyed by retreating German soldiers in 1944 (Szűcs 1978). Though, the mill was closed, its grain storage was operational until 1998. This storage was open on top to subserve ventilation, so a stable food source was given to granivorous birds in the city. For further city developments, it has to be taken into consideration that the size of the urbanized area is a key factor to improve ecosystem health and human interactions with nature (Garaffa *et al.* 2009), so the high proportion of green areas in the city is necessary to maintain the diversity of urban bird communities.

The importance of tree availability

In our research, we found that the density of Eurasian Collared Doves can be linked to the availability of coniferous trees. In North America, Mourning Doves *(Zenaida macroura)* prefer red pine *(Pinus resinosa)* and Norway spruce *(Picea abies)*, and habitat types such as the conifer and medium shrub categories, however, white pine *(Pinus strobus)* and Scotch pine *(Pinus sylvestris)* were not used (Caldwell 1964). As a result, we assume that in elevated levels of predator abundance, so was in Debrecen, doves seek the hideouts provided by coniferous trees. Moreover, if no threat is visible, doves nest freely without any selection for tree species.

In Scotland, Hooded Crows prefer higher coniferous trees afar from human presence (McIvor & Healy 2017), meanwhile in Italy Carrion Crows *(Corvus corone)* – the close relative of Hooded Crow – prefer open trees as nesting sites (Vignoli *et al.* 2013). It is not uncommon that dove species also prefer pine tree species as nesting sites. Taking this data into consideration, since Hooded Crows seem to be more sensitive to human disturbance, they avoid the area of Józsa, resulting a relaxed environment.

There are factors that were not recorded during this study like the availability of food and water sources, noise and light pollution, level of human presence. These can also modify the overall environmental conditions. The village-like structure of Józsa has advantageous conditions like animal breeding, high-percentage of agricultural lands in the neighbouring areas, or the lower level of human presence. Habitat preference values approved that this area plays a prominent role in local dove populations. Meanwhile in 'classic' urban circumstances, doves prefer areas that have a stable food source, and low presence of predators. Wood Pigeons seem to prefer areas with similar tree structure that is presented outside the city.

Does overurbanization degrade bird communities?

In South-eastern Mexico, a study showed that the status of bird communities varies along land-uses, as a representative of urbanization gradient. Only a few generalist species were present in areas with commercial components and evenness was higher in green areas. As urbanization increased bird abundances increased with lower species richness. These descriptive values were also sensible to site-specific habitat characteristics (Ortega-Álvarez & MacGregor-Fors 2009).

We concluded that urban planning can also promote avifauna abundance in the city centre by varying the heights of buildings in urban renewal projects rather than clustering buildings of similar height, or by focusing on the spatial configuration of green spaces (especially their proximity) rather than their area.

In Italy a large-scale sampling was carried out on an urban gradient, where Eurasian Collared Doves showed no connection to the specified habitat types during nest site selection. This result ensures that nesting is connected to tree species rather than urban habitat types (Vignoli *et al.* 2013). In our research, doves showed higher preference values to suburban and residential areas. The multiple overuse of Józsa can be related to the high proportion of agricultural lands that provides a huge amount of food. In the city centre, the lack of food results lower population levels, which can clarify the changes between urban habitat types.

A research carried out in Belarus showed that Wood Pigeons prefer deciduous trees over coniferous (Sakhvon & Kövér 2020), so the further urbanization processes are expected in Hungary and all over Europe to the northern taiga as a spread limit.

However, coniferous tree density and average tree height do affect the structure of urban bird communities. The landscape changing effects of urbanization is a quite fresh phenomenon, not all of its relationships are explored. In this study, we could set up a line of habitat preference of prey and predator species with a special focus on coniferous tree species.

Our results show that there is no overlap in coniferous tree preferences along these three species. Columbidae seek more cover to hide their nest, but Hooded Crows stand alone as predators in cities, so the density of shrubs affects them less. But changes in habitats, such as monodominance of a single tree in urban environment can cause an unexpected tension, so these species can become competitors on nesting trees.

Acknowledgements

The publication is supported by the EFOP-3.6.3-VEKOP-16-2017-00008 project. The project is co-financed by the European Union and the European Social Fund.

References

Allen, A. P. & O'Conner, R. J. 2000. Hierarchical correlates of bird assemblage structure on Northeastern USA lakes. – Environmental Monitoring Assessment 62(1): 15–35. DOI: 10.1023/A:1006244932033

Bagyura, J., Fidlóczky, J., Schwartz, V. & Tóth, L. 2017. Interesting breeding cases of the Raven *(Corvus corax)* in Hungary. – Ornis Hungarica 25(1): 39–43. DOI: 10.1515/orhu-2017-0003

Bankovics, A. 2001. Status of wild Pigeons and Doves in Hungary. – Naturzale 16: 61–70.

Bersier, L. F. & Meyer, D. R. 1994. Bird assemblages in mosaic forests – the relative importance of vegetation structure and floristic composition along the successional gradient. – Acta Oecologica 15: 561–576.

Bersier, L. F. & Meyer, D. R. 1995. Relationships between bird assemblages, vegetation structure, and floristic composition of mosaic patches in riparian forests. – Revue d' Ecologie-la Terre et la Vie 50: 15–33.

Blair, R. B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? – Ecological Applications 9(1): 164–170. DOI: 10.2307/2641176

Blair, R. B. 2001. Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous fauna? – In: Lockwood, J. L. & McKinney, M. L. (eds.) Biotic Homogenization: The Loss of Diversity Through Invasion and Extinction. – Kluwer Academic Publishers, Boston, MA. pp. 33–56.

Caldwell, L. D. 1964. Dove production and nest site selection in Southern Michigan. – The Journal of Wildlife Management 28(4): 732–738. DOI: 10.2307/3798788

Chace, J. F. & Walsh, J. J. 2006. Urban effects on native avifauna: a review. – Landscape and Urban Planning 74(1): 46–69. DOI: 10.1016/j.landurbplan.2004.08.007

Croci, S., Butet, A. & Clergeau, P. 2008. Does urbanization filter birds on the basis of their biological traits? – Condor 110(2): 223–240. DOI: 10.1525/cond.2008.8409

Devictor, V., Julliard, R., Couvet, D., Lee, A. & Jiguet, F. 2007. Functional homogenization effect of urbanization on bird communities. – Conservation Biology 21(3): 741–751. DOI: 10.1111/j.1523-1739.2007.00671.x

Emlen, J. T. 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. – Condor 76(2): 184–197. DOI: 10.2307/1366729

Garaffa, P. I., Filloy, J. & Bellocq, M. I. 2009. Bird community responses along urban–rural gradients: Does the size of the urbanized area matter? – Landscape and Urban Planning 90(1–2): 33–41. DOI: 10.1016/j.landurbplan.2008.10.004

Ives, C. D., Lentini, P. E., Threlfall, C. G., Ikin, K., Shanahan, D. F., Garrard, G. E., Bekessy, S. A., Fuller, R. A., Mumaw, L., Rayner, L., Rowe, R., Valentine, L. E. & Kendal, D. 2016. Cities are hotspots for threatened species. – Global Ecology and Biogeography 25(1): 117–126. DOI: 10.1111/geb.12404

Jokimäki, J. & Suhonen, J. 1993. Effects of urbanization on the breeding bird species richness in Finland: a biogeographical comparison. – Ornis Fennica 70: 71–77.

Jokimäki, J., Suhonen, J., Vuorisalo, T., Kövér, L. & Kaisanlahti-Jokimäki, M-L. 2017. Urbanization and nest-site selection of the Black-billed Magpie *(Pica pica)* populations in two Finnish cities: From a persecuted species to an urban exploiter. – Landscape and Urban Planning 157: 577–585. DOI: 10.1016/j.landurbplan.2016.08.001.

Juhász, L. 1990. A balkáni gerle állományának változása 1980–1990 között hazánk néhány mezőgazdasági régiójában [Population changes in the population on Eurasian Collared Doves between 1980–1990 in some of the agricultural lands of Hungary]. – Debreceni Agrártudományi Egyetem Tudományos Közleményei 1990: 153–169. (in Hungarian)

Kluza, D. A., Griffin, C. R. & DeGraaf, R. M. 2000. Housing developments in rural New England: effects on forest birds. – Animal Conservation 3(1): 15–26. DOI: 10.1111/j.1469-1795.2000.tb00083.x

Kövér, L., Gyüre, P., Balogh, P., Huettmann, F., Lengyel, Sz. & Juhász, L. 2015. Recent colonization and nest site selection of the Hooded Crow (*Corvus corone cornix* L.) in an urban environment. – Landscape and Urban Planning 133: 78–86. DOI: 10.1016/j.landurbplan.2014.09.008

Marzluff, J. M., Bowman, R. & Donelly, R. 2001. A historical perspective on urban bird research: trend, term, and approaches. – In: Marzluff, J. M., Bowman, R. & Donelly, R. (eds.) Avian Ecology and Conservation in an Urbanizing World. – Kluwer Academic Publishers, MA. pp. 1–17.

Máthé, O. & Batáry, P. 2015. Insectivorous and open-cup nester bird species suffer the most from urbanization. – Bird Study 62(1): 78–86. DOI: 10.1080/00063657.2014.1000262

McIvor, G. E. & Healy, S. D. 2017. Nest site selection and patterns of nest re-use in the Hooded Crow *Corvus cornix*. – Bird Study 64(3): 1–12. DOI: 10.1080/00063657.2017.1364220

Meffert, P. J. & Dziock, F. 2013. The influence of urbanisation on diversity and trait composition of birds. – Landscape Ecology 28: 943–957. DOI: 10.1007/s10980-013-9867-z

Meyrier, E., Jenni, L., Bötsch, Y., Strebel, S., Erne, B. & Tablado, Z. 2017. Happy to breed in the city? Urban food resources limit reproductive output in Western Jackdaws. – Ecology and Evolution 7(5): 1363–1374. DOI: 10.1002/ece3.2733

Mills, G. S., Dunning, Jr., J. B. & Bates, J. M. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. – Condor 91(2): 416–428. DOI: 10.2307/1368320

Morelli, F., Benedetti, Y., Ibanez-Alamo, J. D., Jokimäki, J., Mänd, R., Tryjanowski, P. & Møller, A. P. 2016. Evidence of evolutionary homogenization of bird communities in urban environments across Europe. – Global Ecology and Biogeography 25(11): 1284-1293. DOI: 10.1111/geb.12486

O'Connell, T. J., Jackson, L. E. & Brooks, R. P. 2000. Bird guilds as indicators of ecological condition in the central Appalachians. – Ecological Applications 10(6): 1706–1721. DOI: 10.1890/1051-0761(2000)010[1706:BGAIOE]2.0.CO;2

Poague, K. L., Johnson, R. J. & Young, L. J. 2000. Bird use of rural and urban converted railroad rights-of-way in southeast Nebraska. – Wildlife Social Biology 28(4): 852–864. DOI: 10.2307/3783840

Pielowski, Z. 1969. Belt assessment as a reliable method of determining the numbers of Hares. – Acta Theriologica 14(9): 133–140.

Rosenberg, K. V., Terrill, S. B. & Rosenberg, G. H. 1987. Value of suburban habitats to desert riparian birds. – Wilson Bulletin 99(4): 642–654.

Sakhvon, V. & Kövér, L. 2020. Distribution and habitat preferences of the urban Woodpigeon *(Columba palumbus)* in the north-eastern breeding range in Belarus. – Landscape and Urban Planning 201: 103846. DOI: 10.1016/j.landurbplan.2020.103846

Sol, D., González-Lagos, C., Moreira, D., Maspons, J. & Lapiedra, O. 2014. Urbanisation tolerance and the loss of avian diversity. – Ecology Letters 17(8): 942–950. DOI: 10.1111/ele.12297

Szűcs, E. 1978. A debreceni István gőzmalom története [History of 'István' steam mill in Debrecen]. – Hajdú-Bihar Megyei Levéltár Közleményei 12. (in Hungarian)

Vignoli, L., Scirè, S. & Bologna, M. A. 2013. Rural-urban gradient and land use in a millenary metropolis: how urbanization affects avian functional groups and the role of old villas in bird assemblage patterning. – Web Ecology 13(1): 49–67. DOI: 10.5194/we-13-49-2013

Ornis Hungarica 2020. 28(2): 158–203.
DOI: 10.2478/orhu-2020-0024

Evolution of Songbirds (Passeriformes) and their Presence in the Neogene and the Quaternary in the Carpathian Basin

Jenő (E.) Kessler

Received: March 09, 2020 – August 31, 2020 – September 01, 2020

Kessler, J. (E). 2020. Evolution of songbirds (Passeriformes) and their presence in the Neogene and the Quaternary in the Carpathian Basin. – Ornis Hungarica 28(2): 158–203. DOI: 10.2478/orhu-2020-0024

Abstract Songbirds are the largest order of birds with 6456 species, making up more than half of every known bird species. The location and time of their emergence, as well as the method of their spreading, is debated. They are present in the Carpathian Basin from the beginning of the Neogene, with an increasing number of types and species. Due to their diverse ways of life and diets, their presence mirrors the environmental conditions of the given geological periods quite accurately.

Keywords: Perching birds, Tertiary, Quaternary, Paleogene, Neogene, avian fauna

Összefoglalás A verébalakúak a madarak osztályának legnépesebb rendje 6456 fajjal, ami több mint a felét képviseli az összes ismert madárfajnak. Megjelenésük helye, ideje és elterjedésük módja vitatott. A Kárpát-medencében a Neogén elejétől vannak jelen, növekvő típus- és fajszámban. Változatos életmódjuk és táplálkozásuk következtében jelenlétük jól tükrözi az adott földtörténeti időszak környezeti viszonyait.

Kulcsszavak: énekesmadarak, Harmadidőszak, Negyedidőszak, Paleogén, Neogén, madárfauna

Department of Paleontology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c, Hungary, e-mail: kessler_jeno@yahoo.com

Introduction

About half of the extant avian species consists of songbirds, which can be found all around the world, apart from Antarctica, with a large number of species. They supposedly formed in the area of the ancient continent of Gondwana (Australia and surroundig archipelago) but their fossil remains in the Palearctic and Nearctic are only known from the Paleogene-Neogene boundary in small numbers. Extantly, their research received a boost, and so did the number of identified and described extant and extinct taxa (Kessler 2013a, 2013b, 2015).

According to the current status of science, songbirds spread from Australia and its environs to the whole world during the Oligocene. The earliest known Palaearctic remains come from the Upper Oligocene (MP 30) from sites at Coderet and Gannat (Allier) in France (Mourer-Chauviré *et al.* 1989). Typically, these finds already bear the osteomorphological signs indicating passerines (Nagy 2020). Thereafter, fossils from Europe, Asia, and also from North and South America are only known from the Lower Miocene. In South America, passerine remains have been described from the Lower Miocene in Patagonia (Noriega & Chiappe 1993). This could suggest that the spread of the passerines ended around this time.

Fossils from the northern hemisphere from before the Miocene probably do not belong to songbirds, but rather to Coraciiformes species that were dominantly present in the Paleogene (Olson 1985). The first songbird fossils were described by Milne-Edwards (1869–71) from the Lower Miocene of France (named *Motacilla humata, M. major, Lanius miocaenicus*). Brodkorb (1978) noted finds from the Lower Miocene of Florida as well, while Howard (1957) described the species *Palaeoscines turdirostris* from the Late Miocene of California. Numerous finds had been noted from Europe, but only defined to the family or genus level (Ballman in 1972 noted *Alauda* and *Sitta* species from the Early Miocene of France in 1972, while Steadman noted Emberizinae species from the Miocene of the USA in 1982).

Despite having prior finds rich in songbird remains, their definitions only go to the family or genus level at most, with only a few exceptions. One of the main reasons for this is the highly significant phenotypical homogenity, resulting in the morphological or size differences having been handled by experts as unique characteristics. The other reason is the sentiment that species do not modify or shift into new species even after many thousands/tens of thousands of generations. This approach also disregards the fact that Linnaean taxonomy distinguishes between related species primarily based on outer morphological/phenotypical characteristics (the form of the beak, colors of feathers, dimensions, etc.), but skeletal characteristics do not play a part in the diagnostics of species. These differences can only be shown via comparative skeletal examinations; these had not been undertaken until extantly, and even those that have only compared particular skeletal parts (in the articles of Fürbringer, Lambrecht, Jánossy and others, also cited in this work).

The osteological characteristics, however, only hint at movement and physiological roles, apart from the beaks that hint at their diets. As opposed to this, the feathers that have a main role in species diagnostics are significant in camouflage and mating. Typically species with open nests either the color of both males or females is gray-brown, or the color of females brooding at daytime is significantly less garish than that of males. In the case of songbird species brooding in closed nests there is no significant difference between the colors of the two genders, although the color of males might be more vibrant even there. The change in species originating from environmental change mostly has an effect on the feathers during reproduction and camouflage to avoid predators (primarily in times of brooding and raising their young), but this cannot be shown in the case of remains significant to paleontology. Moreover, the changes in skeletal parts (mostly the proportion and size of limbs) can only show differences in movement, which is not necessarily typical when a new species is formed. Non-adaptive new colors, voice or mating dances can be detrimental when searching for a mate (for example, albino specimens have no osteological differences, but the lack of species-specific colors has a significant negative effect in mating).

Paleontological finds do not show the characteristics on which the Linnaean taxonomy is based, and due to their age, molecular genetic classification is also impossible. Thus, the specialists can only define the material and create new genera, species, subspecies based on available osteological characteristics/differences/similarities, or accept the opinion of many that during the last millions of years no shift in species took place regarding these taxonomical types. This latter view not only opposes the theory of evolution, but also disregards the fact that members of the order of songbirds are sexually mature by their first year, forming one or several new generations every year.

It is hard to imagine that during millions of generations, no changes would take place that would form new species with different characteristics to their distant ancestors. This is also refuted by the current diversification of finches on the Galapagos Islands.

In this work, the author examined and identified several thousand skeletal parts of songbirds in the Carpathian Basin from the Lower, Middle and Upper Miocene, the Pliocene and Lower Pleistocene, describing more than 120 new species, mostly from sites located in Hungary. Most of the examined bones come from earlier collections, but they were only identified to the family/genus level at best.

It is a welcome news that possibly due to the newly described species in 2012 and 2015, as well as the osteological guide to the genus level published in 2015, the classification of the remains of the order down to the species level and their publication has seen a steady rise worldwide, resulting in more and more studies of this nature.

Abbreviations: MN 1–5 (23,5–16,5 MY) – Lower Miocene; **MN 6–8** (16,5–11,5 MY) – Middle Miocne; **MN 9–13** (11,5–5,3 MY) – Upper Miocene; **MN 14–15** (5,3–3,2 MY) – Lower Pliocene; **MN 16–17** (3,2–1,8 MY) – Upper Pliocene; **Q1–Q2** (1,8 MY–500.000Y) – Lower Pleistocene; **Q3 (Q3/I–Q3/II)** (500.000–120.000Y) – Middle Pleistocene; **Q4/I** (120.000–15.000Y) – Upper Pleistocene; **Q4/II** (15.000Y) – Holocene; † – extinct/fossil species – subspecies.

In the geochronological sense we use the early, middle and late prefixes when dividing the periods into ages, and in the chronostratigraphic sense we use the lower, middle and upper prefixes when dividing the systems into series.

Systematics

Ord. Passeriformes Linnaeus, 1758
Fam. Alaudidae (Vigors, 1825)

– *Melanocorypha* Boie, 1826

– *Melanocorypha* † *minor* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b).

It corresponds to the extant genus, but dimensions are smaller.

– *Melanocorypha calandra* (Linnaeus, 1766)

Q1: Betfia 9 (Romania) (Gál 2002).

From sites in Europe outside the Carpathian Basin **Q3:** France, Russia, Spain; **Q4:** France, Italy, Moldova, Poland, Spain, Ukraine (Tyrberg 1998).

– *Melanocorypha* sp. indet.

Q1: Beremend 17 (Hungary) (Jánossy 1992, 1996).

From sites in Europe outside the Carpathian Basin:

– ***Melanocorypha bimaculata* (Ménétries, 1832)**

Q3: Azerbaijan (Tyrberg 1998).

– ***Melanocorypha maxima*** **Blyth, 1867**

Q4: Italy (Tyrberg 1998).

– ***Melanocorypha leucoptera*** **(Pallas, 1811)**

Q4: Germany (Tyrberg 1998).

– ***Melanocrorypha yeltoniensis*** **(Forster, 1767)**

Q3: Russia; **Q4**: Ukraine (Tyrberg 1998).

The genus was reported from Bulgaria: *Melanocorypha serdicensis* Boev, 2012 (Upper Miocene, Hrabarsko) and *Melanocorypha donchevi* Boev, 2012 (Upper Pliocene, Varshets) (Boev 2012). One fossil species of larks have been described from the Pleistocene deposits in Israel: *Melanocorypha gracilis* Tchernov, 1968 (Tyrberg 1998).

– *Galerida* Boie, 1828

– *Galerida † cserhatensis* Kessler *et* Hír, 2012

Type locality and age: Litke 2, Lower Miocene (MN 5) (Hungary) (Kessler & Hír 2012);

It largely corresponds to the extant *Galerida cristata*, with small morphological differences.

– *Galerida † pannonica* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b).

Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b).

It corresponds in characteristics and sizes with extant species of the genus.

– *Galerida cristata* (Linnaeus, 1758)

Q1: Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002); **Q2:** Somssich-hegy 2 (Hungary) (Jánossy 1981, 1983, 1986); **Q4/I:** Hámor-Puskaporos Niche (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986); Tatabánya-Kálváriahegy 4. Cave (Gál 2005a, 2005b) (all in Hungary); **Q4/II:** Hosszúhegyi Cave (Hungary) (Jánossy 1979); Peterd-Tordai Defile – Magyar Cave (Petrești, Cheile Turzii-Peștera Ungurească) (Romania) (Kessler & Gál 1998, Gál 2005a). From sites in Europe outside the Carpathian Basin **Q3:** France, Germany, Spain; **Q4:** Bosnia-Herczegovina, Czech Republic, France, Germany, Moldova, Poland, Russia, Spain, Ukraine, United Kingdom.

– *Galerida* sp. indet.

Q1: Beremend 17 (Hungary) (Jánossy 1992, 1996).

From sites in Europe outside the Carpathian Basin:

– *Galerida theklae* (Brehm, 1858)

Q3: Spain; **Q4**: Spain (Tyrberg 1998).

The genus was reported outside the Carpathian Basin in Bulgaria from Varshets (Upper Pliocene, MN 17) as *Galerida bulgarica* Boev, 2012 (Boev 2012). It is also known with extant species only from Middle Pleistocene in European fossil localities (Tyrberg 1998).

– †*Praealauda* Kessler *et* Hír, 2012

– †*Praealauda hevesensis* Kessler *et* Hír, 2012

Type locality and age: Felsőtárkány, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír 2012).

