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Temporal changes in the diet composition of the Eastern Imperial Eagle *(Aquila heliaca)* in Hungary

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Abstract The diet composition of breeding Eastern Imperial Eagles *(Aquila heliaca)* was analysed in Hungary between 2005 and 2017, and compared with two previously published datasets from the periods of 1982–1991 and 1992–2004. Altogether the distribution of 8543 prey items of 126 different species and 29 other taxa were analysed within a 36-years period. We found that the previously abundant Common Hamster *(Cricetus cricetus)* became marginal (7.42%), while European Sousliks *(Spermophilus citellus)* practically disappeared (0.03%) from the diet of Imperial Eagles. Small game species, like the Common Pheasant *(Phasianus colchicus)* and the Brown Hare *(Lepus europaeus)* composed a remarkable part of the diet (11.22% and 28.11% respectively), which raised some conflicts with hunters regionally and probably also contributed to the high prevalence of persecution incidents against the eagles. In parallel with the loss of traditional prey species, corvids (13.10%), pigeons (8.90%), waterbirds (6.83%), other rodents (6.71%), Roe Deers *(Capreolus capreolus)* (5.59%), raptors and owls (4.88%) became regularly detected prey species. The temporal changes of the main prey categories were analysed between 1998 and 2017, when the ratio of Hamster and Pheasant showed significant decrease (-27.29% and -6.38%, respectively). The ratio of Brown Hare also showed slight decrease (-3.98%), but the change was not significant. On the other hand, the ratio of corvids, waterbirds and Roe Deers within the diet showed significant increase (+18.20%, +6.25% and +5.39%, respectively). The observed flexibility in the foraging behaviour of Imperial Eagles greatly facilitate conservation efforts, as they seems to be able to utilize the most abundant prey sources, i.e. they were not depending solely from the status of any single specific prey source. However, eagles could only shift and survive in those regions, where their traditional preys decreased, if alternative species were available for them.

Keywords: raptor, prey, *Cricetus*, *Spermophilus*, *Lepus*, *Phasianus*

Összefoglalás A parlagi sasok *(Aquila heliaca)* táplálék-összetételét vizsgáltuk Magyarországon 2005–2017 között és összehasonlítottuk két korábban publikált időszak (1982–1991, 1992–2004) adatsoraival. A 36 éves időszak alatt összesen 126 különböző fajhoz és további 29 taxonhoz tartozó 8543 zsákmányállatot sikerült beazonosítanunk. Korábban a mezei hörcsög *(Cricetus cricetus)* a leggyakoribb, míg a közönséges ürge *(Spermophilus citellus)* rendszeres zsákmánynak számított, azonban ritka zsákmánnyá váltak a 2005–2017 közötti időszakra (7,42% és 0,03%). Az apróvad-fajok közül a fácán *(Phasianus colchicus)* és a mezei nyúl *(Lepus europaeus)* jelentős részét tették ki a tápláléknak (11,22% és 28,11%), amely egyes területeken ellenérzést keltett a vadászokban, és valószínűleg szerepet játszott a sasok ellen elkövetett bűncselekmények magas gyakoriságában is. A hagyományos zsákmány-fajok visszaszorulásával párhuzamosan a varjú- (13,10%) és galambfélék (8,90%), a vízimadarak (6,83%), az egyéb rágcsálók (6,71%), az őz *(Capreolus capreolus)* (5,59%), valamint a ragadozómadarak és baglyok (4,88%) is rendszeres táplálékká váltak. A fő táplálék-kategóriák időbeli változásai 1998-2017 között kerültek elemzésre, ami alapján a hörcsög és a fácán aránya szignifikáns csökkenést mutatott az utolsó 20 év során (-27,29% és -6,38%). A mezei nyúl aránya is enyhe csökkenést mutatott (-3,98%), de a változás nem volt statisztikailag szignifikáns. Ezzel szemben a varjúfélék, vízimadarak és az őz aránya szignifikáns növekedést mutatott a táplálékban (+18,20%, +6,25% és +5,39%). A megfigyelt flexibilitás a parlagi sasok zsákmányszerző viselkedésében nagyban elősegíti a fajvédelmi törekvéseket, mivel úgy tűnik képesek mindig a legkönnyebben elérhető zsákmány-fajt fogyasztani, így nem függnek kizárólagosan egyik specifikus zsákmány-faj állományváltozásaitól sem. Ugyanakkor a hagyományos zsákmány-fajok visszaszorulásakor a parlagi sasok csak azokon a területeken tudtak váltani és túlélni, ahol alternatív zsákmány-fajok elérhetőek voltak.

Kulcsszavak: ragadozómadár, zsákmány, *Cricetus*, *Spermophilus*, *Lepus*, *Phasianus*

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Introduction

The availability and relative frequency of main prey species are among the most important factors affecting the distribution and breeding success of large raptors (e.g. Newton 1979, Steenhof *et al.* 1997, Katzner *et al.* 2006, Penteriani *et al.* 2006, Schweiger *et al.* 2015). Therefore, the analyses of diet composition and specific actions for the key prey