A new genus and species of the Alaudidae family. Originally, was marked as *Turdus* sp. indet. (Hír *et al.* 2001).

– *Alauda* Linnaeus, 1758

– *Alauda † tivadari* Kessler, 2013

Type locality and age: Polgárdi 4, Late Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). The coracoid is somewhat smaller than in extant species, while the distal fragment of the *tibiotarsus* is equal to it in the size. The extinct species from Felsőtárkány (MN 7–8): *Praealauda hevesensis* Kessler *et* Hír, 2012 differs in its age, sizes and morphological characteristics (Kessler & Hír 2012).

– *Alauda arvensis* Linnaeus, 1758

Q1: Beremend 16 (Hungary) (Jánossy 1992, 1996); Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002); **Q3/I:** Hundsheim (Austria) (Lambrecht 1933, Jánossy 1974a, 1979); **Q4/I:** Hámor-Puskaporos Niche (Hungary) (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986); Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas) (Slovakia) (Lambrecht 1913, 1933);

Q4/II: Ecsegfalva (Hungary) (Pike-Tay *et al.* 2004, Gál 2007); Gyulafehérvár (Alba Iulia) (Gál 2005a, 2005b); Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia) (Kessler 1982) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1**–**2:** France, Ukraine; **Q3**: Austria, Czech Republik, France, Italy, Russia, Spain; **Q4**: Austria, Bulgaria, Czech Republic, Italy, Poland, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

In the Carpathian Basin, the extant genus and species are also known from the Early Pleistocene in Hungary (Beremend 16), Romania (Betfia 9) (Jánossy 1992, Gál 2002). The genus was reported extantly outside the Carpathian Basin in Bulgaria (Upper Pliocene, MN 17, Varshets) as *Alauda xerarvensis* Boev, 2012 (Boev 1996, 2012) and is also known with extant species from the Early Pleistocene from Valerots (France) and Stránská skála (Czech Republic) (Tyrberg 1998). *Alauda gypsorum* Portis, 1887 and *Alauda major* Portis, 1887 (Portis 1887) from the Late Miocene (MN 13) of Seniglia and Gabbro (Italy) were reported in slab as fossil species, but Mlíkovsky (2002) put them into „*Family incertae sedis*".

– *Lullula* Kaup, 1829

– *Lullula † neogradensis* Kessler *et* Hír, 2012

Type locality and age: Mátraszőlős 1, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír 2012).

An extinct *Lullula* species previously was identified as *Pyrrhula* sp. (Gál *et al.* 1999).

– *Lullula †minor* Kessler, 2013

Type locality and age: Polgárdi 4, 5; Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b).

The fossil species differs from extant with its smaller sizes and in some morphological characteristic. The fossil species *Lullula neogradensis* Kessler *et* Hír, 2012 from Mátraszőlős was described based on other bones and its age is much older (Kessler & Hír 2012).

– *Lullula † parva* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b).

It corresponds in characteristics to the extant genus. The fossil species *Lullula neogradensis* Kessler *et* Hír, 2012 from Mátraszőlős 1 and *Lullula † minor* from Polgárdi differ in its age and sizes to Csarnótian and Beremendian specimens.

– *Lullula † minuscula* n. sp.

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). In size corresponds with *Lullula minor* Kessler, 2013 from Polgárdi but is younger in age. It is different in size and in characteristics to *Lullula parva*.

– *Lullula arborea* (Linnaeus, 1758)

Q1: Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002). From sites in Europe outside the Carpathian Basin **Q1–2:** Spain; **Q3:** France, Italy, Spain; **Q4:** Belgium, Bulgaria, Czech Republic, France, Italy, Poland, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

The genus was reported outside the Carpathian Basin in Bulgaria from the Late Miocene Chrabarsko as *Lullula* sp. (Boev 2000), and from the Late Pliocene – Early Pleistocene as *Lullula slivnicensis* Boev, 2012 (Slivnica, MN 17) and *L. balcanica* Boev, 2012 (Varshets, MN 18) based on other skeletal types (Boev 1996, 2012). The extant species *Lullula arborea* was reported from the Late Pliocene and the Early Pleistocene (MN 18) in Mallorca (Spain) (Sondaar *et al.* 1995), but probably they are also fossil species.

– *Calandrella* Kaup, 1829

– *Calandrella † gali* Kessler, 2013

Type locality and age: Polgárdi 4, 5; Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It corresponds in its characteristics to extant species but its size is somewhat different. The genus was reported only from sites in Europe outside the Carpathian Basin:

– *Calandrella cinerea* (J. F. Gmelin, 1789)

Q1–2: Ukraine; **Q4:** Spain, Ukraine (Tyrberg 1998).

– *Calandrella brachydactyla* (Leisler, 1814)

Q3: France, Italy; **Q4:** France, Greece (Tyrberg 1998).

– *Calandrella rufescens* (Viellot, 1820)

Q3: Azerbaijan (Tyrberg 1998).

– *Eremophila* Boie, 1828

– *Eremophila alpestris* (Linnaeus, 1758)

Q4/I: Gencsapáti (Hungary) (Jánossy 1979); **Q4/II:** Grosse Offenbergerhöhle (Austria), (Bocheński & Tomek 1994). From sites in Europe outside the Carpathian Basin **Q1–2:** France; **Q3:** France, Germany, Russia; **Q4:** Belgium, Czech Republic, Germany, Italy, Poland, Russia, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

The genus was reported from Bulgaria: *Eremarida xerophila* Boev, 2012 (Upper Miocene, Hrabarsko); *Eremophila prealpestris* Boev, 2012 (Upper Pliocene, Varshets) (Boev 1996, 2012). The extant species *Eremophila alpestris* (Linnaeus, 1758) was described from the Late Pliocene of Mas Ramboult (France) (Mourer-Chauviré 1975). Finally, Zelenkov (2011) reported the *Eremophila* aff. *E. alpestris* in the Late Pliocene (MN 16) of Beregovaya (Bichursky District, Republic of Buryatia, Russia).

Fam. Hirundinidae Vigors, 1825

– *Hirundo* Linnaeus, 1758

– *Hirundo* † *gracilis* Kesler, 2013

Type locality and age: Polgárdi 4, 5; Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). More slender than the extant species.

– *Hirundo* † *major* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics with extant genus, but its dimensions are larger. This material was reported as *Hirundo* sp. from Csarnóta 2 by Jánossy (1972, 1979). The fossil species *Hirundo* † *gracilis* Kessler, 2012 from Polgárdi is smaller than the Csarnótian specimen.

– *Hirundo rustica* Linnaeus, 1758

Q1: Németóvár 4B (Austria) (Jánossy 1981, Döppes & Rabeder 1997, Mlikovskỳ 1998); Osztramos 8 (Hungary) (Jánossy & Kordos 1976); Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002); **Q2:** Somssich-hegy 2 (Hungary) (Jánossy 1981, 1982, 1983, 1986); Méhész (Vcelare) (Slovakia) (Horáček 1985, Mlikovskỳ 2002); **Q3/I:** Hundsheim (Austria) (Lambrecht 1933, Jánossy 1974a, 1979, Mlikovskỳ 1998, 2002); Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988); Betfia 7/4 (Romania) (Kessler 1975, Jánossy 1979, Gál 2002); **Q4/I:** Budapest-Remetehegyi Niche (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Pilisszántó I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986), Szilvásvárad-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986), Tatabánya-Kálváriahegy 4. Cave (Gál 2005a, 2005b) (all in Hungary); Ohábaponor-Bordu Mare Cave (Ohaba, Peștera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Szegyestel-Măgura Cave (Sighiștel, Peștera Măgura) (Kessler 1982, 1985, Gál 2002) (all in Romania); **Q4/II:** Grosse Offenbergerhöhle (Austria) (Bocheński & Tomek 1994); Hosszúhegyi Cave (Hungary) (Jánossy 1979); Herkulesfürdő-Rablók Cave (Băile Herculane, Peştera Hoţilor) (Kessler 1981, Gál 2002), Révi Caves (Peşterile din Vadu Crișului) (Kessler 1982), Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia) (Kessler 1982) (all in Romania). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic, France, Germany, Italy, Russia, Spain, United Kingdom; **Q4:** Austria, Belgium, Croatia, Czech Republic, France, Germany, Greece, Ireland, Italy, Poland, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Hirundo* sp. foss. indet.

MN 15: Beremend 26 (Hungary) (Kessler 2010); Ivánháza I (Ivanovce I) (Slovakia) (Mlíkovskỳ 2002); **Q1:** Beremend 16 (Hungary) (Jánossy 1992, 1996).

– *Hirundo* sp. indet.

Q2: Nagyharsányhegy 1–4 (Hungary) (Lambrecht 1916, 1933, Jánossy 1978, 1979, 1980); **Q3/II:** Cserépfalu-Hórvölgyi Cave (Hungary) (Jánossy 1979). From sites in Europe outside the Carpathian Basin **Q3:** Italy, Malta; **Q4:** France, Germany, Italy, Poland, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– ***Hirundo rupestris* Scopoli, 1789**

Q4/I: Cserépfalu-Subalyuk Cave (Hungary) (Jánossy 1979).

From sites in Europe outside the Carpathian Basin **Q3:** France, Spain; **Q4:** Belgium, Bulgaria, France, Georgia, Germany, Italy, Poland, Spain, Switzerland (Tyrberg 1998).

– ***Hirundo daurica*** **Linnaeus, 1771**

From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Croatia, France, Germany, Greece, Italy (Tyrberg 1998).

– *Delichon* Moore, 1854

– *Delichon* † *polgardiensis* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It corresponds in its characteristics to extant species but differs in its sizes.

– *Delichon* † *pusillus* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It is smaller as the extant species but mostly corresponds to it in the characteristics.

– *Delichon* † *major* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics with extant species, but has larger sizes.

– *Delichon urbica* (Linnaeus, 1758)

Q1: Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002); **Q4/I:** Tatabánya-Kálváriahegy 4. Cave (Hungary) (Gál 2005a, 2005b); **Q4/II:** Grosse Offenbergerhöhle (Austria) (Bocheński & Tomek 1994); Révi Caves (Peşterile din Vadu Crișului) (Romania) (Kessler 1982). From sites in Europe outside the Carpathian Basin **Q1–2:** Czech Republic (Stránská skála, Mlíkovskỳ 1995) and Spain (Quibas) (Montoya *et al.* 1999); **Q3:** Russia, Ukraine; **Q4:** Croatia, Czech Republic, France, Greece, Ireland, Italy, Russia, Ukraine, United Kingdom (Tyrberg 1998).

– *Riparia* Forster, 1817

– *Riparia* † *minor* Kessler, 2013

Type locality and age: Polgárdi 4, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Differs from extant species in some morphological characteristics and in its smaller sizes.

– *Riparia riparia* (Linnaeus, 1758)

Q1: Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002). From sites in Europe outside the Carpathian Basin, the species is known from the Early Pleistocene (**Q1**) from Czech Republic (Stránská skála) (Mlikovskỳ 1995); **Q3:** France; **Q4:** France, Italy (Tyrberg 1998).

Fam. Paridae Boie, 1826

– *Aegithalos* Hermann, 1804

– *Aegithalos* † *gaspariki* Kessler, 2013

Type locality and age: Polgárdi 4, 5; Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It corresponds more in characteristics and sizes to extant species of the genus.

– *Aegithalos* † *congruis* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It mostly corresponds with extant species in the characteristics and sizes.

– *Aegithalos caudatus* (Linnaeus, 1758)

Q1: Betfia 2 (Romania) (Kormos 1913, Čapek 1917);

The genus is known in fossil material with extant species in **Q1**–**2:** from S'Onix-Mallorca – Spain (Sondaar *et al.* 1995); **Q3:** France; **Q4:** Italy, Poland, Ukraine (Tyrberg 1998).

– *Parus* Linnaeus, 1758

– *Parus* † *medius* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It is among the medium-sized tits.

– *Parus* † *robustus* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It is fossil species with larger dimensions than extant *Parus major*.

– *Parus* † *parvulus* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It is small tit species.

– *Parus coeruleus* Linnaeus, 1758

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/I:** Mixnitz – Drachenhöhle (Austria) (Lambrecht 1933). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic; **Q4:** Germany (Tyrberg 1998).

– *Parus major* Linnaeus, 1758

Q1: Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002); **Q2:** Kiskóh-Medve Cave (Chiscău, Peștera Urșilor) (Romania) (Kessler 1982, Jurcsák & Kessler 1988, Gál 2002); **Q3/I:** Hundsheim (Austria) (Lambrecht 1933, Jánossy 1974a, 1979); Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988); **Q4/I:** Merkenstein (Austria) (Wettstein & Mülhofer 1938); Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988); Kőrösmart (Rîpa) (Romania) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002); **Q4/II:** Hosszúhegyi Cave (Hungary) (Jánossy 1979). From sites in Europe outside the Carpathian Basin **Q1–2:** Spain, Ukraine; **Q4:** Austria, Bosnia-Herczegovina, Croatia, Czech Republic, France, Germany, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Parus lugubris* Temminck, 1820

Q1: Betfia 2 (Romania) (Kormos 1913, Čapek 1917).

– *Parus ater* Linnaeus, 1758

Q3: Tarkő 1 (Hungary) (Jánossy 1979). From sites in Europe outside the Carpathian Basin **Q1–2:** Spain, **Q4:** Czech Republic, France, Ukraine (Tyrberg 1998).

– *Parus palustris* Linnaeus, 1758

Q3: Hundsheim (Austria) (Lambrecht 1933, Jánossy 1974a, 1979). From sites in Europe outside the Carpathian Basin **Q3:** Germany; **Q4:** Austria, Croatia (Tyrberg 1998).

– *Parus montanus* Conrad, 1827

Q4/I: Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988). From sites in Europe outside the Carpathian Basin **Q4:** Austria, France (Tyrberg 1998).

– *Parus cristatus* Linnaeus, 1758

Only from sites in Europe outside the Carpathian Basin **Q1–2:** Spain; **Q3:** France, Spain; **Q4:** France, Poland, Ukraine (Tyrberg 1998).

– *Parus* sp.

Q3/II: Uppony I/1 (Hungary) (Jánossy 1979); **Q4/I:** Érd (Hungary) (Jánossy 1979). From sites in Europe outside the Carpathian Basin **Q4:** Ukraine (Tyrberg 1998).

– *Panurus* Koch, 1816

– *Panurus biarmicus* (Linnaeus, 1758)

From sites in Europe outside the Carpathian Basin **Q4:** Germany (Tyrberg 1998). The family is known outside the Carpathian Basin only from the Late Pliocene from Varsets (MN 17, Bulgaria) as *Parus* sp. (Boev 2000).

Fam. Sittidae Bonaparte, 1831

– *Sitta* Linnaeus, 1758

– *Sitta † gracilis* Kessler, 2013

Type locality and age: Polgárdi 4, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Its size is smaller than in extant species.

– *Sitta † pusilla* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). The dimensions of fossil species are smaller than those of extant species. The *Sitta gracilis* from Polgárdi was described also on the basis of carpometacarpus. It is larger than the Csarnótian specimen and differs from it in shape of the *processus extensorius*; that of the Polgárdi specimen is shorter than in the Csarnótian remains. The *processus alularis* is more pointed. The characteristics correspond in general to extant species. Jánossy (1995) reported these bones as *Sitta* sp.

– *Sitta † villanyensis* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics and size with extant species and differs in these to extinct species from Polgárdi and Csarnóta, which are much smaller. Previously was reported as *Sitta* sp. foss. indet. (Kessler 2010).

– *Sitta europaea* Linnaeus, 1758

Q1: Németóvár 4B (Austria) (Jánossy 1981); Betfia 9 (Romania) (Gál 2002); **Q2:** Somssich-hegy 2 (Hungary) (Jánossy 1981, 1982, 1983, 1986); **Q4/I:** Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988); **Q4/II:** Bodajk-Rigólyuk (Hungary) (Kordos 1984); Szkerisoara-Coiba Mare Cave (Scărişoara, Peştera Coiba Mare) (Romania) (Kessler 1985). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic, Ukraine; **Q4:** Austria, Bosnia-Herczegovina, Bulgaria, Croatia, Czech Republic, France, Poland, Ukraine (Tyrberg 1998).

– Sittidae gen *et* sp. foss. indet.

MN 6: Kőalja 2 (Subpiatra 2) (Romania) (Kessler & Venczel 2009).

The genus is known outside the Carpathian Basin only from the Early Pliocene (MN 16) from Rebielice Królowskie I. (Poland) as *Sitta* sp. (also with smaller sizes) (Jánossy 1974b) and from the Late Pliocene from Varsets (MN 17, Bulgaria) (Boev 1996, 2000). The fossil species *Sitta senogalliensis* Portis, 1887 from Senigallia (Upper Miocene, MN 13, Italy) was put by Mlíkovsky (2002) into *"Family incertae sedis"*.

Fam. Certhiidae Vigors, 1825

– *Certhia* Linnaeus, 1758

– *Certhia † janossyi* Kessler *et* Hír, 2012

Type locality and age: Rudabánya, Upper Miocene (MN 9) (Hungary) (Kessler & Hír 2012). It corresponds with extant species in the characteristics and sizes.

– *Certhia † immensa* Kessler, 2012

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). The sizes are larger than in extant species. The fossil material was reported previously as *Certhia* sp. (Kessler 2010).

– *Certhia familiaris* Linnaeus, 1758

Q1: Betfia 2 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002). From sites in Europe outside the Carpathian Basin as *Certhia* sp. **Q4:** France, Germany (Tyrberg 1998).

– Certhiidae gen. *et* sp. foss. indet.

MN 6: Kőalja 2 (Subpiatra 2) (Romania) (Kessler & Venczel 2009).

The family and genus was reported with fossil species only from the Carpathian Basin.

Fam. Tichodromidae Swainson, 1827

– *Tichodroma* Illiger, 1811

– *Tichodroma † capeki* Kessler, 2013

Type locality and age: Polgárdi 4, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Its characteristics correspond to extant species. The family and genus were reported as fossil and extant species only from the Carpathian Basin and from **Q4:** Italy, Poland (Tyrberg 1998).

Fam. Muscicapidae Vigors, 1825

– *Muscicapa* Linnaeus, 1766

– *Muscicapa † leganyii* Kessler *et* Hír, 2012

Type locality and age: Felsőtárkány, Middle Miocene (MN 7–8) (Jánossy 1979) (Kessler & Hír 2012). Other locality and age: Felnémet 2/3, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír 2012).

It corresponds with extant species sizes.

– *Muscicapa † miklosi* Kessler, 2013

Type locality and age: Polgárdi 4, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics and sizes to extant species of the genus.

– *Muscicapa † petényii* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics and in dimensions to extant species of *Muscicapa (Ficedula)* genus.

– *Muscicapa* aff. *striata* (Pallas, 1764)

Q1: Betfia 9 (Romania) (Gál 2002); **Q3/I:** Hundsheim (Austria) (Lambrecht 1933, Jánossy 1974a, 1979); **Q4/II:** Bodajk-Rigó Niche (Kordos 1984), Hosszúhegyi Cave (Jánossy 1979) (all in Hungary).

From sites in Europe outside the Carpathian Basin **Q4:** Belgium, Greece (Tyrberg 1998).

– *Ficedulla albicollis* (Temminck, 1815)

From sites in Europe outside the Carpathian Basin **Q3:** France, Germany; **Q4:** France, Ukraine (Tyrberg 1998).

– *Ficedula hypoleuca* (Pallas, 1764)

From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** France (Tyrberg 1998). The genus is known in Late Pliocene – Early Pleistocene boundary (MN 17–18) from S'Onix – Mallorca (Spain) as *Muscicapa striata* (Pallas, 1764) (Sondaar *et al.* 1995); from Varshets (Bulgaria) as *Muscicapa* sp. (Boev 1996, 2000); from Mas Ramboult (France) as *Ficedula hypoleuca* (Pallas, 1764) (Mourer-Chauviré 1975) and as *Ficedula* sp. from Montoussé (France) (Clot *et al.* 1976).

– *Erithacus* Cuvier, 1801

– *Erithacus* † *horusitskyi* Kessler *et* Hír, 2012

Type locality and age: Mátraszőlős 1, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír 2012). In size, it is similar to *Erithacus* and *Saxicola* species, except for size of the length of proximal epiphysis, while in shape it is more similar to *Erithacus*. Previously was reported as *Parus* sp. (Gál *et al*. 1999).

– *Erithacus* † *minor* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics to extant species, but it is smaller.

– *Erithacus rubecula* (Linnaeus, 1758)

Q1: Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kesssler 1975, Jánossy 1979, Gál 2002); **Q3/I:** Hundsheim (Austria) (Mlíkovskỳ 2009); **Q4/I:** Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988); **Q4/II:** Hosszúhegyi Cave (Hungary) (Jánossy 1979); Szegyestel-völgyi Caves (Peșteri din Valea Sighiștelului) (Romania) (Kessler 1982). From sites in Europe outside the Carpathian Basin **Q1–2:** Spain; **Q3:** France, Italy, United Kingdom; **Q4:** Austria**,** Croatia, France**,** Georgia, Germany, Greece, Ireland, Italy, Spain, Serbia, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– *Erithacus* sp.

Q1: Beremend 17 (Jánossy 1992, 1995).

– *Luscinia* Forster, 1817

– *Luscinia* † *praeluscinia* Kessler *et* Hír, 2012

Type locality and age: Litke 2, Lower Miocene (MN 5) (Hungary) (Kessler & Hír 2012). In size, it is closest to the extant *Luscinia luscinia*.

– *Luscinia* † *jurcsaki* Kessler *et* Venczel, 2011

Type locality and age: Kőalja 2 (Subpiatra) (Romania), Middle Miocene (MN 6) (Hungary) (Kessler & Venczel 2011).

The distal fragment of the femur typically refers to the family of flycatchers (Muscicapidae). It was previously reported as such (Kessler & Venczel 2009). Within this, it differs in size from the larger genus *Muscicapa, Saxicola, Erithacus, Phoenicurus* and much smaller than the genus *Oenanthe* and *Monticola*.

– ***Luscinia* † *denesi* Kessler, 2013**

Type locality and age: Polgárdi 4, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics to the extant genus. Previously was reported as *Luscinia* sp. (Jánossy 1991, 1995).

– *Luscinia* † *pliocaenica* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). The characteristics of bones correspond to extant genus despite the damages; however, they have larger dimensions than in extant species.

– *Luscinia luscinia* (Linnaeus, 1758)

Q1: Betfia 9 (Romania) (Gál 2002). From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Austria, Germany, Italy, Spain, United Kingdom (Tyrberg 1998).

– *Luscinia megarhynchos* C. L. Brehm, 1831

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/II:** Bodajk-Rigólyuk (Hungary) (Kordos 1984). From sites in Europe outside the Carpathian Basin **Q4:** Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Luscinia svecica* (Linnaeus, 1758)

Q3/I: Hundsheim (Austria) (Mlíkovskỳ 2009). From sites in Europe outside the Carpathian Basin **Q4:** Germany (Tyrberg 1998).

– *Luscinia* sp.

Q1: Németóvár 4B (Deutsch-Altenburg) (Austria) (Jánossy 1981) (after Mlikovskỳ 1998 is *Sylvia atricapilla*). From sites in Europe outside the Carpathian Basin **Q4:** Germany (Tyrberg 1998).

The genus was reported outside the Carpathian Basin as *Luscinia svecica* (Linnaeus, 1758) by Jánossy from Rebielice I. (Upper Pliocene, Poland) (Jánossy 1974) and from Stránská skála (**Q1**, Czech Republic) (Jánossy 1972).

– *Saxicola* Bechstein, 1892

– *Saxicola* † *lambrechti* Kessler, 2013

Type locality and age: Polgárdi 4, 5; Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics and sizes to extant species of the genus.

– *Saxicola* † *baranensis* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Its characteristic corresponds to extant genus and has larger sizes than extant species.

– *Saxicola* † *parva* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Kessler 2013a, 2013b). It is smaller than *S. baranensis*. The characteristics and dimensions correspond to smaller species of the extant genus. It is smaller than *S. baranensis*.

– *Saxicola* † *magna* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Its characteristic corresponds to extant genus and has larger sizes than extant species.

– *Saxicola rubetra* (Linnaeus, 1758)

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/II:** Körösbánlaki Cave (Romania) (Kessler 1982). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic, France, Spain; **Q4:** Czech Republic, France, Ireland, Russia, Ukraine, United Kingdom (Tyrberg 1998).

– *Saxicola torquata* (Linnaeus, 1766)

Q1: Betfia 2 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002); **Q4/I:** Gencsapáti (Hungary) (Jánossy 1979). From sites in Europe outside the Carpathian Basin **Q4:** Germany (Tyrberg).

The genus is known outside the Carpathian Basin more from Early Pleistocene (**Q1**) from Voigstedt (Germany) (Jánossy 1965) and from Quibas (Spain) (Montoya *et al*. 1999).

– *Monticola* Boie, 1822

– *Monticola* † *pongraczi* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds mostly in characteristics and size to extant species.

– *Monticola saxatilis* (Linnaeus, 1766)

Q4/I: Barcarozsnyó Gura Cheii Cave (Peștera Gura Cheii-Râşnov) (Romania) (Gál 1998, 2002). The genus is known only the Middle and the Late Pleistocene to extant species from France, Spain (Tyrberg 1998).

– *Monticola solitarius* (Linnaeus, 1758)

The extant species is known only outside of Carpathian Basin **Q3:** France; **Q4:** France, Greece, Spain (Tyrberg 1998).

– *Phoenicurus* Forster, 1817

– *Phoenicurus* † *erikai* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics to extant genus, but it is similar in size to smaller extant species.

– *Phoenicurus* † *baranensis* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Its characteristic corresponds to the extant genus but has larger dimensions.

– *Phoenicurus phoenicurus* (Linnaeus, 1758)

Q3/I: Hundsheim (Austria) (Jánossy 1974a). From sites in Europe outside the Carpathian Basin **Q3:** France, Germany; **Q4:** Czech Republic, France, Germany, Russia, Ukraine, United Kingdom (Tyrberg 1998).

– *Phoenicurus ochrurus* (Gmelin, 1789)

Q4/II: Grosse Offenbergerhöhle (Austria) (Bocheński & Tomek 1994).

The genus was reported only from Quibas – Spain (Lower Pleistocene, **Q1**) (Montoya *et al*. 1999).

– *Oenanthe* Viellot, 1816

– *Oenanthe* † *kormosi* Kessler, 2013

Type locality and age: Polgárdi 4, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). In its characteristics and sizes close to the extant species *Oenanthe oenanthe* (Linnaeus, 1758) but is somewhat larger than that and alsoother species inthe family, but it is smaller than *Monticola.*

– *Oenanthe* † *pongraczi* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It mostly corresponds in charachteristics to extant species *Oenanthe oenanthe* but is larger.

– *Oenanthe oenanthe* (Linnaeus, 1758)

Q3/I: Hundsheim (Austria) (Lambrecht 1933, Jánossy 1979); **Q4/II:** Grosse Offenbergerhöhle (Austria) (Bocheński & Tomek 1994); Hosszúhegyi Cave (Hungary) (Jánossy 1979).

– *Oenanthe hispanica* (Linnaeus, 1758)

The extant species was reported outside of Carpathian Basin from **Q3:** France; **Q4:** Greece (Tyrberg 1998).

– *Oenanthe leucura* (J. F. Gmelin, 1789)

Q4: France (Tyrberg 1998).

The earliest report of the genus outside the Carpathian Basin is only the Early Pleistocene (**Q1**) from Stránská skála (Czech Republic) (Jánossy 1972); Montoussé 5. (France) (Clot *et al*. 1976); Quibas (Spain) (Montaya *et al.* 1999).

The fossil species indicated here from Polgárdi, Csarnóta 2 and Beremend 26 was reported previously as Muscicapidae sp. foss. indet. (Kessler 2010).

Fam. Turdidae Rafinesque, 1815

– **†*Turdicus* Kretzoi, 1962**

– †*Turdicus matraensis* Kessler *et* Hír, 2012

Type locality and age: Mátraszőlős 3, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír 2012).

Their features are partly consistent with the new genus described by Miklós Kretzoi from the Betfia 5 (Lower Pleistocene) site by a left coracoid (1962), as the bone is more graceful (?) than the extant species. However, it differs in size from the genus type species (*Turdicus tenuis* Kretzoi, 1962), which is similar in size to that of the Mistle Thrush *(Turdus viscivorus)*.

– †*Turdicus pannonicus* Kessler, 2013

Type locality and age: Polgárdi, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It presents morphological characteristics corresponding to the genus and intermediate dimensions between *Turdicus matraensis* and *T. tenuis*.

– † *Turdicus tenuis* Kretzoi, 1962

Type locality and age: Betfia 5, Q2 (Romania) (Kretzoi 1962).

The original diagnosis is that it is typically a gracillary bone. Unfortunately, the holotype has been lost, and image-size and dimensions have not been reported, so it is considered as ‘nomen nudum’ (Brodkorb 1978, Mlikovskỳ 2002).

The fossil genus has not yet been identified from the area outside the Carpathian Basin, but here it is continuously present from the Middle Miocene to the Lower Pleistocene.

– *Turdoides* Cretzschmar 1826

– *Turdoides* † *borealis* Jánossy, 1979

Type localities and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Jánossy 1979); other locality and age: Osztramos 1, Pliocene (MN 16) (Hungary) (Jánossy 1979). It is smaller in size than *Turdus philomelos* and *T. iliacus*. The genus had not been labeled elsewhere from fossil material.

– *Turdus* Linnaeus, 1758

– *Turdus* † *miocaenicus* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Its size and characteristics are very similar to extant larger trushes' *(Turdus pilaris/ viscivorus/torquatus)* size.

– *Turdus † polgardiensis* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). In size, it is similar to medium-size thrushes *(Turdus merula)*. In the morphological characteristics, it is more similar to larger species of the genus.

– *Turdus † major* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Its characteristics are similar to extant species and has the size of *T. torquatus*.

– *Turdus † medius* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristies to extant genus, and in dimensions to *Turdus merula.*

– *Turdus † praeminor* Kessler, 2019 / *syn: Turdus minor* Kessler 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristies to extant genus, and in dimensions to *Turdus philomelos,* but it is smaller. Originally was named as *T. minor*, but since the name is already reserved for one of the extant species in the Bahamas Islands, it has been renamed.

– *Turdus torquatus* Linnaeus, 1758

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/I:** Kőrösmart (Rîpa) (Romania) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002); **Q4/II:** Teufelslucke (Austria) (Soergel 1966). From sites in Europe outside the Carpathian Basin; **Q3:** France, Germany, Spain; **Q4:** Austria, Bulgaria, Croatia, Czech Republic, France, Germany, Italy, Poland, Spain, United Kingdom (Tyrberg 1998).

– *Turdus merula* Linnaeus, 1758

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q3/I:** Tarkő 1 (Hungary) (Jánossy 1979); Betfia 7/4 (Romania) (Kessler 1975, Jánossy 1979, Gál 2002); **Q4/I:** Krapina (V. Malez 1973, 1984, V. Malez-Bačić 1975), Velika Pecina (V. Malez 1975, 1984, 1988), Veternica (V. Malez 1973, 1988, V. Malez-Bačić 1975) (all in Croatia); Tatabánya-Kálváriahegy 4. Cave (Hungary) (Gál 2005a, 2005b); Kőrösmart (Rîpa) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura), Szegyestel-Tibocoaia Cave (Sighiștel) (Kessler 1982, 1985, Gál 2002) (all in Romania); **Q4/II:** Teufelslucke (Austria) (Soergel 1966); Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Legény Cave (Kormos 1914), Miskolc-Névtelen Cave (Kessler 2010) (all in Hungary); Körösbánlaki Cave (Peştera din Bălnaca) (Kessler 1982), Püspökfürdő Lake (lacul din Băile Episcopești) (Kessler 1974b, 1985), Révi Caves (Peşterile din Vadu Crişului), Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia), Szegyestelvölgyi Caves (Peșteri din Valea Sighiștelului) (Kessler 1982), Szkerisoara-Coiba Mare Cave (Scărişoara, Peştera Coiba Mare) (Kessler 1982, Jurcsák & Kessler 1986, 1988), Vargyasi-szoros – Homoródalmási Caves (Peșteri din Defileul Vârghișului) (Jurcsák & Kessler

1986, 1988) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1–2:** France; **Q3:** Azerbaijan, Czech Republic, France, Italy, Spain, Ukraine, United Kingdom; **Q4:** Austria, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Ireland, Italy, Luxemburg, Montenegro, Moldova, Poland, Serbia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Turdus philomelos* C. L. Brehm, 1831

Q1: Németóvár (Austria) (Jánossy 1981); Beremend 16 (Hungary) (Jánossy 1992); Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q3/I:** Hundsheim (Austria) (Lambrecht 1933, Jánossy 1974a, 1979); Süttő 1–4 (Hungary) (Jánossy 1979); **Q4/I:** Merkenstein (Austria) (Wettstein & Mühlhofer 1938); Budapest-Remetehegyi Niche (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Hámor-Herman Ottó Cave (Lambrecht 1915, 1933), Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986) (all in Hungary); Barcarozsnyó (Peștera Gura Cheii-Râşnov) (Gál 1998, 2002), Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura), Szegyestel-Tibocoaia Cave (Sighiștel, Peştera Tibocoaia) (Kessler 1982, 1985, Gál 2002) (all in Romania); Óruzsin-Antal Cave (Oruzer) (Slovakia) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933); **Q4/II:** Legény Cave (Kormos 1914), Ordacsehi-Kistöltés (Gál 2004, 2005b) (all in Hungary); Peterd-Tordai Defile, Magyar Cave (Petreşti, Cheile Turzii-Peștera Ungurească) (Kessler & Gál 1998, Gál 2005b), Remetelórév-Bólyikői Cave (Lorău-Peştera din Piatra Boiului) (Kessler 1982), Révtizfalusi Cave (peştera din Zece Hotare) (Kessler 1985), Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia), Szegyestel-völgyi Caves (Peşteri din Valea Sighiştelului) (Kessler 1982), Vársonkolyosi Caves (peşteri din (Şuncuiuș)) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1–2:** Bulgaria; **Q3:** Ukraine; **Q4:** Belgium, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Ireland, Italy, Portugal, Poland, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– *Turdus iliacus* Linnaeus, 1766

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q2:** Nagyharsányhegy 1–4 (Hungary) (Kessler 2010); **Q3/I:** Hundsheim (Austria) (Lambrecht 1933, Jánossy 1979); **Q4/I:** Barcarozsnyó (Romania) (Gál 1998, 2002); Hámor-Puskaporos (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986), Szilvásvárad-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986) (all in Hungary); Barcarozsnyó – Gura Cheii Cave (Peștera Gura Cheii-Râşnov) (Romania) (Gál 1998, 2002); **Q4/II:** Teufelslucke (Austria) (Soergel 1966). From sites in Europe outside the Carpathian Basin **Q1–2:** France, Spain; **Q3:** Azerbaijan, France, Italy, Spain, Ukraine, United Kingdom; **Q4:** Austria, Belgium, Czech Republic, France, Greece, Germany, Ireland, Italy, Portugal, Poland, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– Turdus iliacus / T. musicus (=philomelos)

Q4/I: Szilvásvárad-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986) (all in Hungary);

– Turdus viscivorus / T. torquatus

Q4/I: Varbó-Lambrecht Kálmán Cave (Hungary) (Jánossy 1964,1979);

– *Turdus viscivorus* Linnaeus, 1758

Q1: Németóvár (Deutsch-Altenburg) (Austria) (Jánossy 1981); Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q3/I**: Hundsheim (Lambrecht 1933, Jánossy 1974a, 1979), Merkenstein (Wettstein & Mühlhofer 1938) (all in Austria); Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988); **Q4/I:** Krapina (Lambrecht 1915, V. Malez 1973, 1984), Velika pec na Lipi (V. Malez 1975, 1984, V. Malez-Bačić 1975, 1979) (all in Croatia); Budapest-Remetehegyi Niche (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Csobánka-Kiskevélyi Cave (Lambrecht 1912, 1915, 1933, Jánossy 1979), Felsőtárkány-Peskő Cave (Lambrecht 1912, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Niche (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986), Hámor-Herman Ottó Cave (Lambrecht 1915, 1933), Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986), Répáshuta-Balla Cave (Lambrecht 1912, 1933), Szilvásvárad-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986) (all in Hungary); Barcarozsnyó-Gura Cheii Cave (Peștera Gura Cheii-Râşnov) (Gál 1998, 2002), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Szegyestel-Măgura Cave, Szegyestel-Tibocoaia Cave (Peștera Tibocoaia) (Sighiștel) (Kessler 1982, 1985, Gál 2002) (all in Romania); Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas) (Slovakia) (Lambrecht 1913, 1933); **Q4/II:** Teufelslucke (Austria) (Soergel 1966); Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Felsőtárkány-Petényi Cave (Jánossy 1979), Hosszúhegyi Cave (Jánossy 1979) (all in Hungary); Herkulesfürdő-Rablók Cave (Băile Herculane, Peştera Hoţilor) (Kessler 1981, Gál 2002), Körösbánlaki Cave (Peştera din Bălnaca) (Kessler 1982), Peterd-Tordai Defile – Magyar Cave (Petrești, Cheile Turzii-Peștera Ungurească) (Kessler & Gál 1998, Gál 2005a), Révi Caves (Peşterile din Vadu Crişului) (Kessler 1982), Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia) (Kessler 1982), Szkerisoara-Sasok Cave (Scărişoara, Peştera Vulturilor) (Kessler 1982, Jurcsák & Kessler 1986, 1988), Vársonkolyos-Izbîndiş Cave, Vársonkolyos-Kis Magyar Cave (Şuncuiuş, Peştera Izbîndiş; Peştera Napiştileu),Vársonkolyosi Caves (Şuncuiuş) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1–2:** France, Spain; **Q3:** Czech Republic, France, Italy, Russia, Spain; **Q4:** Belgium, Croatia, Czech Republic, France, Germany, Greece, Ireland, Italy, Moldova, Poland, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Turdus pilaris* Linnaeus, 1758

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q3/II:** Süttő 1–4 (Hungary) (Jánossy 1979); **Q4/I:** Bajót-Öregkő (Kormos 1914), Budapest-Remetehegyi Niche (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Felsőtárkány-Peskő Cave (Lambrecht 1912, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Niche (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986), Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986), Répáshuta-Balla Cave (Lambrecht 1912, 1933), Szilvásvárad-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986) (all in Hungary); Hidegszamos-Csont Cave (Someşul Rece-Peştera cu Oase) (Lambrecht 1915), Kőrösmart (Rîpa) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002), Nándor-Nándori Cave (Nandru-Peştera

Curata) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura) (Kessler 1982, 1985, Gál 2002) (all in Romania); Óruzsin-Antal Cave (Oruzer) (Slovakia) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933); **Q4/II:** Teufelslucke (Austria) (Soergel 1966); Felsőtárkány-Petényi Cave (Jánossy 1979); Legény Cave (Lambrecht 1914), Répáshuta-Rejteki Niche (Jánossy 1962, 1979, 1986) (all in Hungary); Peterd-Tordai-Defile – Magyar Cave (Petrești, Cheile Turzii-Peștera Ungurească) (Kessler & Gál 1998, Gál 2004), Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia), Szegyestel-völgyi Caves (peşteri din Valea Sighiştelului) (Kessler 1982), Szkerisoara-Sasok Cave (Scărişoara, Peştera Vulturilor).

(Kessler 1982, Jurcsák & Kessler 1986, 1988), Vargyasi-szoros – Homoródalmási Caves (peșteri din Defileul Vârghișului) (Jurcsák & Kessler 1986, 1988), Vársonkolyos-Izbîndiş Cave (Şuncuiuş, Peştera Izbîndiş) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic, France, Germany, Italy, Spain; **Q4:** Austria, Belgium, Croatia, Czech Republic, France, Germany, Greece, Ireland, Italy, Portugal, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– Turdus pilaris / T. merula

Q4/I: Szamosfalva (Someșeni) (Romania) (Kormos 1913, Lambrecht 1933);

– *Turdus* sp. foss. indet.

MN 7–8: Felsőtárkány (Hungary) (Hír *et al.* 2001); **MN 13:** Polgárdi 4 (Hungary) (Jánossy 1991, 1995 – as: *Turdus iliacus*); **MN 15:** Ivánháza I (Ivanovce I) (Slovakia) (Švec in Fejfar & Heinrich 1985, Mlíkovskỳ 2002); **MN 15:** Csarnóta 2 (Jánossy 1979 – as: *Turdus viscivorus*), Beremend 26 (Kessler 2010) (all in Hungary); **MN 16:** Betfia 13 (Romania) (Kessler 1975, Gál 2002);

– *Turdus* sp. indet.

Q1: Németóvár 4B (Deutsch-Altenburg) (Austria) (Jánossy 1981, Döppes & Rabeder 1997, Mlíkovskỳ 1998); Beremend 17 (Hungary) (Kessler 2010); Betfia 9 (Romania) (Gál 2002); **Q2:** Nagyharsányhegy 1–4 (Hungary) (Lambrecht 1916, 1933, Jánossy 1979); **Q3/I:** Hundsheim (Austria) (Mlíkovskỳ 2009); **Q3/II:** Süttő 1–4 (Hungary) (Kessler 2009); **Q4/I:** Csobánka-Kiskevélyi Cave (Lambrecht 1912, 1915, 1933, Jánossy 1979), Felsőtárkány-Peskő Cave (Lambrecht 1912, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Niche (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986), Száraz-Gerence (Jánossy 1979, 1986) (all in Hungary); Kőrösmart (Rîpa) (Romania) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002). From sites in Europe outside the Carpathian Basin **Q1–2:** Croatia, Germany; **Q3:** Czech Republic, Gerorgia, Grece, Germany, Italy, Poland, Spain, Turkey; **Q4:** Austria, Belgium, Bosnia-Herczegovina, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Ireland, Italy, Malta, Moldova, Poland, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

The genus it is known outside of the Carpathian Basin from Credinta – Romania (Middle Miocene, MN 8) as *Turdus* sp. (Gál & Kessler 2006), while from the Late Pliocene from Rebielice Królowskie I. – Poland (Jánossy 1974b), Varshets-Bulgaria (Boev 1996, 2000), Sandalja I. – Croatia (V. Malez-Bacic 1979).

Fam. Oriolidae Boie, 1826

– *Oriolus* Linnaeus, 1758

– *Oriolus* † *beremendensis* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds partially with charateristics and size of the extant species.

– *Oriolus oriolus* (Linnaeus, 1758)

Q1: Betfia 9 (Romania) (Gál 2002); **Q3:** Vindija (V. Malez 1973, 1988) (Croatia); **Q4/I:** Budapest-Remetehegyi Niche (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986) (all in Hungary); **Q4/II:** Peterd-Tordai-Defile – Magyar Cave (Petreşti, Cheile Turzii-Peştera Ungurească) (Kessler & Gál 1998, Gál 2005a), Révi Caves (Peşterile din Vadu Crișului) (Kessler 1982) (all in Romania).

The family and genus have no other extinct species. The extant species *Oriolus oriolus* is known from some localities from the Late Pleistocene (**Q4**) in Europa: Bosnia-Herczegovina, Croatia, Czech Republic, France, Germany, Italy (Tyrberg 1998).

Fam. Sylviidae Vigors, 1825

– *Acrocephalus* Naumann, 1811

– *Acrocephalus* † *major* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics and sizes to extant larger species of the genus.

– *Acrocephalus* † *minor* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Corresponds in characteristic to smaller species of the genus. The fosil species from Polgárdi was reported previously as *Acrocephalus* sp. by Jánossy (1991, 1995).

– *Acrocephalus* † *kretzoii* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Its characteristics correspond to extant genus but in dimensions more similar to a larger species.

– *Acrocephalus* † *kordosi* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Its characteristics correspond to extant genus, but its dimensions place it among the smaller species.

– *Acrocephalus* sp. foss. indet.

MN 9: Rudabánya (Hungary) (Jánossy 1993); **MN 16:** Beremend 26 (Hungary) (Kessler 2010); **Q1:** Betfia 9 (Romania) (Gál 2002).

– *Acrocephalus palustris* (Bechstein, 1811)

Q1: Betfia 2 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002). From sites in Europe outside the Carpathian Basin **Q4:** France (Tyrberg 1998).

– *Acrocephalus paludicola* (Viellot, 1817)

From sites in Europe outside the Carpathian Basin **Q4:** France (Tyrberg 1998).

– *Acrocephalus schoenobaenus* (Linnaeus, 1758)

From sites in Europe outside the Carpathian Basin **Q4:** United Kingdom (Tyrberg 1998).

– *Acrocephalus scirpaceus* (Hermann, 1894)

From sites in Europe outside the Carpathian Basin **Q4:** Spain (Tyrberg 1998).

– *Acrocephalus arundinaceus* (Linnaeus, 1758)

From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Austria, France, Romania (Tyrberg 1998).

– *Acrocephalus* sp.

Q4/II: Ecsegfalva (Hungary) (Pike-Tay *et al.* 2004, Gál 2007).

From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic **Q4:** France (Tyrberg 1998).

– *Cettia* Bonaparte, 1838

– *Cettia* † *janossyi* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics and sizes to extant species. This material was reported previously as *Cettia* sp. by Jánossy (1991).

– *Cettia* † *kalmani* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Its characteristics correspond to extant species, but the fossil species is bigger in sizes than extinct species from Polgárdi *Cettia janossyi* or than the extant species. The genus was reported only from the Carpathian Basin.

– ***Hippolais* C. von Baldenstein, 1827**

– *Hippolais* † *veterior* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Its characteristics mostly correspond to those of extant genus.

– *Hippolais* sp. foss. indet.

MN 15: Csarnóta 2 (Hungary) (Jánossy 1979); **Q1:** Betfia 2 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002). The genus was reported outside the Carpathian basin only from France (Upper Pleistocene, **Q4**) with extant species *Hippolais icterina* (Vieillot, 1817) (Tyrberg 1998).

– *Sylvia* Scopoli, 1769

– *Sylvia* † *intermedia* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). The bones belong to medium-size species. The fossil material was reported previously as *Sylvia* sp. by Jánossy (1991).

– *Sylvia* † *pusilla* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). The bones belong to one smaller species.

– *Sylvia atricapilla* (Linnaeus, 1758)

Q1: Betfia 9 (Romania) (Gál 2002); Németóvár (Austria) (Jánossy 1981). From sites in Europe outside the Carpathian Basin **Q1–2:** Spain; **Q3:** France; **Q4:** Czech Republic, France, Spain, United Kingdom (Tyrberg 1998).

– *Sylvia communis* Latham, 1787

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** France (Tyrberg 1998).

– *Sylvia borin* (Boddaert, 1783)

Q3: Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, M. Malez & Rukavina 1979); **Q4/I:** Velika pec na Lipi (Croatia) (V. Malez 1975, 1984, V. Malez-Bačić 1975, 1979). From sites in Europe outside the Carpathian Basin **Q3:** United Kingdom; **Q4:** Croatia (Tyrberg 1998).

– *Sylvia curruca* (Linnaeus, 1758)

Q4/I: Óruzsin-Antal Cave (Oruzer, Antal Cave, Slovakia) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933). From sites in Europe outside the Carpathian Basin **Q4:** Russia (Tyrberg 1998).

– *Sylvia melanocephala* (J. F. Gmelin, 1788)

From sites in Europe outside the Carpathian Basin **Q3:** France (Tyrberg 1998).

– *Sylvia hortensis* (J. F. Gmelin, 1788)

From sites in Europe outside the Carpathian Basin **Q4:** France (Tyrberg 1998).

– *Sylvia nisoria* (Bechstein, 1785)

From sites in Europe outside the Carpathian Basin **Q3:** France (Tyrberg 1998).

– *Sylvia* sp. foss. indet.

MN 15: Beremend 26 (Hungary) (Kessler 2010); **Q1:** Betfia 9 (Gál 2002).

– *Sylvia* sp.

From sites in Europe outside the Carpathian Basin **Q3:** France, Italy; **Q4:** Bosnia-Herczegovina, Greece, United Kingdom (Tyrberg 1998).

– *Locustella* Kaup, 1829

– *Locustella* † *kordosi* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Corresponds in characteristics to species of extant genus.

– *Locustella* † *janossyi* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics to extant genus and in dimensions with smaller-sized extant species.

– *Locustella* † *magna* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics to extant species, but it is larger.

– *Locustella fluviatilis* (Wolf, 1810)

Q1: Betfia 9 (Romania) (Gál 2002).

– *Locustella* sp. foss. indet.

MN 9: Rudabánya (Hungary) (Kretzoi 1975, Jánossy 1993).

Outside of the Carpathian Basin the genus is known only from the Late Pleistocene (**Q4**) of the Czech Republic as *Locustella naevia* (Boddaert, 1783) (Tyrberg 1998).

– *Phylloscopus* Boie, 1826

– *Phylloscopus* † *miocaenicus* Kessler *et* Hír, 2012

Type locality and age: Felsőtárkány, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír 2012).

By its characteristics, it belongs to the genus *Phylloscopus* of the Sylviidae family.

– *Phylloscopus* † *venczeli* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics to extant species of the genus.

– *Phylloscopus* † *pliocaenicus* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Its characteristic corresponds to the extant genus.

– *Phylloscopus* sp. indet.

Q3/I: Hundsheim (Austria) (Lambrecht 1933, Jánossy 1974, 1979).

Outside of Carpathian Basin the genus is known the Late Pliocene from Varsets (MN 17, Bulgaria) as *Phylloscopus* sp. (Boev 1996, 2000); from Cerdzenica – Bulgaria (Lower Pleistocene, **Q1**) (Boev 2000) and in the Late Pleistocene (**Q4**) with extant species *(Phylloscopus bonelli, P. collybita, P. trochilus, P. sibilatrix)* from Czech Republic, France, Italy, Switzerland (Tyrberg 1998).

– *Regulus* Vieillot, 1807

– *Regulus* † *plioceanicus* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics to extant species, but it is larger in its sizes.

– *Regulus* sp.

Q3/I: Hundsheim (Austria) (Lambrecht 1933, Jánossy 1974, 1979); **Q4/II:** Répáshuta-Rejteki Niche (Hungary) (Jánossy 1962, 1979, 1986).

The genus is known from the extinct species *Regulus bulgaricus* Boev, 1999 from Varshets – Bulgaria (Late Pliocene, MN 17) (Boev 1999). The extant species was reported from S'Onix – Mallorca, Spain (Early Pleistocene, **Q1**) (Sondaar *et al.* 1995) and as *Regulus regulus* and *Regulus ignicapilus* from Czech Republic, Poland Spain and Switzerland of the Late Pleistocene from Europa (Tyrberg 1998).

– **Sylviidae gen. *et* sp. foss. indet.**

MN 6: Kőalja 2 (Subpiatra) (Romania) (Kessler & Venczel 2009).

The family is identified from the Miocene and Pliocene only in the Carpathian Basin and in Bulgaria.

Fam. Motacillidae Vigors, 1825

– *Anthus* Bechstein, 1807

– *Anthus* † *antecedens* Kessler *et* Hír, 2012

Type locality and age: Felsőtárkány, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír 2012). It is assigned to pipits with larger stature.

– *Anthus* † *híri* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It corresponds in its characteristics to the extant genus *Anthus,* its sizes are between extant *A. spinoletta* and *A. trivialis,* it belongs to the pipits with a smaller stature.

– *Anthus* † *baranensis* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in its characteristics to smaller-size extant species.

– *Anthus pratensis* (Linnaeus, 1758)

Q4/I: Krapina (Croatia) (V. Malez 1973, 1984, V. Malez-Bačić 1975), Hámor-Puskaporos Niche (Hungary) (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986). From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Austria, Bosnia-Herczegovina, Croatia, Czech Republic, France, Ireland, Spain, United Kingdom (Tyrberg 1998).

– *Anthus cervinus* (Pallas, 1811)

Q3/I: Hundsheim (Austria) (Jánossy 1974).

– *Anthus trivialis* (Linnaeus, 1758)

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/I:** Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988); Hámor-Puskaporos Niche (Hungary) (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986), Hidegszamos-Csont Cave (Someşul Rece, Peştera cu Oase) (Romania) (Lambrecht 1915); **Q4/II:** Herkulesfürdő-Rablók Cave (Băile Herculane, Peştera Hoţilor) (Romania) (Kessler 1981, Gál 2002). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic, France; **Q4:** Bulgaria, Croatia, France, Georgia, Italy, Poland, Ukraine, United Kingdom (Tyrberg 1998).

– *Anthus spinoletta* (Linnaeus, 1758)

Q2: Kövesvárad (Hungary) (Jánossy 1963); **Q4/I:** Óruzsin-Antal Cave (Oruzer, Antal Cave, Slovakia) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933). From sites in Europe outside the Carpathian Basin; **Q3:** France, Germany, Spain; **Q4:** Austrias, France, Spain, Switzerland, United Kingdom (Tyrberg 1998).

– *Anthus* sp. foss. indet.

MN 16: Beremend 15 (Hungary) (Jánossy 1992); **Q1:** Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania).

– *Anthus* sp.

Q4/I: Mixnitz-Drachenhöhle (Austria) (Lambrecht 1933); Pilisszántói I. Niche (Hungary) (Lambrecht 1915, 1933, Jánossy 1979, 1986). From sites in Europe outside the Carpathian Basin; **Q3:** Czech Republic, Georgia, Italy; **Q4:** Belgium, Georgia, Switzerland, Ukraine (Tyrberg 1998).

On outside the Carpathian Basin the genus is known from Rebielice Królowskie 1 – Poland (Upper Pliocene MN 16) (Jánossy 1974); Varseths – Bulgaria (Upper Pliocene, MN 16, MN 17) (Boev 1996, 2000). The fossil species *Anthus bosniaskii* Pycraft 1909 from Gabbro – Italy (Upper Miocene, MN 13) was put by Mlíkovský into „*Family incertae sedis*" (Mlíkovský 2002).

– *Motacilla* Linnaeus, 1758

– *Motacilla* † *intermedia* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). The sizes are intermediate between *M. alba* and *M. cinerea*, but in morphological characteristics it resembles *M. alba*. In several characteristics, it exhibits the mixture of *Anthus* and *Motacilla* types. The remains were reported as *Motacilla* sp. by Jánossy (1991, 1995).

– *Motacilla* † *minor* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in its characteristics with extant *Motacilla flava* but has intermediate dimensions between *M. flava* and *M. cinerea*.

– *Motacilla* † *robusta* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It is more robust than the extant species.

– *Motacilla flava* Linnaeus, 1758

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/I:** Kőrösmart (Rîpa) (Romania) (Jánossy in Hamar & Csák 1969, Kessler 1974, Gál 2002). From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Croatia, France, Switzerland (Tyrberg 1998).

– *Motacilla alba* Linnaeus, 1758

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q4/I:** Pilisszántói I. Niche (Hungary) (Lambrecht 1915, 1933, Jánossy 1979, 1986); **Q4/II:** Körösbánlaki Cave (Peştera din Bălnaca), Kőrösmart (Rîpa) (Kessler 1982), Révi Caves (Peşterile din Vadu Crișului), Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia) (Kessler 1982) (all in Romania). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic, France, Russia; **Q4:** Austria, Czech Republic, Croatia, France, Germany, Poland, Russia, Ukraine, United Kingdom (Tyrberg 1998).

– *Motacilla cinerea* Tunstall, 1771

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/II:** Szegyestel-völgyi Caves (peşteri din Valea Sighiştelului) (Romania) (Kessler 1982). From sites in Europe outside the Carpathian Basin **Q4:** Croatia, United Kingdom (Tyrberg 1998).

– *Motacilla* sp. foss. indet.

MN 7–8: Mátraszőlős 1 (Hungary) (Kessler & Hír 2012);

The fossil species from Polgárdi and Beremend 26 were reported previously as *Motacilla* sp. foss. indet. by Jánossy (1991, 1995) and Kessler (2010).

– *Motacilla* sp.

Q3/I: Hundsheim (Austria) (Lambrecht 1933, Jánossy 1979, Mlikovskỳ 1998, 2002). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic; **Q4:** France, Germany, United Kingdom (Tyrberg 1998).

The genus was described outside of the Carpathian Basin from Varshets – Bulgaria (Upper Pliocene, MN 17) by Boev (1996, 2000), and from Stránská skálá – Czech Republic (Lower Pleistocene, MQ1) by Mlíkovský (1995). The fossil species *Motacilla humata* Milne-Edwards 1871 and *Motacilla major* Milne-Edwards 1871 (Milne-Edwards 1871) from Saint-Gerand-le-Puy – France (Lower Miocene, MN 2) has a disputed situation (Mlíkovský 2002).

Fam. Bombycillidae Swainson, 1832

– *Bombycilla* Swainson, 1832

– *Bombycilla* † *hamori* Kessler *et* Hír, 2012

Type locality and age: Litke 2, Lower Miocene (MN 5) (Hungary) (Kessler & Hír 2012). Other locality and age: Felsőtárkány, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír

2012). Based on morphological characteristics, it is a fossil species with smaller size than the extant *Bombycilla garrulus*.

– *Bombycilla* † *brevia* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b).

The dimensions are much smaller than in the extant species.

– *Bombycilla* † *kubinyii* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in its characteristics and size to extant species. This species was reported initially as *Bombycilla* sp. foss. indet. by Kessler (2010).

– *Bombycilla garrulus* (Linnaeus, 1758)

Q3/I: Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988); **Q4/I:** Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988); Szilvásvárad-Istállóskői Cave (Hungary) (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986); Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura) (Romania) (Kessler 1982, 1985, Gál 2002).From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Belgium, Bosnia-Herczegovina, Croatia, Czech Republic, France, Italy, Poland, United Kingdom (Tyrberg 1998).

– *Bombycilla* sp. foss. indet.

MN 15: Csarnóta 2 (Hungary) (Kessler 2010a); **Q1:** Beremend 17 (Hungary) (Jánossy 1992); Betfia 9 (Romania) (Gál 2002).

The family and genus are known from fossil species in the Neogene only from the Carpathian Basin.

Fam. Troglodytidae Vieillot, 1807

– *Troglodytes* Vieillot, 1807

– *Troglodytes* † *robustus* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). The fossil species differs to the extant in its larger size.

– *Troglodytes troglodytes* (Linnaeus, 1758)

Q4/I: Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988).

The genus is known to extant species from S'Onix – Mallorca – Spain (Early Pleistocene, MN 18) (Sondaar *et al*. 1995) and from **Q3:** France; **Q4:** Croatia, France, Poland, United Kingdom (Tyrberg 1998).

Fam. Cinclidae Cabanis, 1847

– *Cinclus* Borkhausen, 1897

– *Cinclus* † *major* Kessler *et* Hír, 2012

Type locality and age: Litke 2, Lower Miocene (MN 5) (Hungary) (Kessler & Hír 2012). The features of the bone are similar to those of the extant species, but their dimensions are slightly larger.

– *Cinclus* † *gaspariki* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). The remains in general correspond in characteristics to the extant species.

– *Cinclus* † *minor* Kessler, 2013

Type locality and age: Csarnóta 2, Middle Pliocene (MN 15–16) (Hungary) (Kessler 2013a, 2013b). It is smaller than the extant species.

– *Cinclus cinclus* (Linnaeus, 1758)

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/I:** Merkenstein (Austria) (Wettstein & Mühlhofer 1938), Hámor-Herman Ottó Cave (Lambrecht 1915, 1933), Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986) (all in Hungary); Barcarozsnyó-Gura Cheii Cave (Peștera Gura Cheii-Râşnov) (Romania) (Gál 1998, 2002); **Q4/II:** Grosse Offenbergerhöhle (Austria) (Bocheński & Tomek 1994); Peterd-Tordai-Defile-Magyar Cave (Petrești, Cheile Turzii-Peştera Ungurească) (Kessler & Gál 1998, Gál 2005a), Vársonkolyos-Izbindis Cave (Şuncuiuş, Peştera Izbîndiş) (Kessler 1977, Gál 2002) (all in Romania).

It is also known in the Middle Pleistocene (**Q3**) from localities in France and Germany, and in the Late Pleistocene (**Q4**) in Austria, Belgium, Czech Republic, France, Germany, Italy, United Kingdom (Tyrberg 1998).

Fam. Prunellidae Richmond, 1908

– *Prunella* Vieillot, 1818

– *Prunella* † *freudenthali* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). The sizes of the *humerus* corresponds to the extant species *P. modularis*. The sizes of *ulna* and *femur* is slightly smaller than in the extant species.

– *Prunella* † *kormosi* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a). Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a). It is larger than the extant *P. modularis* but smaller than *P. collaris.*

– *Prunella modularis* (Linnaeus, 1758)

Q4/I: Grosse Badlhöhle (Austria) (Fladerer 1993); Eskülllő-Igric Cave (Aștileu, Peştera Igriţa) (Romania) (Kessler 1985). From sites in Europe outside the Carpathian Basin **Q1–2:** Spain; **Q3:** France, Italy; **Q4:** Austria, Germany, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Prunella collaris* (Scopoli, 1769)

Q4/II: Herkulesfürdő-Zoltán Cave (Băile Herculane, Peştera Zoltan) (Gál 2002), Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974, Fischer & Stephan 1977) (all in Romania). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic, France, Greece, Spain; **Q4:** Austria, France, Germany, Greece, Italy, Spain, Switzerland (Tyrberg 1998).

The genus is not known outside the Carpathian Basin with fossil species.

Fam. Laniidae Swainson, 1834

– *Lanius* Linnaeus, 1758

– *Lanius* † *schreteri* Kessler *et* Hír, 2012

Type locality and age: Felsőtárkány, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír 2012).

Other locality: Felnémet 2/3, Middle Miocene (MN 7–8) (Hungary) (Kessler & Hír 2012). Based on its characteristics, it is equivalent to *Lanius excubitor*, though larger than it.

– *Lanius* † *capeki* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). In general, it corresponds in characteristics and sizes to the extant *L. collurio.*

– *Lanius* † *hungaricus* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in size to extant *Lanius collurio*.

– *Lanius* † *major* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). The remains derive from two different-sized specimens. The humerus is mostly smaller than the extant *L. excubitor,* the carpometacarpus and tarsometatarsus derived from the large specimens.

– *Lanius* † *intermedius* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It has intermediate dimensions between extant species *L. minor* and *L. collurio,* and differs in characteristics to the much smaller *L. hungaricus* Kessler, 2012 from Csarnóta.

– *Lanius excubitor* Linnaeus, 1758

Q1: Betfia 9 (Romania) (Gál 2002); **Q3/II:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988); **Q4/I:** Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura) (Romania) (Kessler 1982, 1985, Gál 2002); **Q4/II:** Kevélynyergi Cave (Hungary) (Kessler 2010); Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia) (Romania) (Kessler 1982). From sites in Europe outside the Carpathian Basin **Q4:** Austria, Croatia, France, Germany, Poland, Spain, Switzerland (Tyrberg 1998).

– *Lanius collurio* Linnaeus, 1758

Q2: Betfia 7 (Romania) (Kessler 1975, Gál 2002); **Q4/I:** Merkenstein (Austria) (Wettstein & Mühlhofer 1938); Budapest-Remetehegyi Niche (Hungary) (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986). From sites in Europe outside the Carpathian Basin **Q4:** Austria, Bulgaria, Czech Republic, France, Germany, Moldova, Ukraine, United Kingdom (Tyrberg 1998).

– *Lanius minor* Gmelin, 1788

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q4/I:** Pilisszántói I. Niche (Hungary) (Lambrecht 1915, 1933, Jánossy 1979, 1986); Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura) (Romania) (Kessler 1982, 1985, Gál 2002); **Q4/II:** Révi Caves (Peşterile din Vadu Crișului) (Romania) (Kessler 1982). From sites in Europe outside the Carpathian Basin **Q1–2:** Greece; **Q4:** Spain (Tyrberg 1998).

– *Lanius senator* Linnaeus, 1758

Q4: Pilisszántó 1 (Lambrecht 1915, 1933, Jánossy 1986), Puskaporos (Lambrecht 1933, Jánossy 1986) (all in Hungary). From sites in Europe outside the Carpathian Basin **Q3:** France, Italy, Spain; **Q4:** Austria, France, Spain (Tyrberg 1998).

– *Lanius* sp.

From sites in Europe outside the Carpathian Basin **Q4:** Austria, Bosnia-Herczegovina, Spain (Tyrberg 1998).

– *Lanius* sp. foss. indet.

MN 16: Betfia 13 (Romania) (Kessler 1975, Gál 2002 – as *Lanius collurio*);

The fossil species from Beremend 26 were reported previously as *Lanius* sp. foss. indet. by Kessler (2010).

– Laniidae gen. *et* sp. foss. indet.

MN 6: Kőalja 2 (Subpiatra) (Romania) (Kessler & Venczel 2009).

The family and genus are known outside the Carpathian Basin from the Late Pliocene from of Varshets (MN 17, Bulgaria) as *Lanius* sp. (Boev 1996, 2000); from Petralona 24 – Greece (Lower Pleistocene) as *Lanius* cf. *minor* Gmellin, 1788 by Kretzoi (1977). The fossil species *Lanius miocaenus* Milne-Edwards, 1871 (Milne-Edwards 1869–71) from Saint-Gérand-le-Puy – France (Lower Miocene, MN 2) was put into "*Family incertae sedis"* by Mlíkovský (2002).

Fam. Sturnidae Vigors, 1825

– *Sturnus* Linnaeus, 1758

– *Sturnus* † *kretzoii* Kessler *et* Hír, 2012

Type locality and age: Rudabánya, Upper Miocene (MN 9) (Hungary) (Kessler & Hír 2012). The features of the remains correspond to the extant genus, but their dimensions are much smaller.

– *Sturnus* † *brevis* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It differs in its smaller sizes from the extant species.

– *Sturnus* † *pliocaenicus* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It differs to known extinct and extant species with much larger dimensions.

– *Sturnus* † *baranensis* Kessler, 2013

Type locality and age: Beremend 26, Middle Pliocene (MN 15–16) (Hungary) (Kessler 2013a, 2013b). It differs from extant species in its intermediate dimensions between *S. vulgaris* and *S. roseus*.

– *Sturnus vulgaris* Linnaeus, 1758

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q2:** Betfia 5 (Romania) (Kessler 1975, Jánossy 1979, Gál 2002); **Q3/II:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, M. Malez & Rukavina 1979); **Q4/I:** Bajót, Herman Ottó Cave, Csobánka-Kiskevélyi Cave (Lambrecht 1912, 1915, 1933, Jánossy 1979), Hámor-Puskaporos Niche (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986), Hámor-Herman Ottó Cave (Lambrecht 1915, 1933), Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986), Tatabánya-Kálváriahegy 4. Cave (Gál 2005a, 2005b), Varbó-Lambrecht Kálmán Cave (Jánossy 1964, 1979) (all in Hungary); Nándor-Nándori Cave (Nandru-Peştera Curata) (Romania) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003); **Q4/II:** Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Szendrő (Gál 2005b, Tassi 2006) (all in Hungary); Herkulesfürdő-Rablók Cave (Băile Herculane, Peştera Hoţilor) (Kessler 1981, Gál 2002), Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler

1974, Fischer & Stephan 1977), Körösbánlaki Cave (Peştera din Bălnaca) (Kessler 1982), Révi Caves (Peşterile din Vadu Crișului) (Kessler 1982) (all in Romania). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic France, Malta, United Kingdom; **Q4:** Austria, Bosnia-Herzegovina, Croatia, France, Germany, Greece, Italy, Poland, Eussia, Spain, Switzerland, Ukarine, United Kingdom (Tyrberg 1998).

– *Sturnus roseus* (Linnaeus, 1758)

Q4/I: Pilisszántói I. Niche (Hungary) (Lambrecht 1915, 1933, Jánossy 1979, 1986). From sites in Europe outside the Carpathian Basin **Q4:** France, Italy (Tyrberg 1998).

– *Sturnus unicolor* Temminck, 1820

From sites in Europe outside the Carpathian Basin **Q4:** France, Spain (Tyrberg 1998).

– *Sturnus* sp.

Q1: Beremend 16, 17 (Hungary) (Jánossy 1992); **Q4/I:** Szilvásvárad-Istállóskői Cave (Hungary) (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986). From sites in Europe outside the Carpathian Basin **Q3:** Italy, Spain, Turkey; **Q4:** France, Germany, Greece, Italy, Spain, United Kingdom (Tyrberg 1998).

The family and genus were described outside the Carpathian Basin as *Sturnus* sp. in the Late Pliocene and the Early Pleistocene localities from Varseths – Bulgaria (MN 17 – MQ1) by Boev (1996, 2000), West Runton and Boxgrove – England (Harrison 1979, Harrison & Stewart 1999) and Prezletice – Czech Republic (Čapek 1917, Jánossy 1983, 1992).

Fam. Passeridae Illiger, 1811

– *Passer* Koch, 1816

– *Passer † hiri* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Its size is smaller than the extant species but corresponds to it in its characteristics.

– *Passer † minusculus* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Is very little in comparison to extant species of the genus but corresponds it in its characteristics.

– *Passer † pannonicus* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds mostly in dimensions and characteristics to extant species. The extinct species from Polgárdi and Csarnóta are smaller.

– *Passer montanus* (Linnaeus, 1758)

Q1: Betfia 2 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002); **Q2**: Betfia 5 (Romania) (Kessler 1975, Jánossy 1979, Gál 2002); **Q3:** Uppony I/1 (Hungary) (Jánossy 1979); **Q4/I:** Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988); **Q4/II:** Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia) (Romania) (Kessler 1982). From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Bulgaria, France, Italy, Ukraine, United Kingdom (Tyrberg 1998).

– *Passer domesticus* (Linnaeus, 1758)

Q4/I: Hámor-Puskaporos (Hungary) (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986); **Q4/II:** Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Legény Cave (Lambrecht 1914) (all in

Hungary). From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Czech Republic, France, Ireland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Passer* sp.

From sites in Europe outside the Carpathian Basin **Q3:** Ukraine; **Q4:** Bosnia-Herczegovina, Germany, Italy, Spain (Tyrberg 1998).

The earliest report of the family and the genus is from Saint-Gérand-le-Puy – France (Lower Miocene, MN 2) as *Passer* sp. (Mourer-Chauviré 1995), but it is not known in other localities from Neogene.

Fam. Fringillidae Leach, 1820

– *Serinus* Koch, 1916

– *Serinus serinus* (Linnaeus, 1766)

Q1: Németóvár 4B (Deutsch-Altenburg) (Austria) (Jánossy 1981). From sites in Europe outside the Carpathian Basin **Q3:** France, United Kingdom (Tyrberg 1998).

– *Serinus citrinella* (Pallas, 1764)

From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** France, Poland (Tyrberg 1998).

– *Serinus* sp.

From sites in Europe outside the Carpathian Basin **Q3:** Italy; **Q4:** France (Tyrberg 1998).

– *Serinus* sp. foss. indet.

MN 16: Beremend 15 (Hungary) (Jánossy 1992, 1996);

The genus *Serinus* sp. was reported from Saint-Gerand-le Puy – France (Lower Miocene, MN 2), (Mourer-Chauviré 1995).

– *Carduelis* Brisson, 1760

– *Carduelis* † *kretzoii* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It corresponds in its sizes to extant smaller and medium size extant species of the genus, such as *C. carduelis*, *C. flammea* and *C. spinus.*

– *Carduelis* † *lambrechti* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Its size corresponds to extant *Carduelis chloris.*

– *Carduelis* † *parvulus* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in characteristics to genus and in dimensions to little sized species.

– *Carduelis* † *medius* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics and sizes with one medium sized extant species of the genus.

– *Carduelis chloris* Linnaeus, (1758)

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/I:** Merkenstein (Austria) (Wettstein & Mühlhofer 1938); Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Szegyeste-Măgura Cave (Sighiştel, Peştera Măgura) (Kessler 1982, 1985, Gál 2002) (all in Romania); **Q4/II:** Révi Caves (Peşterile din Vadu Crişului), Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia), Szegyestel-völgyi Caves (peşteri din Valea Sighiştelului) (Kessler 1982) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1–2:** France; **Q3:** France, Italy, Malta; **Q4:** Bosnia-Hercezgovina, France, Germany, Greece, Ireland, Italy, Poland, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Carduelis carduelis* (Linnaeus, 1758)

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/I:** Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988). From sites in Europe outside the Carpathian Basin **Q1–2:** Spain; **Q3:** Czech Republic, France; **Q4:** France, Germany, Italy, Poland, Russia, Ukraine, United Kingdom (Tyrberg 1998).

– *Carduelis spinus* (Linnaeus, 1758)

Q1: Betfia 9 (Romania) (Gál 2002). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic; **Q4:** France, Germany, United Kingdom (Tyrberg 1998). From sites in Europe outside the Carpathian Basin **Q1–2:** France; **Q4:** Czech Republic, Russia (Tyrberg 1998).

– *Carduelis cannabina* (Linnaeus, 1758)

Q1: Betfia 9 (Romania) (Gál 2002); **Q4/I:** Kőrösmart (Rîpa) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002); Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura) (Kessler 1982, 1985, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q3:** France, Ukraine; **Q4:** Austria, Czech Republic, France, Germany, Ireland, Italy, Poland, Spain, United Kingdom (Tyrberg 1998).

– *Carduelis flammea* (Linnaeus, 1758)

Q4/I: Merkenstein (Austria) (Wettstein & Mühlhofer 1938). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic; **Q4:** France, Germany, United Kingdom (Tyrberg 1998). From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Austria, France, Italy, Spain, United Kingdom (Tyrberg 1998).

– *Carduelis* sp. indet.

Q1: Beremend 17 (Hungary) (Jánossy 1992); Betfia 9 (Romania) (Gál 2002); **Q4/I:** Tatabánya-Kálvária-hegy 4. Cave (Hungary) (Gál 2005a, 2005b). From sites in Europe outside the Carpathian Basin **Q1–2:** France; **Q3:** Italy; **Q4:** Belgium, Czech Republic, Russia (Tyrberg 1998).

The genus was described outside of the Carpathian Basin from the Late Pliocene – Early Pleistocene, (MN 17–MQ1) in Varshets and Cerzenica. Bulgaria by Boev (1996, 2000), Quibas and S'Onix-Spain by Montoya *et al.* (1999) and Sondaar *et al.* (1995); Mas Ramboult – France by Mourer-Chauviré (1995) and Stránská skála – Czech Republic by Jánossy (1972).

– *Pinicola* Vieillot, 1807

– *Pinicola † kubinyii* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It is smaller in dimensions than the extants species.

– *Pinicola enucleator* (Linnaeus, 1758)

Q1: Németóvár 4B (Deutsch-Altenburg) (Austria) (Jánossy 1981); **Q4/I:** Merkenstein (Austria) (Wettstein & Mühlhofer 1938); Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986), Szilvásvárad-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986) (all in Hungary); **Q4/II:** Herkulesfürdő-Zoltán Cave (Băile Herculane, Peştera Zoltan) (Romania) (Gál 2002). From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** France, Italy, Spain, United Kingdom (Tyrberg 1998).

– *Pinicola* sp.

Q3/I: Hundsheim (Austria) (Lambrecht 1933, Jánossy 1974a, 1979); Tarkő (Kessler 2010), Vértesszőlős 2 (Jánossy 1974a, 1979) (all in Hungary).

– *Coccothraustes* Brisson, 1760

– *Coccothraustes* † *major* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It differs from extant species in its dimensions and larger size and corresponds much in its characteristics. It should be noted that we do not come across this genus in other songbird-rich materials (Polgárdi, Csarnóta).

– *Coccothraustes coccothraustes* (Linnaeus, 1758)

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q3/I:** Hundsheim (Austria) (Mlíkovskỳ 2009); **Q3/II:** Süttő 1–4 (Hungary) (Jánossy 1979); **Q4/I:** Merkenstein (Wettstein & Mühlhofer 1938), Velika Pecina (V. Malez 1975, 1984, 1988), Velika pec na Lipi (V. Malez 1975, 1984, 1993, V. Malez-Bacic 1975, 1979) (all in Croatia); Hámor-Herman Ottó Cave (Lambrecht 1915, 1933), Szilvásvárad-Istállóskői Cave (Labrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986) (all in Hungary); Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura) (Kessler 1982, 1985, Gál 2002) (all in Romania); Óruzsin-Antal Cave (Oruzer, Antal Cave) (Slovakia) (Nehring 1880, Róth 1881, Lambrecht 1933); **Q4/II:** Körösbánlaki Cave (Peştera din Bălnaca) (Kessler 1982), Remetelórév-Bólyikői Cave (Lorău-Peştera din Piatra Boiului), Szegyestel-Drăcoaia Cave (Sighiştel, Peştera Drăcoaia), Szegyestel-völgyi Caves (peşteri din Valea Sighiştelului) (Kessler 1982), Vársonkolyos-Kis-Magyar Cave (Şuncuiuş, Peştera Napiştileu), Vársonkolyosi Caves (peşteri din Şuncuiuș) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1–2:** Spain; **Q3:** Czech Republic, France, Italy, Malta, Spain; **Q4:** Austria, Bosnia-Herczegovina, Croatia, France, Germany, Greece, Ireland, Italy, Moldova, Poland, Portugal, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

The genus was reported with extinct species only from Bulgaria (Varshets and Slivnita, Upper Pliocene – Early Pleistocene, MN 17–Q1) as *Coccothraustes simeonovi* Boev 1998 and *C. balcanicus* Boev, 1998 (Boev 1998).

– *Pyrrhula* Linnaeus, 1758

– *Pyrrhula* † *gali* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics to extant species and genus.

– *Pyrrhula* † *minor* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics to extant genus but differs in dimensions.

– *Pyrrhula pyrrhula* Linnaeus, 1758

Q1: Betfia 9 (Romania) (Gál 2002); **Q3:** Uppony I/1 (Hungary) (Jánossy 1979); **Q4/I:** Merkenstein (Austria) (Wettstein & Mühlhofer 1938); Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988); Budapest-Remetehegyi Niche (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Hámor-Puskaporos Niche (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986), Hámor-Herman Ottó Cave (Lambrecht 1915, 1933), Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986), Répáshuta-Balla Cave (Lambrecht 1912, 1933) (all in Hungary); Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura) (Romania) (Kessler 1982, 1985, Gál 2002); **Q4/II:** Legény Cave (Hungary) (Lambrecht 1914); Herkulesfürdő-Rablók Cave (Băile Herculane, Peştera Hoţilor) (Kessler 1981, Gál 2002), Kazánszoros-Climente Cave (Kessler 1981, Gál 2002), Szegyestel-völgyi Caves (Peşteri din Valea Sighiştelului) (Kessler 1982), Szkerisoara-Coiba Mare Cave (Scărişoara, Peştera Coiba Mare) (Kessler 1982, Jurcsák & Kessler 1986, 1988) (all in Romania). From sites in Europe outside the Carpathian Basin **Q3:** Croatia, Czech Republic, France, Italy; **Q4:** Austria, Bulgaria, Croatia, France, Germany, Greece, Ireland, Italy, Poland, Spain, United Kingdom (Tyrberg 1998).

– ***Pyrrhula* sp. foss. indet.**

MN 15: Beremend 26 (Hungary) (Kessler 2010a); based on maxillae and mandibles.

The genus was reported outside the Carpathian Basin from the Late Pliocene – Early Pleistocene, (MN 17 – MQ1) in Varshets – Bulgaria by Boev (1996, 1997) and Stránská skála – Czech Republic by Jánossy (1972a).

– *Fringilla* Linnaeus, 1758

– *Fringilla † kormosi* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It is large size *Fringilla* species.

– *Fringilla † petenyii* Kessler, 2013

Type locality and age: Csarnóta 2, Middle Pliocene (MN 15–16) (Hungary) (Kessler 2013a, 2013b). Its characteristics and dimensions correspond to the extant genus.

– *Fringilla montifringilla* Linnaeus, 1758

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q4/I:** Budapest-Remetehegyi Niche (Hungary) (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986); Kőrösmart (Rîpa) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II:** Teufelslucke (Austria) (Soergel 1966); Répáshuta-Rejteki Niche (Hungary) (Jánossy 1962, 1979, 1986). From sites in Europe outside the Carpathian Basin **Q4:** Czech Republic, France, Germany, Italy, Spain, United Kingdom (Tyrberg 1998).

– *Fringilla coelebs* Linnaeus, 1758

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q2:** Kiskóh-Medvék Cave 2 (Chișcău, Peștera Urșilor) (Romania) (Kessler 1982, Jurcsák & Kessler 1988, Gál 2002); **Q4/I:** Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988); Esküllő-Igric Cave (Aștileu, Peştera Igriţa) (Romania) (Kessler 1985); **Q4/II:** Kazánszoros-Climente Cave (Kessler1981, Gál 2002), Révi Caves (Peşterile din Vadu Crișului) (Kessler 1982), Szkerisoara-Coiba Mare Cave (Scărişoara, Peştera Coiba Mare) (Kessler 1982, Jurcsák & Kessler 1986, 1988) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1–2:** Spain, Ukraine; **Q3:** Croatia, France, Spain; **Q4:** Austria, Bulgaria, Croatia, Czech Republic, France, Germany, Ireland, Italy, Poland, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– *Fringilla* sp. foss. indet.

Localities and age: Litke 2, Lower Miocene (MN 5), Mátraszőlős 2, Middle Miocene (MN 7–8) (Kessler & Hír 2012b) (all in Hungary).

The genus is known outside of the Carpathian Basin from the Lower Pliocene (MN 16) from Hostalets de Pierola – Spain as *Fringilla* sp. (Villalta 1963), from the Late Pliocene – Early Pleistocene (MN 17–MQ1) from Varshets – Bulgaria (Boev 1996, 1997); S'Onix (Mallorca) – Spain (Sondaar *et al.* 1995) and Tarchankut – Ukraine (Vojitsvens'ky 1967) as *F.* cf. *coelebs* Linnaeus, 1758.

– *Montifringilla* Adams, 1858

– *Montifringilla nivalis* (Linnaeus, 1766)

Q4/II: Grosse Offenbergerhöhle (Bocheński & Tomek 1994); Teufelslucke (Soergel 1966) (all in Austria). From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Austria, France, Germany, Italy, Poland, Spain, Ukraine (Tyrberg 1998).

– *Loxia* Linnaeus, 1758

– *Loxia † csarnotanus* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Other locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Its characteristics correspond with the extant genus, but has smaller dimensions.

– *Loxia curvirostra* Linnaeus, 1758

Q1: Betfia 9 (Romania) (Gál 2002); **Q3/I:** Hundsheim (Mlíkovskỳ 2009); **Q4/I:** Budapest-Remetehegyi Niche (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Hámor-Puskaporos Niche (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986), Hámor-Herman Ottó Cave (Lambrecht 1915, 1933), Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986), Szilvásvárad-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986) (all in Hungary); Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura) (Romania) (Kessler 1982, 1985, Gál 2002); **Q4/II:** Herkulesfürdő-Zoltán Cave (Băile Herculane, Peştera Zoltan) (Romania) (Gál 2002). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic; **Q4:** Bulgaria, Croatia, Czech Republic, France, Italy, Poland, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Loxia leucoptera* J. F. Gmelin, 1789

From sites in Europe outside the Carpathian Basin **Q4:** Italy (Tyrberg 1998).

– *Loxia pytyopsittacus* Borkhausen, 1793

From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** Czech Republic, France, Italy (Tyrberg 1998).

– *Loxia* sp.

Q4/I: Merkenstein (Wettstein & Mühlhofer 1938).

From sites in Europe outside the Carpathian Basin **Q3:** Italy; **Q4:** Switzerland (Tyrberg 1998).

The genus was reported as *Loxia* sp. from Saint-Gerand-le Puy-France (Lower Miocene, MN 2) (Mourer-Chauviré 1995) and as *Loxia patevi* Boev, 1999 from Varshets – Bulgaria (Upper Pliocene, MN 17) (Boev 1999).

– Fringillidae gen. *et* sp. indet

Q4/I: Répáshuta-Balla Cave (Hungary) (Lambrecht 1912, 1933).

The fossil species from this family from Polgárdi 4, 5, Csarnóta 2 and Beremend 26 were innitialy indicated as Fringillidae gen. *et* sp. indet. by Kessler (2010).

Fam. Emberizidae Vigors, 1831

– *Emberiza* Linnaeus, 1758

– *Emberiza* † *bartkoi* Kessler *et* Hír, 2012

Type locality and age: Litke 2, Lower Miocene (MN 5) (Hungary) (Kessler & Hír 2012). In size it resembles a medium-to-large goldfinch.

***Emberiza* † *pannonica* Kessler, 2013**

Type locality and age: Polgárdi 5; Upper Miocene (MN 13) (Kessler 2013a, 2013b). It corresponds to medium-sized extant species *(E. citrinella, E. cia, E. cyrlus)*. The fossil species *Emberiza bartkoi* Kessler *et* Hír, 2012 from Litke 2 – Hungary (Lower Miocene, MN 5) seems similar in it sizes to Polgárdi specimen but was described from a distal fragment of a *humerus*.

– *Emberiza* † *polgardiensis* Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). In its sizes it is similar to the smaller extant species *(E. schoeniclus)*.

– *Emberiza* † *media* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds to characteristics of extant genus.

– *Emberiza* † *parva* Kessler, 2013

Type locality and age: Csarnóta 2, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). Corresponds in its characteristics to extant genus.

– *Emberiza* † *gaspariki* Kessler, 2013

Type locality and age: Beremend 26, Pliocene (MN 15) (Hungary) (Kessler 2013a, 2013b). It corresponds in its characteristics to extant species but has larger dimensions.

– *Emberiza cirlus* Linnaeus, 1766

Q4/I: Velika Pecina (V. Malez 1975, 1984, 1988). From sites in Europe outside the Carpathian Basin **Q4:** Italy, Spain (Tyrberg 1998).

– *Emberiza calandra* Linnaeus, 1758

Q1: Betfia 2 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002), Betfia 9 (Kessler 1975, Gál 2002) (all in Romania); **Q4/I:** Hámor-Puskaporos Cave (Lambrecht 1916, 1933, Jánossy 1979, 1986), Pilisszántói I. Niche (Lambrecht 1915, 1933, Jánossy 1979, 1986) (all in Hungary); **Q4/II:** Miskolc-Felső forrás (Hungary) (Kessler 2010). From sites in Europe outside the Carpathian Basin the species is unknown.

– *Emberiza citrinella* Linnaeus, 1758

Q1: Betfia 9 (Romania) (Gál 2002); **Q3:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, M. Malez & Rukavina 1979); Uppony I/1 (Hungary) (Jánossy 1979); **Q4/I:**

Velika Pecina (Croatia) (V. Malez 1975, 1984, 1988); Varbó-Lambrecht Kálmán Cave (Hungary) (Jánossy 1964, 1979); **Q4/II:** Teufelslucke (Austria) (Soergel 1966); Herkulesfürdő-Zoltán Cave (Băile Herculane, Peştera Hoţilor) (Romania) (Gál 2002). From sites in Europe outside the Carpathian Basin **Q3:** Czech Republic, France, Spain; **Q4:** Austria, Croatia, Czech Republic, France, Germany, Ireland, Italy, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Emberiza schoeniclus* Linnaeus, 1758

Q4/I: Merkenstein (Austria) (Wettstein & Mühlhofer 1938); Hámor-Puskaporos Cave (Hungary) (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986). From sites in Europe outside the Carpathian Basin **Q4:** Czech Republic, Italy, Poland, United Kingdom (Tyrberg 1998).

– *Emberiza cia* Linnaeus, 1766

From sites in Europe outside the Carpathian Basin **Q4:** Italy, Spain, Ukraine (Tyrberg 1998).

– *Emberiza hortulana* Linnaeus, 1758

From sites in Europe outside the Carpathian Basin **Q3:** France; **Q4:** France, Italy, Ukraine (Tyrberg 1998).

– *Emberiza melanocephala* Scopoli, 1769

From sites in Europe outside the Carpathian Basin **Q3:** Spain; **Q4:** Spain (Tyrberg 1998).

– *Emberiza* sp.

Q2: Nagyharsányhegy 1–4 (Hungary) (Jánossy 1979) **Q4/I:** Novi I, III (Slovakia) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933, Jánossy 1979); **Q4/II:** Grosse Offenbergerhöhle (Austria) (Bocheński & Tomek 1994).

The genus is known outside the Carpathian Basin from the Late Pliocene – Early Pleistocene (MN 17–MQ1) sediments from Varshets and Slivnita – Bulgaria (Boev 1996, 1997, 2000) and Stránská skála – Czech Republic (Jánossy 1972).

– *Plectrophenax* Stejneger, 1882

– *Plectrophenax veterior* † Kessler, 2013

Type locality and age: Polgárdi 5, Upper Miocene (MN 13) (Hungary) (Kessler 2013a, 2013b). It corresponds in its characteristics to the extant species.

– *Plectrophenax nivalis* (Linnaeus, 1758)

Q4/I: Merkenstein (Austria) (Wettstein & Mühlhofer 1938); Budapest-Remetehegyi Niche (Kormos & Lambrecht 1914, Lambrecht 1933, Jánossy 1979, 1986), Cserépfalu-Subalyuk Cave (Jánossy 1979), Hámor-Puskaporos Niche (Lambrecht 1912, 1916, 1933, Jánossy 1979, 1986) (all in Hungary). From sites in Europe outside the Carpathian Basin **Q3:** France, Ukraine; **Q4:** Czech Republic, France, Germany, Italy, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– Calcarius Bechstein, 1802

– *Calcarius lapponicus* (Linnaeus, 1758)

From sites in Europe outside the Carpathian Basin **Q4:** Austria, United Kingdom (Tyrberg 1998).

– Emberizidae gen *et* sp. indet.

Q3/I: Betfia 7/4 (Romania) (Kessler 1975); **Q4/I:** Tatabánya-Kálváriahegy 4. Cave (Hungary) (Gál 2005a, 2005b).

– Passeriformes fam., gen *et* sp. foss. indet.

MN 4: Oberdorf (Austria) (Mlíkovskỳ 1998); **MN 5:** Litke 2 (Hungary) (Kessler & Hír 2012); **MN 6:** Dévényújfalu (Devinska Nova Ves) (Slovakia) (Mlíkovskỳ 2002); Kőalja 2 (Subpiatra) (Romania) (Kessler & Venczel 2009); **MN 7–8:** Mátraszőlős 1 (Kessler & Hír 2012), Mátraszőlős 2 (Gál *et al.* 2000, Kessler & Hír 2012), Felsőtárkány (Hír *et al.* 2001, Kessler & Hír 2012), Felsőtárkány-Felnémet (Kessler & Hír 2012) (all in Hungary); **MN 13:** Polgárdi (Hungary) (Kessler 2010); **MN 15:** Beremend 26 (Kessler 2010), Csarnóta 2, 4 (Kessler 2010) (all in Hungary); **MN 16:** Beremend 38 (Kessler 2010), Osztramos 7 (Jánossy 1979) (all in Hungary).

Many bones from this material afterwards were identified to the species level (Kessler & Venczel 2011, Kessler & Hír 2012, Kessler 2013a, 2013b).

Conclusions

The order of songbirds (Passeriformes) is the most numerous one in the avian fauna of the Carpathian Basin, as well as of other areas. This is also the case regarding fossil material, although due to the rudimentary nature of collection methods, as well as difficulties concerning their identification, their numbers only grew in the most extant years. Currently, the remains of 58 genera (3 of which are extinct) in 16 families have been identified to the species level (208 + 2 species, of which 118 extinct + 2 extinct subspecies). This is supplemented by 23 extinct and 20 extant taxa, which were only identified to the family or genus level.

From the territory of current-day Hungary, new 114 extinct taxa represent Neogene Passeriformes, including the material from Polgárdi (39 taxa), Csarnóta (35 taxa) and Beremend (24 taxa), as well as those described from North Hungary (15 taxa) and Romania (Subpiatra – Kőalja) (1 taxon).

– The family Alaudidae is one of the most populated, since it is represented by one extinct genus, 10 extinct and 5 extant species in the fossil material. Extinct ones are known from the Early Miocene up to the Early Pliocene, while extant ones are known from the Quaternary. Their size is between that of sparrows and thrushes, they mostly live in open areas and nest on the ground, hence they relatively often fall prey to predators.

– The family Hirundinidae is also well represented by 6 extinct species and 4 extant ones. Although they are swift flyers, they typically live in groups, so they are also often parts of predators' diets. Extinct species are only from the Late Miocene and the Early Pliocene, while extant species are present in every phase of the Quaternary.

– The family Paridae is represented by small sedentary insectivore species. 5 extinct and 7 extant species were identified from the fossil materials. Similar to the Hirundinidae, extinct representatives are only found in the Late Miocene and Early Pliocene, while extant ones are from the Quaternary. Although this phenomenon appears in the case of numerous other families as well, its causes are unclear. It can be due to improper taphonomic conditions, the relatively low number of fossil material, or the improper geological classification of the sites.

– Sittidae, Certhidae and Tichodromidae are families with similar ways of life and sizes, with few species. While the former two families are sedentary insectivores living on barks of woodland trees, the sole representative of the third family is migratory and lives on the ledges of cliffs, and differs with its pompous colors from its brown relatives. Even though they are only represented by 4 species in the current fauna, and only two of those are present in the fossil material in the Early and Late Pleistocene and Holocene, 6 extinct species are known from the Late Miocene and Early Pliocene, as well as two pieces of not fully identified material from the Middle Miocene. Their remains also prove the presence of their habitats (woodlands, as well as bare ledges of cliffs) in these time periods

– The family Muscicapidae is one of the richest regarding the number of species. Apart from the 18 extinct species, the remains of 11 extant species were identified from the time period between the Early Miocene and Early Pliocene, as well as from the Quaternary. Of them, nightingales and flycatchers are represented by one extinct species each in every era. They are sparrow-sized, grey or brown migratory insectivores living among bushes or trees. Their presence proves these former conditions.

– The Turdidae family is quite well represented within the fossil material with one extinct genus, 9 extinct species and 6 extant species. The existence of the extinct and much-debated genus *(Turdicus)* was proven from materials from Lower, Middle, and Upper Miocene materials. Such is also the case with the extinct species *(Turdoides borealis)* of the northern genus. The extant *Turdus* genus is represented by 5 extinct species in the Late Miocene and Early Pliocene material, while extant species are more numerous; they are sedentary or migrate, due to their sizes and high numbers they often fall prey to predators.

– The Sylviidae family is another populated one. Apart from 16 extinct species (as well as several finds from the Miocene that had not been fully identified), it is only represented by 4 extant species within the fossil material. The extinct species, as with the families discussed so far, were classified from the Late Miocene and Early Pliocene. Whitethroats, warblers, grasshopper warblers, leaf warblers, icterine warblers and kinglets have gray-brown feathers, they are insectivores and migrate. They live among bushes and trees, thus, their presence indicates this kind of habitat.

– The Motacillidae family (wagtails and pipits), however, consists of birds, about the size of sparrows or larger, living in open areas. They are insectivores and mostly migratory. Apart from 5 extinct species and a few not fully identified finds, they are represented by 8 extant species. Extinct ones were classified from the Middle Miocene to the Early Pleistocene material, thus, representatives of the family from the Middle Miocene to extant times are continuously present in the Carpathian Basin.

– Oriolidae, Bombycillidae, Cinclidae and Troglodytidae are all typically single-species families. Despite this, they are also present within the fossil material, both with their extinct and extant species. Bombycillidae and Cinclidae have three extinct species each, while Oriolidae and Troglodytidae have one each. What is more, the former ones were present from the Early Miocene to the Early Pliocene, while the latter ones only from the Early Pliocene and the Late Miocene. Extant species are known from almost the whole timeframe of the Quaternary. Considering appearance, size and way of life, however, they are quite different families. While the Golden Oriole is a species of relatively larger size (similar to larger blackbirds) with colorful feathers, it lives in woodlands, it is insectivore and migratory. The bohemian waxwings are seed-eating, migrating birds of the taiga with sizes of smaller blackbirds. Wrens are rather small birds with brownish feathers, living and nesting on the ground of bushy areas; they feed on insects and are sedentary. The Dipper is a species living around creeks, looking for prey in their beds. Their size is similar to blackbirds, and they are sedentary. Their presence proves that these habitats were present in the total timespan of the Neogene and the Quaternary inside the Carpathian Basin.

– Prunellidae are sparrow-sized birds living among woodlands and bushes with gray-brown feathers. They are represented by a few extinct as well as extant species within the fossil material. While the extinct species are birds of the Late Miocene and Early Pliocene, the extant ones are only known from the Late Pleistocene and the Holocene.

– Members of the Laniidae family typically live in bushy/open areas. Their size is between that of sparrows and thrushes, their diet consists of invertebrates, and they are migratory. They are represented by 5 extinct and 4 extant species. The extinct ones lived in the timeframe of the Middle Miocene and Early Pliocene, while extant ones in the whole of the Quaternary. Their not fully identified extinct types are known from the Middle Miocene, as well as the Early and Late Pliocene.

– Extant forms of the Sturnidae family represent two completely different types that are present in the Quaternary, with one species each. The Common Starling lives in the woods and in open areas and reed beds, roams in large flocks, and feeds on insects and fruit, while the Rosy Starling is a migrating insectivore that lives in open areas. The former is present in the whole of the Quaternary, while the latter is only known from the Late Pleistocene. The 4 extinct species were defined and described with different sizes from the Late Miocene and the Early Pliocene.

– The Passeridae and Fringillidae families are closely related, and have many similarities as well. The latter is also rich in species. Three extinct species are known of the former family from the Late Miocene and Early Pliocene (apart from two extant species identified from the Quaternary). The latter family, however, is represented by 11 extinct species from the Late Miocene and Early Pliocene as well, but also by several not fully identified taxa from the Early and Middle Miocene and the Late Pliocene. The remains of 12 extant species were identified from the Quaternary. Their sizes vary between sparrows and smaller blackbirds, they are usually colorful seed-eating sedentary species. In nesting periods, they live in woodland area, in these times they also eat insects (with the exception of *Loxia*). They are quite frequent within the fossil material as well.

– The Emberizidae family consists of species living in more open areas, feeding on insects and seeds, and are mostly sedentary. Their sizes range from sparrows to starlings. They are represented by 6 extinct and 5 extant species. The former are known from the Late Miocene and Early Pliocene, while the latter are known from the Quaternary, from several sites.

Acknowledgements

The author wishes to express his deep gratitude to referees for their help in the revision of the text and to József Vuts and Lóránd Abos for the language revision.

References

Bocheński, Z. M. & Tomek, T. 1994. Fossil and subfossil bird remains from five Austrian caves. – Acta Zoologica Cracoviensia 37: 347–358.

Boev, Z. N. 1996. Tertiary avian localities of Bulgaria. – In: Mlíýkovský, J. (ed.) Tertiary avian localities of Europe. – Acta Universitatis Carolinae, Geologica 39: 541–545.

Boev, Z. N. 1997. Chauvireria balcanica gen. n., sp. n. (Phasianidae – Galliformes) from the Middle Villafranchian of Western Bulgaria. – Geologica Balcanica 27: 69–78.

Boev, Z. N. 1998. Late Pliocene hawfinches (*Coccothraustes* Brisson, 1760) (Aves: Fringillidae) from Bulgaria. – Historia Naturalis Bulgarica 9: 87–99.

Boev, Z. N. 1999. Earliest finds of crossbills (genus *Loxia*) (Aves: Fringillidae) from Varshets (NW Bulgaria). – Geologica Balcanica 29(3–4): 51–57.

Boev, Z. N. 2000. Neogene avifaunas of Bulgaria. – Vertebrata Palasiatica 38 (Suppl.): 2–10.

Boev, Z. N. 2012. Neogene Larks (Aves: Alaudidae (Vigors, 1825) from Bulgaria. – Acta Zoologica Bulgarica 64(3): 295–318.

Brodkorb, P. 1960. How many species of birds have existed? – Bulletin of the Florida State Museum, Biological Sciences 5: 41–53.

Čapek, V. 1917. A püspökfürdői preglaciális madárfauna [The Preglaciale bird fauna from Püspökfürdő]. – Barlangkutatás 5: 66–74. (in Hungarian)

Clot, A., Chaline, J., Heintz, E., Jammot, D., Mourer-Chauviré, C. & Rage. J. C. 1976. Montoussé 5 (Hautes-Pyrénées), un nouveau remplissage de fissure à faune de vertébrés du Pléstocène inférieur [Montoussé 5 (Hautes-Pyrénées), a new fissure filling with vertebrate fauna of the Lower Pleistocene]. – Géobios 9: 511–514. (in French)

Döppes, D. & Rabeder, G. (eds.) 1997. Pliozäne und Pleistozäne Faunen Österreichs. – Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften [Pliocene and Pleistocene Fauns of Austria – Communications from the Commission for Quaternary Research of the Austrian Academy of Sciences]. Vol. 10. – Wien (in German)

Fischer, K. & Stephan, B. 1977. Vogelknochenfunde aus Quartären Ablagerungen Südwestrumaniens [Bird bones from Quaternary deposits in Southwest Romania]. – Annalen für Ornithologie 1: 79–90. (in German)

Fladerer, F. A. 1993. Neue Daten aus jung- und mittelpleistozänen Höhlensedimenten im Raum Peggau-Deutschfeistritz, Steiermark [New data from young and Middle Pleistocene cave sediments in the area Peggau-Deutschfeistritz, Styria]. – Fundberichte aus Österreich 31: 369–374. (in German)

Freudenthal, M. & Kordos, L. 1989. *Cricetus polgardiensis* sp. nov. and *Cricetus kormosi* Schaub, 1930 from the Late Micene Polgárdi localities (Hungary). – Scripta Geologica 89: 71–95.

Gál, E. 1998. Avifauna fosilă a peșterii Gura Cheii de la Râșnov (Jud Brașov) [Fossil bird fauna of the Gura Cheii Cave from Râșnov (Brașov County)]. – Studia Universitatis Babeș-Bolyai, Biologia 43(1–2): 88–93. (in Romanian)

Gál, E. 2002. Avifauna pleistocena a Romaniei [Notpublished doctoral thesis: Pleistocene birds faunas from Romania]. – Bucuresti (in Romanian)

Gál, E. 2003. Bird remains from two Romanian caves: Curata Cave (Nandru) and Bordu Mare Cave (Ohaba Ponor). – ICAZ 2002, Abstracts, 56.

Gál, E. 2004. The Neolitic avifauna of Hungary within the context of the Carpathian Basin. – Antaeus 27: 273–286.

Gál, E. 2005a New evidence of fowling and poultry keeping in Pannonia, Dacia and Moesia during the period of the Roman Empire. – In: Gruppe, G. & Peters, J. (eds.) Feathers, grit and symbolism. Birds and humans in the Ancient Old and New Worlds. – Proceedings of the 5th Meeting of the ICAZ Bord Working Group, Munich, Germany, 26–30 July 2004. – Documenta Archaeobiologiae 3. Verlag Marie Leidorf GmbH.Rahden/Westf., pp. 301–316.

Gál, E. 2005b Animal remains from archaeological excavations in North-Eastern Hungary. – In: Gál, E., Juhász, I. & Sümegi, P. (eds.) Environmental Archaeology in North-Eastern Hungary. – Varia Archaeologica Hungarica 19: 139–174.

Gál, E. 2007. Fowling in lowlands. Neolithic and Chalcolithic bird exploitation in South-East-Romania and the Great Hungarian Plain. – Archaeolinqua, Series Minor 24., Budapest

Gál, E., Hír, J., Kessler, E., Kókay, J., Mészáros, L. & Venczel, M. 1998–1999. Középső-miocén ősmaradványok, a Mátraszőlős, Rákóczi-kápolna alatti útbevágásból. I. A Mátraszőlős 1. lelőhely [Middle Miocene fossils from the sections at the Rákóczi Chapell at Mátraszőlős. I. Mátraszőlős 1. site]. – Folia Historico Naturalia Musei Matraensis 23: 33–78. (in Hungarian with English Summary)

Gál, E., Hír, J., Kessler, E., Kókay, J. & Vencel, M. 2000. Középső-miocén ősmaradványok a Mátraszőlős, Rákóczi-kápolna alatti útbevágásból. II. A Mátraszőlős 2. lelőhely [Middle Miocene fossils from the sections at the Rákóczi Chapell at Mátraszőlős. I. Mátraszőlős 2. site]. – Folia Historico Naturalia Musei Matraensis 23: 33–78. (in Hungarian with English Summary)

Gál, E. & Kessler, E. 2006. Songbird remains from the Miocene (Middle Sarmatian) site Credinta (Dobrogea, South-East Romania). – In: Csiki, Z. (ed.) Volume dedicated to Dan Grigorescu on his 65th birthday. – University of Bucharest Printing House

Harrison, C. J. O. & Stewart, J. R. 1999. Avifauna. – In: Roberts, M. B. & Parffit, S. A. (eds.) A Middle Pleistocene hominid site at Eartham Quarry, Boxgrove, West Sussex. – English Heritage Archaeological Report (London) 17: 187–196.

Harrison, C. J. O. 1979. Small non-passerine birds of the Lower Tertiary as exploiters of ecological niches now occupied by passerines. – Nature 281: 562–563.

Hír, J., Kókay, J., Venczel, M., Gál, E. & Kessler, E. 2001. Előzetes beszámoló a felsőtárkányi „Gödör-kert" őslénytani lelőhelykomplex újravizsgálatáról [A preliminary report on the revised investigation of the paleontological locality complex "Gödör-kert" at Felsőtárkány, Northern Hungary]. – Folia Historico-Naturalia Musei Matraensis 25: 41–65. (in Hungarian with English Summary)

Horáček, I. 1985. Survey of the fossil vertebrate localities Včeláre 1–7. – Časopis pro Mineralogii a Geologii 30: 353–366.

Jánossy, D. 1952. Az Istállóskői barlang aurignaci faunája [The Aurignacian cave fauna from Istállóskő]. – Földtani Közlöny 82(4–6): 181–203. (in Hungarian)

Jánossy, D. 1954. Fossile Ornis aus der Höhle von Istállóskő [Fossile birds from the Istállóskő Cave]. – Aquila 55–58: 205–223. (in German)

Jánossy, D. 1955. Die Vogel-und Saugetierreste der Spätpleistozänen Schichten der Höhle von Istállóskő [The bird and mammalian remains of the Late Pleistocene Layers of the Istállóskő Cave]. – Acta Archaeologica Academiae Sciencentiarum Hungaricae 5: 149–181. (in German)

Jánossy, D. 1962. Eine fossile Vogelfauna aus den Mosuterien-Schichten der Subalyuk-Höhle im Bükk-Gebirge [A fossil avifauna from the Mousterian layers of Subalyuk cave in the Bükk Mountains]. – Aquila 67–68., 175–188. (in German)

Jánossy, D. 1965. Vogelreste aus den altpleistozänen Ablagerungen von Voigtstedt in Thüringen [Bird remains from the old Pleistocene deposits of Voigtstedt in Thuringia]. – Paläontologische Abhandlungen (A) 2: 336–361. (in German)

Jánossy, D. 1972. Die mittelpleistozäne Vogelfauna der Stránská Skála [The Middle Pleistocene bird fauna of Stranská Skálá]. – Anthropos 21(12): 35–64. (in German)

Jánossy, D. 1974a Die mittelpleistozäne Vogelfauna von Hundsheim (Niederösterreich) [The Middle Pleistocene avifauna of Hundsheim (Lower Austria)]. – Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschftliche Klasse, Abteilung I. 182: 211–257. (in German)

Jánossy, D. 1974b Upper Pliocene and Lower Pleistocene bird remains from Poland. – Acta Zoologica Cracoviensia 19: 531–564.

Jánossy, D. 1978. Új finomrétegtani szint Magyarország pleisztocén őslénytani sorozatában [A new fine stratigrafic level in Paleontological series at Hungarian Pleistocene]. – Földrajzi Közlemények 26(1–3): 161–174. (in Hungarian)

Jánossy, D. 1979. Plio-pleistocene Bird Remains from the The Carpathian Basin. IV. Anseriformes, Gruiformes, Charadriiformes, Passeriformes. – Aquila 85: 11–39.

Jánossy, D. 1980. Plio-pleistocene Bird Remains from the The Carpathian Basin. VI. Systematical and Geographical Catalogue. – Aquila 87: 9–22.

Jánossy, D. 1981. Die altpleistozänen Vogelfaunen von Deutsch-Altenburg 2 und 4 (Niederösterreich) [The Early Pleistocene bird fauna of Deutsch-Altenburg 2 and 4 (Lower Austria)]. – Beiträge zur Palaontologie von Österreich 8: 375–391. (in German)

Jánossy, D. 1982. Új adatok az európai madárfauna kialakulásáról [New data on the evolution of European bird fauna]. – Földtani Közlemények 112: 449–453. (in Hungarian)

Jánossy, D. 1983. Die mittelpleistozäne Vogelfauna von Přezletice bei Prag (ČSSR) [The Pleistocene bird fauna of Přezletice near Prague (CSSR)]. – In: Heinrich, W-D. (ed.) Wirbeltier-Evolution und Faunenwandel im Känozoikum [Vertebrate Evolution and Faunal Change in the Cenozoic]. – Schriftenreihe für Geologische Wissenschaften 19–20: 247–269. (in German)

Jánossy, D. 1986. Pleistocene vertebrate faunas of Hungary. – Budapest, Akadémiai Kiadó & Amsterdam, Elsevier

Jánossy, D. 1991. Late Miocene bird remains from Polgárdi (W-Hungary). – Aquila 98: 13–35.

Jánossy, D. 1992. Lower Pleistocene bird remains from Beremend (S-Hungary, Loc. 15. and 16.). – Aquila 99: 9–25.

Jánossy, D. 1993. Bird remains from the Upper Miocene (MN 9) of Rudabánya (N-Hungary). – Aquila 100: 53–70.

Jánossy, D. 1995. A Late Miocene avifauna from Polgárdi, western Hungary. – In*:* Peters, D. S. (ed.) Acta Palaeornithologica. – Courier Forschunsinstitut Senckenberg 181: 203–206.

Jánossy, D. 1996. Lower Pleistocene vertebrate faunas from the localities 16 and 17 of Beremend (Southern Hungary). – Fragmenta Mineralogica et Paleontologica 18: 91–102.

Jánossy, D. & Kordos, L. 1976. Az Osztramos gerinces lelőhelyeinek faunisztikai és karszt-morfológiai áttekintése (1974-ig) [The faunistical and karst-morphological review of paleontological localities for Vertebrates at Osztramos (to 1974)]. – Fragmenta Mineralogica et Palaeontologica 8: 39–72. (in Hungarian and English)

Jurcsák, T. & Kessler, E. 1986. Evoluţia avifaunei pe teritoriul României (I) [Evolution of avifauna on Romanian territory]. – Crisia 16: 577–615. (in Romanian with English Summary)

Jurcsák, T. & Kessler, E. 1988. Evoluţia avifaunei pe teritoriul României (III) [Evolution of the avifauna in the territory of Romanian, Part III.]. – Crisia 18: 647–688. (in Romanian with English Summary)

Kessler, E. 1974a Date noi asupra avifaunei fosile a Dealului Burzău – Râpa [New data to fossil bird fauna from Burzau Hill (Village Rîpa)]. – Nymphaea 2: 159–167. (in Romanian)

Kessler, E. 1974b Contribuţii noi la avifauna depozitelor hidrotermale postglaciare de la Băile 1 Mai – Oradea, jud. Bihor [New contributions to postglaciale avifauna and hydrothermal sediments from Băile 1 Mai – Oradea, Bihor County]. – Tibiscus 11: 123–128. (in Romanian)

Kessler, E. 1975. Contribuţii noi la studiul avifaunei fosile de la Betfia, jud. Bihor [New contributions to fossile avifauna from Betfia, Bihor County]. – Nymphaea 3: 53–59. (in Romanian)

Kessler, E. 1977. Avifauna postglaciară de la Vadu Crişului, jud. Bihor [Postglaciar avifauna from Vadu Crişului, Bihor County]. – Tibiscus (1977): 255–260.

Kessler, E. 1981. Noi date privind avifauna pleistocenă a Văii Ierului (jud. Bihor) [New data on the Pleistocene bird fauna of Valea Ierului (Bihor County)]. – Nymphaea 8–9: 259–264. (in Romanian)

Kessler, E. 1982. Avifauna fosilă şi subfosilă a Munţilor Apuseni [Fossil and subfossil bird fauna from Apuseni Mountains]. – Nymphaea 10: 171– 181. (in Romanian)

Kessler, E. 1985b Contribuţii noi la studiul avifaunelor cuaternare din România [New contributions to the study of Quaternary bird faunas in Romania]. – Crişia 15: 485–491. (in Romanian)

Kessler, J. 2010. Új eredmények a Kárpát-medence neogén és negyedidőszaki madárvilágához, III. rész [New results with regard to the Neogene and Quaternary Avifauna of the Carpathian basin. Part III.]. – Földtani Közlöny. 140(1): 53–72. (in Hungarian)

Kessler, J. & Hír, J. 2012. Észak-Magyarország madárvilága a miocénben II. [The avifauna in North Hungary during the Miocene, Part II.]. – Földtani Közlöny 141(2): 149–168. (in Hungarian with English Summary)

Kessler, E. 2013a Neogene songbirds from Hungary (Aves, Passeriformes) faunae from Hungary. – Hantkeniana 2013: 37–149.

Kessler, J. 2013b A Kárpát-medence madárvilágának őslénytani kézikönyve [Palaeornithological Handbook of birds fauna from Carpathian Basin]. – Könyvműhely Kiadó Miskolc (in Hungarian)

Kessler, E. & Gál, E. 1998. Resturi fosile si subfosile de pasari in siturile paleolitice si neolitice din Cheile Turzii si Cheile Turenilor (Judetul Cluj) [Fossil and sub-fossil remains of birds in the Paleolithic and Neolithic sites of the Turzii Gorge and the Gorges of Tureni (Cluj County)]. – Angvistia 3: 9–122. (in Romanian)

Kessler, J. & Hír, E. 2012. Észak-Magyarország madárvilága a miocénben II. rész [The avifauna in North Hungary during the Miocene. Part II.]. – Földtani Közlöny 142(2): 149–168. (in Hungarian)

Kessler, E. & Venczel, M. 2009. Bird remains from the Middle Miocene of Subpiatră (W-Romania). – Nymphaea, Folia naturae Bihariae 36: 27–36.

Kessler, E. & Venczel, M. 2011. A new passeriform bird from the Middle Miocene of Subpiatră (W-Romania). – Nymphaea, Oradea, 38: 17–22.

Kordos, L. 1984. A bodajki Rigó-lyuk újholocén kitöltésének vizsgálata [Investigating the Holocene filling of the Bodajk-Rigó Hole]. – Folia Musei Historico-Naturalis Bakonyensis 3: 31–42. (in Hungarian)

Kormos, T. 1911. Die pliozäne Knochenfund bei Polgárdi (vorläufiger Bericht) [The pliocene bone find at Polgárdi (preliminary report)]. – Földtani Közlöny 41: 171–189. (in German)

Kormos, T. 1913. Kleinere Mitteilungen aus dem ungarischen Pleistozän [Small releases from the Hungarian Pleistocene]. – Centralblatt für Mineralogie, Geologie und Palaontologie 1913: 13–17. (in German)

Kormos, T. 1914. Az 1913. évben végzett ásatásaim eredményei [The results of the excavations carried in the year 1913]. – A Magyar Királyi Földtani Intézet 1913. évi jelentése, pp. 498–505., 531–540. (in Hungarian)

Kretzoi, M. 1952. Die Raubtiere der Hipparion-fauna von Polgárdi [The predators of the Hipparion fauna of Polgárdi]. – Jahrbuch Ungarische Geological Anstalt 40: 1–12. (in German)

Kretzoi, M. 1956. A Villányi hegység alsó pleisztocén gerinces faunái [Ostrich remains from Kisláng, Fejér County]. – Geologica Hungarica 27: 1–264. (in Hungarian)

Kretzoi, M. 1962. A csarnótai fauna és faunaszint [The fauna and fauna level of the Csarnóta]. – A Magyar Állami Földtani Intézet Évi Jelentése az 1959. évről, pp. 297–395. (in Hungarian)

Kretzoi, M. 1969. A magyarországi quarter és pliocén szárazföldi biosztratigráfiájának vázlata [Outline of terrestrial biostratigraphy of the Hungarian Quaternary and Pliocene]. – Földrajzi Közlemények 18(3): 179–204. (in Hungarian)

Kretzoi, M. 1975. Fontosabb szórványleletek a MÁFI gerinces gyüjteményében (2 studies) [The most important Vertebrate finds of the Hungarian Geological Institute]. – A Magyar Állami Földtani Intézet Évi jelentése 1975 évről, pp. 401–415. (in Hungarian)

Kretzoi, M. 1977. The fauna of small vertebrates of the Middle Pleistocene at Petralona. – Anthropos (Athena) 4: 131–143.

Lambrecht, K. 1912. Magyarország fossilis madarai – Die fossilen Vögel Ungarns [The Fossil birds of Hungary]. – Aquila 19: 288–320. (in Hungarian and German)

Lambrecht, K. 1913. Neueren Daten zur fossilen Ornis unseren Höhlen [Extant data for fossil birds in our caves]. – Barlangkutatás 1: 173. (in German)

Lambrecht, K. 1915. Fossilis nagy fülesbagoly (*Bubo maximus* Flemm.) és egyéb madármaradványok a magyarországi pleisztocénből [Fossil's Big Eared Owl (*Bubo maximus* Flemm.) and other bird remains in Hungarian Pleistocene]. – Aquila 22: 177–187. (in Hungarian)

Lambrecht, K. 1916. Az első magyar preglaciális madárfauna. Die erste ungarische praglaziale Vogelfauna [The first Hungarian Preglaciale bird fauna]. – Aquila 22: 165–172. (in Hungarian and German)

Lambrecht, K. 1933. Handbuch der Palaornithologie [Handbook of Palaeornithology]. – Gebrüder Borntraeger, Berlin (in German)

Malez, M. 1961. Pecinska hijena iz indije kod Voce [The Cave Hyaenas come from Vindija Cave]. – Geologiceskij Vjesnik 14: 221–244. (in Croatian)

Malez, V. 1973. Fosilne ptice Jugoslavije [Fossil birds from Yugoslavia]. – Unpublished Dissertation, Zagreb University, pp. 1–97. (in Croatian)

Malez, M. 1975. Ornitofauna iz kvartarnih naslaga velike pecine na ravnoj gori u sjeve-rozapadnoj Hrvatskoj [Ornithofauna from the Quaternary sediments of a large cave on a flat mountain in Northwestern Croatia]. – Larus 26–28: 45–54. (in Croatian)

Malez, M. & Rukavina, D. 1975. Kristurbacijske pojave u gornjopleistocenskim nasla-gama pecine Vindije kod Donje Voce u sjeverozapadnoj Hrvatskoj [Cristurbation appearance in Upper Pleistocene at Vindija cave in Northwestern Croatia]. – Rad Hazu knj. 371: 245–265. (in Croatian)

Malez, V. 1973. Fosilne ptice Jugoslavije [Fossil birds from Yugoslavia]. – Unpublished Dissertation, Zagreb University, pp. 1–97. (in Croatian)

Malez, V. 1984. Paleornitološki ostaci iz kvartarnih naslaga nekih spilja Hrvatske i Slovenije [Paleornithological remains from the Quaternary Sediments of some Croatian and Slovenian caves]. – In: Deveti jugoslavenski speleoloski kongres, Zbornik predavanja, pp. 711–719. (in Croatian)

Malez, V. 1988. Pleistocenska ornitofauna iz spilje Vindije u sjevernozapadnoj Hrvatskoj [Pleistocene bird fauna from Vindija cave in Northwestern Croatia]. – Rad Jugoslavenske Akademije Znanosti i Umjetnosti, Varazdin 2: 31–203. (in Croatian)

Malez-Bačic, V. 1979. Pleistocenska ornitofauna iz Šandalje u Istri te njezino stratigrafsko i paleoekološko značenje [Pleistocene bird fauna from Šandalja in Istria and its stratigraphic and paleoecological significance]. – Palaeontologia Jugoslavica 21: 1–46. (in Croatian)

Milne-Edwards, A. 1869–1871. Recherches anatomiques et paléontologiques pour servir àl'histoire des oiseaux fossiles de la France, Vol. 2. [Anatomical and paleontological research to serve the history of fossil birds of France, Vol. 2.]. – Paris, G. Masson (in French)

Mlíkovský, J. 1989. Ptáci staršího a středního pleistocénu Československa: současný stav aperspektivy výzkumu [Birds of the Early and Middle Pleistocene of Czechoslovakia: The Current State of Research

Approach]. – In: Seitl, L. (ed.) Současný stav a perspektivy výzkumu kvartéru v ČSSR [The Current State and Perspectives of the Quaternary Research in Czechoslovakia]. – Brno: Moravské muzeum & Universita J. E. Purkyně, pp. 63–67. (in Czech)

Mlíkovský, J. 1995. Early Pleistocene birds of Stránská skála: 1. Musil's talus cone. – In: Musil, R. (ed.) Stránská skála Hill: Excavations of open-air sediments 1964–1972. – Anthropos (Brno) 26: 111–126. (in Czech)

Mlíkovský, J. (ed.) 1996. Tertiary avian localities of Europe. – Acta Universitatis Carolinae, Geologica 39: 517–848.

Mlíkovský, J. 1998. Early Pleistocene birds of Deutsch-Altenburg, Austria. – Acta Societatis Zoologicae Bohemicae 62: 135–141.

Mlíkovský, J. 2002. Cenozoic Birds of the World. Part 1: Europe. – Ninox Press, Praha

Mlíkovský, J. 2009. Middle Pleistocene birds of Hundsheim, Austria. – Journal of the National Museum (Prague), Natural History Series 177(7): 69–82.

Montoya, P. 1999. La fauna del Pleistoceno inferior de la Sierra de Quibas (Abanilla, Murcia) [The fauna of the Lower Pleistocene of the Sierra de Quibas (Abanilla, Murcia)]. – Estudios Geológicos 55 (3–4): 127–161. (in Spanish)

Montoya, P. 2001. Une faune très diversifiée du Pléistocène inférieur de la Sierra de Quibas (province de Murcia, Espagne) [A very diverse fauna from the Lower Pleistocene of the Sierra de Quibas (province of Murcia, Spain)]. – Comptes Rendus de l'Académie des Sciences (Paris), Sciences de la Terre et des Planètes 332: 387–393. (in French)

Mourer-Chauviré, C. 1975. Les oiseaux du Pléistocène moyen et supérieur de France [The Middle and Upper Pleistocene birds of France]. – Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 64: 1–624. (in French)

Mourer-Chauviré, C. 1995. Dynamics of the avifauna during the Paleogene and the Early Neogene of France. Settling of the extant fauna. – Acta Zoologica Cracoviensia 38(3): 325–342.

Mourer-Chauviré, C., Hugueney, M. & Jonet, P. 1989. Découverte de Passeriformes dans l'Oligocène supérieur de France [Discovery of Passeriformes in the Upper Oligocene of France]. – Comptes Rendus Hebdomadaires de l'Académie des Sciences (Paris), Sciences de la Terre et des Planètes 309: 843–849. (in French)

Nagy, J. 2020. Biologia Futura: rapid diversification and behavioural adaptation of birds in response to Oligocene–Miocene climatic conditions. – Biologia Futura 71: 109–121.

Nehring, A. 1880. Uebersicht über vierundzwanzig mitteleuropäische Quartär-Faunen [Survey of twenty-four Central European Quaternary fauna]. – Zeitschrift der Deutschen Geologischen Gesellschaft 32: 468–509. (in German)

Noriega, J. I. & Chiappe, L. 1993. An Early Miocene Passeriform from Argentina. – The Auk 110(4): 936–938.

Pike-Tay, A., Bartosiewicz, L., Gál, E. & Whitle, A. 2004. Body part representation and seasonility: sheep/goat, bird and fish remains from Early Neolithic Ecsegfalva 23 SE Hungary. – Journal of Taphonomy 2(4): 221–246.

Pongrácz, L. 1999. A beremendi Szőlő-hegy természettudományi kutatásának 150 éve [150 years of natural science research on Beremend Szőlő-Hill]. – Petényi emlékkönyv, Beremend

Portis, A. 1887. Contribuzioni alla ornitolitologia italiana. Parte II. [Contributions to Italian ornitholithology. Part II.]. – Memorie Regia Accademia Scienze (Torino) (2) 38: 181–203. (in Italian)

Róth, S. 1881. Szepesmegye néhány barlangjának leirása [Description of some caves in Szepes County]. – Mathematikai és Természettudományi Közlemények 16: 613–648. (in Hungarian)

Soergel, E. 1966. Die Vogelreste [The Bird Remains]. – In: Ehrenberg, K. (ed.) Die Teufels-oder Fuck-senlucke bei Eggenburg (NÖ) [The Devil or Fuck senlucke at Eggenburg (NA)]. – Denkschriften der Mathematisch-Naturwissenschftliche Klasse der Österreichischen Akademie der Wissenschaften, pp. 93–107. (in German)

Sondaar, P. Y., Mcminn, M., Segui, B. & Alcover, J. A. 1995. Interès paleontològic del jaciments càrstic de les Gimnésies i les Pitiüses [Paleontological interest of the karstic deposits of the Gymnasiums and the Pitiusas]. – Endins 20: 155–170. (in Spanish)

Tassi, M. 2006. Szendrő-Felsővár állatcsontanyaga [Animal bone material form Szendrő- Felsővár]. – Visegrádi Múzeumok Közleményei: 15–30. (in Hungarian)

Tchernov, E. 1980. The Pleistocene Birds of Ubeidiya, Jordan Valley. – In: The Pleistocene of the Central Jordan Valley. The excavation at Ubeidiya. – The Israel Academy of Sciences Humanities, Jerusalem, pp. 1–83.

Tyrberg, T. 1998. Pleistocene birds of the Palearctic: a catalogue. – Cambridge, Mass.: Nuttall Ornithological Club

Villalta, J. F. de 1963. Las aves fósiles del Mioceno español [Fossil birds of the Spanish Miocene]. – Boletín de la Real Sociedad Española de Historia Natural Geología 61: 263–285. (in Spanish)

Vojinstvens'kyj, M. A. 1967. Iskopaemaja ornitofauna Ukrainy [The fossil avifauna of Crimea]. – Prirodnaja Obstanovka i Fauni Prollogo 3: 3–76. (in Russian)

Wettstein, O. V. & Mühlhofer, F. 1938. Die Fauna der Höhle von Merkenstein in N-Ö [The fauna of the Merkenstein cave in North Austria]. – Archiv Naturgeschichte, New Series 7(4): 514–558. (in German)

Zelenkov, N. 2011. Neogene Birds of Central Asia. – PhD Thesis, Paleontological Institute, RAN, Moscow

Zelenkov, V. N. & Kurochkin, E. N. 2012. The first representative Pliocene assemblages of passerine birds in Asia (Northern Mongolia and Russian Transbaikalia). – Geobios 45(3): 323–334. DOI: 10.1016/j.geobios.2011.10.001

sciendo

Ornis Hungarica 2020. 28(2): 204–211.
DOI: 10.2478/orhu-2020-0025

Attributes of Eurasian Green Woodpecker *(Picus viridis)* nest cavities in Hungary

Gerard Gorman

Received: September 28, 2020 – Revised: October 2, 2020 – Accepted: October 05, 2020

Gorman, G. 2020. Attributes of Eurasian Green Woodpecker *(Picus viridis)* nest cavities in Hungary. – Ornis Hungarica 28(2): 204–211. DOI: 10.2478/orhu-2020-0025

Abstract Thirty-three nest cavities of Green Woodpeckers *(Picus viridis)* in Hungary were documented over a period of 15 years (2006–2020). Thirteen different tree species were used. All documented cavities were in the main trunks of trees. The mean cavity height was 5.6 m and 1.5 m standard deviation and ranged from 2 to 9 m. Tree trunk diameters ranged between 36–55 cm with a mean of 43.1 cm and 4.2 cm standard deviation. A southerly orientation of cavity entrances prevailed with a mean direction of 187° clockwise from north. The results suggest that cavity-entrance orientation was non-random.

Keywords: woodpecker nesting cavity, cavity location, cavity height, cavity entrance orientation

Összefoglalás Összesen 33 magyarországi zöld küllő *(Picus viridis)* odúról készült dokumentáció 15 év alatt, 2006–2020-ig. A madarak minden vizsgált esetben a fák törzsébe vájták az odúkat, ehhez összesen 13 különböző fafajt választottak. A röpnyílás átlagos magassága a talajtól számítva 5,6 m volt 1,5 m-es szórással, 2–9 m-es kiterjedéssel. A mellmagassági törzsátmérő 36–55 cm közé esett 43,1 cm-es átlaggal és 4,2 cm-es szórással. Az odúk délies tájolásúak voltak (átlagban 187°, északról számolva, az óramutató járása szerint). Az eredmények alapján megállapítható, hogy a röpnyílások tájolása nem véletlenszerű.

Kulcsszavak: harkály költőodú, az odú helye, odúmagasság, röpnyílás tájolása

Independent Researcher, Hungarian Woodpecker Working Group, c/o MME BirdLife Hungary, Budapest, Hungary, e-mail: picidae.gerard@gmail.com

Introduction

The global distribution of Green Woodpecker *(Picus viridis)* falls almost entirely within the Western Palearctic region with approximately 95% of its total population considered to be within Europe (BirdLife 2020). The species is found from Britain in the west to Russia and Turkmenistan in the east, and from Norway, Sweden and Estonia in the north to Italy, the Balkans and Turkey in the south, and in the southeast to Iran and Iraq. It is absent from Finland and islands such as Gotland, Corsica, Sardinia, Malta, Crete, Cyprus and Ireland, although vagrant individuals have been observed on some of these islands. The species is resident, non-migratory and typically highly sedentary, although post-breeding dispersal of juveniles takes place (Glutz & Bauer 1994, Winkler *et al.* 1995, Gorman 2004, 2020).

The Green Woodpecker is polytypic, with three subspecies generally recognised: *viridis* in Britain, southern Scandinavia and continental Europe (including Hungary) and western Russia; *karelini* in Italy, the southern Balkans, the Caucasus and to Turkmenistan; and *innominatus*, which occurs solely in the Zagros Mountains in Iran and Iraq (del Hoyo & Collar 2014, Gorman 2014, 2020).

The species inhabits a diversity of wooded habitats across this range, which covers three eco-climatic regions: the temperate, Mediterranean and the boreal zones. Typical breeding habitats occupied include open forests and woodlands, riparian woods, parkland, orchards and large gardens. Green Woodpeckers mostly frequent deciduous trees, but in some areas mixed deciduous-coniferous woodlands are used. Dense forests are avoided. In all areas, adjacent grasslands, where birds can forage for terrestrial ants, are essential (Alder & Marsden 2010). In Europe, Green Woodpeckers occur in both lowlands and uplands, to around 2,000 m, only occasionally higher (Gorman 2020).

Although there have been declines locally, often owing to grassland and/or wooded habitat degradation, the overall trends for this species are positive and it is not considered to be threatened. In the *IUCN Red List of Threatened Species*, Green Woodpecker is classified as *Least Concern* (BirdLife 2016).

Green Woodpecker nest cavity characteristics, particularly orientation of entrance holes, have not been widely studied. Existing data have generally been published as part of broader studies on other woodpecker and cavity-nesting bird species (Aulén 1988, Hågvar *et al.* 1989, Blume 1996, Kosiński & Kempa 2007, Zhou *et al.* 2012). Cavity orientation in this species had not been previously studied in Hungary and the aim of this work was to gather data to improve the knowledge and understanding of its habitat requirements.

Methods

This study was restricted to nest cavities that were used by Green Woodpeckers in Hungary. The study area covered six hill ranges across the north of the country. Namely, from west to east, the Gerecse, Buda, Pilis, Bükk, Aggtelek and Zemplén. These low ranges (the highest points in each are all below 1,000 m above sea-level) are characterized by deciduous forests and woodlands. The research was conducted between 2006 and 2020. The search for cavities was carried out from March to May in each year as this is the period when Green Woodpeckers mostly excavate and occupy them, although cavities are sometimes excavated at other times of the year (Gorman 2011). Sites where Green Woodpeckers had been observed previously were investigated and cavities found by observing the behaviour of birds, such as individuals persistently calling, indulging in courtship behaviour or carrying food for nestlings, and by looking for signs of excavation, such as fresh woodchips below trees. Trees with cavities excavated in previous years were also checked. A total of thirty-three (33) cavities were documented. The study did not deal with breeding success, rather the five main aims were: (1) to determine tree species used; (2) to document cavity locations, whether on trunks or limbs; (3) to measure the height of cavity entrances above ground level; (4) to measure the trunk diameters at breast height (DBH) of trees with cavities; (5) to document the orientation of cavity entrances. Cavity height was estimated using simple trigonometry. The diameter of cavity trees was calculated by means of the standard method of DBH, with measurements taken using calipers at 1.3 m above the ground from the base of the trunk. Cavity orientation was calculated with a compass, using sixteen standard points (N, NNE, NE, ENE, etc.). The randomness of orientation was assessed using a Rayleigh test of uniformity (Pewsey *et al.* 2013) as implemented in the package 'circular' in R (Lund & Agostinelli 2011, R Development Core Team 2015).

Results and discussion

Some attributes of thirty-three nest cavities and their locations were documented. All cavity trees were in open wooded areas dominated by broadleaved trees. All cavities documented were newly excavated: none were from previous years that were being reused. New cavities can be recognized by their entrances having clean edges with no renewed tree growth, and light-coloured wood (Gorman 1995). Most cavity entrances were circular in shape, although four were vertically oval and one horizontally oval in shape. Cavity entrance dimensions were not measured.

Trees used

Across their range Green Woodpeckers do not seem to show any significant preference for particular tree species, rather they are only associated with specific trees locally. The openness of a woodland or forest and availability of ant prey is probably more important for this species (Spitznagel 1990, Rolstad *et al.* 2000, Riemer *et al.* 2010). The variety of trees found across the range of the species varies significantly. Almost any tree is used for nesting providing the bole is large enough to house a cavity. An area of soft wood, usual due to fungal decay, facilitates easier excavation. Nevertheless, broadleaved trees are generally selected over coniferous (Glue & Boswell 1994). In this study, nest cavities were found in thirteen different tree species (number of times used in brackets): common alder *Alnus glutinosa* (1), ash *Fraxinus excelsior* (5), beech *Fagus sylvatica* (3), elm *Ulmus minor* (2), hornbeam *Carpinus betulus* (2), horse chestnut *Aesculus hippocastanum* (1), oaks *Quercus* spp. (5), poplar *Populus* spp. (4), plane *Platanus* spp. (1), small-leaved lime *Tilia cordata* (3), sycamore *Acer pseudoplatanus* (1), walnut *Juglans regia* (2) and willow *Salix* spp. (3). All cavities were in broadleaved trees with none in coniferous species. There was no clear dominance by one tree species (see *Table 1*). While no tree species dominated the sample, this was not tested for selection by Green Woodpeckers due to lack of data on relative tree species availability from within the study area.

Cavity location

All cavities found were placed in foliage-free sections on the main trunk of trees and were below canopy level, with a clear flyway to the entrance. No cavities were found in branches. All were in living trees, but in parts with soft and/or deadwood and with the presence of fungi evident.

Table 1. Summary of cavities used by Green Woodpeckers
1. táblázat A zöld küllők által használt odúk adatai

Year	Location	Tree species	Height above ground (approx. metres)	Tree-trunk width (DBH) in cm	Cavity-entrance orientation
2006	Pilis Hills	Ash	7	40	SW
2006	Zemplén Hills	Oak spp.	5.5	46	SSW
2007	Bükk Hills	Elm	6	38	SE
2008	Buda Hills	Poplar spp.	6.5	40	S
2008	Pilis Hills	Oak spp.	5	45	NE
2008	Buda Hills	Ash	7	44	SW
2009	Pilis Hills	Oak spp.	4.5	42	SE
2009	Bükk Hills	Willow spp.	6	42	NW
2010	Buda Hills	Poplar spp.	5	40	S
2011	Zemplén Hills	Walnut	3	38	SE
2011	Pilis Hills	Beech	9	55	SSE
2012	Buda Hills	Oak spp.	5	48	WSW
2012	Bükk Hills	Hornbeam	6.5	40	WSW
2012	Bükk Hills	Ash	6	38	SSW
2013	Gerecse Hills	Willow spp.	5	36	S
2013	Zemplén Hills	Beech	6	45	W
2013	Pilis Hills	Sycamore	5	44	SSE
2014	Aggtelek	Ash	5	40	E
2014	Bükk Hills	Plane	4	42	SW
2015	Zemplén Hills	Lime	7.5	50	S
2015	Buda Hills	Elm	5.5	42	WSW
2015	Pilis Hills	Beech	8	45	ESE
2016	Aggtelek	Hornbeam	3.5	38	SW
2016	Zemplén Hills	Oak spp.	7	50	SE
2016	Gerecse Hills	Poplar sp.	4	44	SW
2017	Zemplén Hills	Willow spp.	3	42	SE
2017	Bükk Hills	Lime	7	50	S
2017	Zemplén Hills	Walnut	2	45	W
2018	Bükk Hills	Common Alder	7	44	ESE
2018	Zemplén Hills	Ash	7	45	SW
2019	Gerecse Hills	Poplar spp.	6.5	38	E
2019	Buda Hills	Horse Chestnut	5	44	S
2020	Bükk Hills	Lime	6	45	SW

Cavity height

Entrance-hole heights of Green Woodpeckers can vary considerably, from as low as 1 m above ground level to as high as 9 m, but most are located between 2–5 m (Glue & Boswell 1994, Glutz & Bauer 1994, Solti 2010). In this study, there was also significant variation in the heights of cavities above ground level. The highest cavity entrance was located at 9 m, the lowest 2 m. The most frequently documented height was 5 m (7 cavities: 21.21%) with the mean of 5.6 m and standard deviation 1.5 m.

Tree trunk width

The widest diameter (DBH) of a cavity tree was 55 cm and the narrowest 36 cm. The most frequently documented diameter was 45 cm (6 cavities: 18.18%), with a mean of 43.1 cm and standard deviation of 4.2 cm.

Cavity entrance orientation

Of the thirty-three cavities, twenty-two (66.67%) faced southwards (SE, SSE, S, SSW, SW). The most frequent alignment was SW with seven (21.21%) cavities. Four cavities were orientated towards the east (E, ESE), five westwards (WSW, W, WNW), one cavity was orientated towards the NW and one to the NE. The cavity orientation was non-random and significantly biased toward the south (Rayleigh test r=0.57, p<0.001) with a mean direction of 187 degrees clockwise from north *(Figure 1)*.

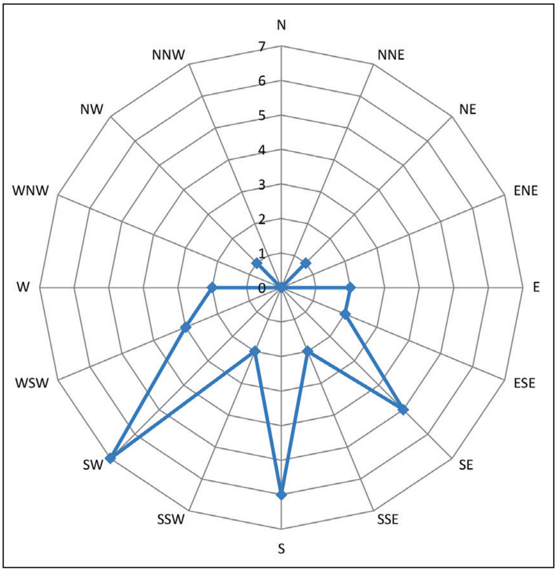


Figure 1. Orientation of Green Woodpecker cavity entrances as frequencies of cardinal points
1. ábra A zöld küllő költőodúk tájolása 16 alégtáj szerint

Conclusions

This paper summarizes some attributes of thirty-three nest cavities of Green Woodpeckers in Hungary over a period of fifteen years. Cavities were found in thirteen different tree species, but there was no evidence that these species held any specific significance for Green Woodpeckers.

As is the case with most picids when selecting a cavity location, it is likely that ease of excavation seemed to be more important than any link to a specific tree species. Most woodpeckers, Green Woodpecker included, invest a substantial amount of time and energy in excavating cavities and, despite being morphologically adapted to excavate timber, it is known that they tend to select parts of trees where it is relatively easy for them to do so with dead or dying sections usually chosen. The hardness of the interior wood of trees is considered to be a key element in cavity site selection (Kosiński & Winiecki 2004, Kosiński *et al.* 2006, Kosiński & Kempa 2007, Matsuoka 2010, Lorenz *et al.* 2015). Dying or living trees with weak and soft areas resulting from decay, due to fungal or insect infestation, or wounds from lightning strikes, strong winds, frost and the like, present better opportunities for cavity excavation than those that are healthy and sound. Studies of two species that are often sympatric with Green Woodpecker in continental Europe, Black Woodpecker *Dryocopus martius* (Zahner *et al.* 2012, Puverel *et al.* 2019) and Grey-headed Woodpecker *Picus canus* (Gorman 2019) have indicated that trees affected with fungal rot are regularly chosen for cavities. Although it was not possible to verify the presence or extent of decay in every cavity tree in the present study, most tended to be more fungus-afflicted than surrounding trees. At least thirty (90.91%) of the thirty-three showed obvious signs of rot in the area of trunk that housed the cavity. Nesting trees were also always amongst the biggest trees in the area, with large enough boles to house a cavity. It was suspected that the location, condition and relative size of each tree, rather than its species, resulted in it being selected for a nest cavity.

The openness of nesting habitat and accessibility of prey, particularly terrestrial ants, is known to be critical for Green Woodpeckers (Spitznagel 1990, Rolstad *et al.* 2000, Riemer *et al.* 2010). The extent to which the surrounding vegetation influenced the selection of cavity trees at the sites documented was not examined in detail, however, at each locations, the surrounding habitat clearly offered suitable foraging opportunities, in the form of various short-grassed habitats.

A frequent question that researchers have sought to answer is whether the entrance orientation of woodpecker cavities is determined by compass direction. Studies globally have yielded contrasting conclusions. One evaluation of cavity-entrance orientation from eighty populations of twenty-three species of woodpecker throughout the Northern Hemisphere concluded that the orientation was influenced by regional climatic forces and was typically non-random (Landler *et al.* 2014). In the present study of Green Woodpecker cavities, a southerly alignment and orientation of entrances prevailed, and the results suggest that cavity-entrance orientation was non-random. A study, also conducted in Hungary, of cavities of a close relative, the Grey-headed Woodpecker, produced similar results (Gorman 2019).

The reasons for this choice of direction are unclear with a number of factors likely to be implicated. Notably, prevailing wind direction may be involved: in Hungary it is from a north-westerly direction (Hungarian Meteorological Service, undated). Temperature, average rainfall levels and degree of sunlight may also influence the orientation of cavities; those facing southwards and eastwards receive more sun, hence illumination and warmth, in the morning hours. The higher number of entrances facing southwards suggests that early-morning warming is preferred. However, a compromise may exist. Local conditions and circumstances may result in some factors outweighing and overriding others. For example, the southward-facing sides of tree trunks may not necessarily catch the most sun and warmth owing to the surrounding environment: other trees, bushes or buildings may all result in shade. Furthermore, woodpeckers, when making cavities, may disregard compass direction in order to conserve excavation energy output. Cavities facing away from the south may be created because to do so requires less effort. A section of tree where a cavity can be more easily excavated, because the wood is softest, may be selected, although it may not be ideal in terms of entrance orientation.

Acknowledgements

The author wishes to thank Danny Alder and Ken Smith for their helpful comments and assistance with statistics, and also two anonymous referees for their constructive remarks.

References

Alder, D. & Marsden, S. 2010. Characteristics of feeding-site selection by breeding Green Woodpeckers *Picus viridis* in a UK agricultural landscape. – Bird Study 57(1): 100–107. DOI: 10.1080/00063650903437511

Aulén, G. 1988. Ecology and distribution history of the White-backed Woodpecker *Dendrocopos leucotos* in Sweden. – PhD Thesis, SLU Uppsala, Sweden, Report 14.

BirdLife International 2016. *Picus viridis*. The IUCN Red List of Threatened Species 2016. – Accessed: 01/09/2020.

BirdLife International 2020. Species factsheet: *Picus viridis*. – www.birdlife.org. Accessed: 01/09/2020.

Blume, D. 1996. Schwarzspecht, Grauspecht, Grünspecht [Black, Grey & Green Woodpeckers]. – Neue Brehm-Bücherei Heft 300. 5. überarb. Auflage. Westarp Wissenschaften, Magdeburg (in German)

del Hoyo, J. & Collar, N. J. 2014. HBW and BirdLife International Illustrated Checklist of the Birds of the World. Vol. 1. – Lynx Edicions, Barcelona

Glue, D. E. & Boswell, T. 1994. Comparative nesting ecology of the three British breeding woodpeckers. – British Birds 87: 253–269.

Glutz von Blotzheim, U. N. & Bauer, K. M. (eds.) 1994. Handbuch der Vogel Mitteleuropas. Band 9. Columbiformes-Piciformes [Handbook of the Birds of Central Europe, Vol. 9.]. – AULA-Verlag Gmbh, Wiesbaden (in German)

Gorman, G. 1995. Identifying the presence of woodpecker (Picidae) species on the basis of their holes and signs. – Aquila 102: 61–67.

Gorman, G. 2004. Woodpeckers of Europe. A study of the European Picidae. – Coleman, Chalfont St. Peter, UK.

Gorman, G. 2011. Green Woodpecker excavating a cavity in autumn. – British Birds 104: 276.

Gorman, G. 2014. Woodpeckers of the World: the complete guide. – Helm, London, UK.

Gorman, G. 2019. Characteristics of Grey-headed Woodpecker *(Picus canus)* cavities in Hungary. – Aquila 126: 33–39.

Gorman, G. 2020. The Green Woodpecker – A monograph on *Picus viridis*. – Picus Press, UK.

Hågvar, S., Hågvar, G., Hailman, E. D. & Hailman, J. P. 1989. The direction of the hole in Norwegian woodpecker nests. – Fauna Norvegica Series C 12: 106–107.

Hungarian Meteorological Service (undated): Wind conditions of Hungary. – Accessed: https://www.met.hu/en/eghajlat/magyarorszag_eghajlata/altalanos_eghajlati_jellemzes/szel/ (01/09/2020)

Kosiński, Z. & Winiecki, A. 2004. Nest-site selection and niche partitioning among the Great Spotted Woodpecker *Dendrocopos major* and Middle Spotted Woodpecker *Dendrocopos medius* in riverine forest of Central Europe. – Ornis Fennica 81(4): 145–156.

Kosiński, Z., Ksit, P. & Winiecki, A. 2006. Nest site of Great Spotted Woodpeckers *Dendrocopos major* and Middle Spotted Woodpeckers *Dendrocopos medius* in near-natural and managed riverine forests. – Acta Ornithologica 41(1): 21–32. DOI: 10.3161/000164506777834624

Kosiński, Z. & Kempa, M. 2007. Density, distribution and nest-sites of woodpeckers Picidae, in a managed forest of Western Poland. – Polish Journal of Ecology 55(3): 519–533.

Landler, L., Jusino, M. A., Skelton, J. & Walters, J. R. 2014. Global trends in woodpecker cavity entrance orientation: latitudinal and continental effects suggest regional climate influence. – Acta Ornithologica 49(2): 257–266. DOI: 10.3161/173484714X687145

Lorenz, T. J., Vierling, K. T., Johnson, T. R. & Fischer, P. C. 2015. The role of wood hardness in limiting nest site selection in avian cavity excavators. – Ecological Applications 25(4): 1016–1033. DOI: 10.1890/14-1042.1

Lund, U. & Agostinelli, C. 2011. Package 'circular': circular statistics. – R package version 0.4-3.

Matsuoka, S. 2010. Great Spotted Woodpeckers *Dendrocopos major* detect variation in wood hardness before excavating nest holes. – Ornithological Science 9(1): 67–74. DOI: 10.2326/osj.9.67

Pewsey, A., Neuhauser, M. & Ruxton, G. D. 2013. Circular Statistics in R. – OUP, Oxford

Puverel, C., Abourachid, A., Böhmer, C., Leban, J-M., Svoboda, M. & Paillet, Y. 2019. This is my spot: what are the characteristics of the trees excavated by the Black Woodpecker? A case study in two managed French forests. – Forest Ecology and Management 453: 117621. DOI: 10.1016/j.foreco.2019.117621

R Development Core Team 2015. A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria

Riemer, S., Schulze, C. H. & Frank, G. 2010. Population density and habitat use of the Green Woodpecker *Picus viridis* in Donau-Auen National Park (Lower Austria). – Vogelwarte 48(3): 275–282. (in German with English Summary)

Rolstad, J., Løken, B. & Rolstad, E. 2000. Habitat selection as a hierarchical spatial process: the Green Woodpecker at the northern edge of its distribution range. – Oecologia 124(1): 116–129. DOI: 10.1007/s004420050031

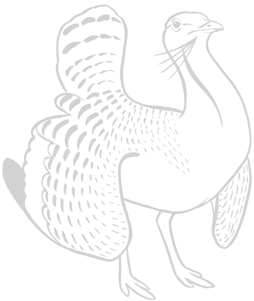
Solti, B. 2010. A Mátra Múzeum madártani gyüjteménye III. Németh Márton tojásgyűjtemény [The ornithological collection of the Mátra Museum III Márton Németh's egg collection]. – Folia Historico-naturalia Musei Matraensis Suppl. 5: 1–275. (in Hungarian)

Spitznagel, A. 1990. The influence of forest management on woodpecker density and habitat use in floodplain forests of the Upper Rhine Valley. – In: Carlson, A. & Aulén, G. (eds.) Conservation and Management of Woodpecker Populations. – Swedish University of Agricultural Sciences, Dept of Wildlife Ecology, Report 17. Uppsala

Winkler, H., Christie, D. A. & Nurney, D. 1995. Woodpeckers: A guide to the woodpeckers, piculets and wrynecks of the World. – Pica Press, Robertsbridge, UK.

Zahner, V., Sikora, L. & Pasinelli, G. 2012. Heart rot as a key factor for cavity tree selection in the Black Woodpecker. – Forest Ecology and Management 271: 98–103. DOI: 10.1016/j.foreco.2012.01.041

Zhou, C., Zhou, D., Kong, X. & Deng, W. 2012. Differentiating nest sites characteristics of four sympatric cavity-nesting birds. – Biodiversity Science 20(6): 716–724. DOI: 10.3724/SP.J.1003.2012.09068



Ornis Hungarica 2020. 28(2): 212–214.
DOI: 10.2478/orhu-2020-0026

First record of Lichtenstein's Sandgrouse *Pterocles lichtensteinii* in Lebanon, 2020

Michel Sawan

Received: June 18, 2020 – Revised: August 17, 2020 – Accepted: August 31, 2020

Sawan, M. 2020. First record of Lichtenstein's Sandgrouse *Pterocles lichtensteinii* in Lebanon, 2020. – Ornis Hungarica 28(2): 212–214. DOI: 10.2478/orhu-2020-0026

Abstract The Lichtenstein's Sandgrouse *(Pterocles lichtensteinii)* is a nomadic, mostly nocturnal species. Its world range includes several countries in Africa, as far south as Kenya, and Asia as far east as Pakistan, but within the Middle East, it is a resident in Egypt, Southern Israel and Jordan, Saudi Arabia, Yemen, Oman and Southern Iran. Like other members of its family, it is found in very dry habitats including wadis and stony deserts. Seeing a flock of them in Lebanon is extraordinary. They were sighted for the first time in the country. The dry hot wind in that time of the year might have brought them there. A poacher shot the flock and killed six birds during night hunting.

Keywords: Liechtenstein's Sandgrouse, first record, new species in Lebanon, night poaching, *Pterocles lichtensteinii*

Összefoglalás A csíkos pusztaityúk *(Pterocles lichtensteinii)* egy nomadizáló, éjszakai életmódot folytató faj. Elterjedési területe Afrikában Kenyáig, Ázsiában a Közel-Keletig, Pakisztánig terjed. Állandó faj Egyiptomban, Izrael déli részén, Jordániában, Szaúd-Arábiában, Jemenben, Ománban és Irán déli részén. A rokon fajokhoz hasonlóan száraz élőhelyeken, vádikban, köves sivatagokban fordul elő. Libanoni előfordulása ismert elterjedési területén kívülre esik. Ez az első ismert megkerülése, amiben valószínűleg szerepet játszott az ebben az időszakban fújó meleg, száraz szél. Egy orvvadász belelőtt a csapatba és megölt 6 példányt egy éjszakai vadászat során.

Kulcsszavak: szudáni pusztaityúk, *Pterocles lichtensteinii*, első előfordulás, új faj Libanonban, orvvadászat

e-mail: michelsawan@hotmail.com

Lichtenstein's Sandgrouse *(Pterocles lichtensteinii)* is a nomadic, mostly nocturnal species, reaching 25 cm in length, in the family Pteroclidae. Its world range includes several countries in Africa, from Morocco through the Sahara to Chad *(P. l. targius)* and from South Sudan as far south as Central Kenya *(P. l. sukensis)*, and Asia as far east as Iran and Pakistan *(P. l. arabicus)*, but within the Middle East *(P. l. lichtensteinii)*, it is a resident in Egypt, Southern Israel and Jordan, Saudi Arabia, Yemen (*P. l. ingramsi*, only resident in EC Yemen), and Oman (BirdLife International 2016, de Juana & Kirwan 2020).

Like other members of its family it is found in very dry habitats including wadis and stony deserts. Their nocturnal nature and their habit of drinking before dawn and after dusk means that they are often very hard to spot. The five geographical races are currently classed as being of Least Concern by Birdlife International (2016). The closest subspecies to Lebanon *(P. l. lichtensteinii)* normally occurs in Southern Israel and, prior to the events described below, this species had never been recorded from Lebanon.

At 11 p.m. on the 19th of January 2020, I was called by a young man (a hunter) who had been hunting Song Thrushes *(Turdus philomelos)* at night when he saw a very fast-flying flock of about 12 birds. He fired at the flock landed on the ground and killed three birds and caught another three alive.

I identified the birds as a nominate subspecies of the Liechtenstein's Sandgrouse *(P. l. lichtensteinii)*, that is endemic from Israel to Somalia and Socotra. It was the first observation of this species in Lebanon. I used the Collins Field Guide (Svensson *et al.* 1999) to confirm the identification of the species because the area where these birds were shot is a passage of the Black-Bellied Sandgrouse *(Pterocles orientalis)* too, since the poacher showed me photos of one that was killed earlier a couple of months ago. The location they were shot was in Bqaiaa, Aakkar District, North Lebanon.

The resulting photo *(Figure 1)* shows one male (in the middle) and two females (on each side). Liechtenstein's Sandgrouse has never been recorded in Lebanon before, therefore, this is the first record. On examining the birds, it was obvious that they had been shot with shotgun pellets. The male shown in *Figure 1.* had obviously been hit in the chest by many pellets (the damage is just visible in the photo) and one of the females had a paralysed leg due to a pellet in the femur.

Figure 1. Lichtenstein's Sandgrouse *(Pterocles lichtensteinii)* caught by a poacher in Akkar, Lebanon at 11 pm on the 19th of January 2020, photo: Michel Sawan

1. ábra Csíkos pusztaityúkok Libanonban, Akkar közelében 2020. január 19-én, este 11 órakor orvvadász által fogva, illetve lőve (fotó: Michel Sawan)

This species is resident throughout its entire distribution. Although it is nomadic the nearest known populations being over 550–600 km away in Southern Israel, and the nearest known recorded vagrancy being in Iraq (Porter *et al.* 1996) and as it would be a new addition to the Lebanese bird list, it is important to exclude the possibility that these birds were smuggled into the country, or had arrived here by some reasons other than a natural one.

The hunter often shows me his prey and consults me when he shoots a new species or encounters a species he has not seen before. He has shown me many of his prey, including Black-bellied *(Pterocles orientalis)* and Pin-tailed Sandgrouse *(P. alchata)* that I have reported previously. However, since he made me promise not to reveal his name or his true identity, none of these photos can be posted.

It is highly unlikely that these birds were smuggled, either by the hunter or by anybody else because of his poor financial background. The fact that the birds had obviously been shot, and that three were already dead before I saw them also rules out any possibility of their origin as smuggled birds. The origin of these birds obviously cannot be established with any certainty but given the nomadic nature of the species, it is possible that they might have come from the nearest known populations in Southern Israel and Jordan. However, it is possible that other populations close to the location of this sighting remain yet to be discovered.

This species likes desert or semi-desert habitat, but although many areas of suitable habitat can be found very close to the location of this sighting, both in Northern Lebanon and in Syria (the Syrian border is less than 60 km away). These have been inaccessible to most people for several years due to security reasons and even before that were very little visited, so it is possible that small breeding populations exist in either or both of these countries. Also, because of the nocturnal habits of Lichtenstein's Sandgrouse, and the relatively small number of knowledgeable birdwatchers in Lebanon and Syria, particularly in the areas where it might occur, it would not be very surprising for a small population being unnoticed, particularly if it was more recently established.

It was never ranked as a gamebird here because it did not exist on the bird lists in Lebanon. Like many birds that are shot during night hunting, they did not have a chance to stay and breed maybe in the next few months. This will open the doors for further studies to confirm the possible breeding of the species in Lebanon. Night poaching and illegal hunting are common and are threats to many non-gamebirds during the migration seasons.

Acknowledgements

I would like to thank Mr. Colin Conroy for reviewing and helping editing the article. And I want to thank Dr. Ghassan Jaradi and Mr. Martin Kaech for the confirmation of my identification for the birds.

References

de Juana, E. & Kirwan, G. M. 2020. Lichtenstein's Sandgrouse *(Pterocles lichtensteinii)*. Version 1.0. – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds.) Birds of the World. – Cornell Lab of Ornithology, Ithaca, NY, USA, DOI: 10.2173/bow.licsan1.01

BirdLife International 2016. *Pterocles lichtensteinii*. – In: IUCN Red List of Threatened Species: e. T22693028A93379543. – DOI: 10.2305/IUCN.UK.2016-3.RLTS.T22693028A93379543.en

Porter, R. F., Christiansen, S. & Schiermacker-Hansen, P. 1996. Field Guide to the Birds of the Middle East. – Poyser, London

Svensson, L., Mullarney, K., Zetterstroöm, D. & Grant, P. 2009. Collins Bird Guide. 2nd ed. – Harper Collins, London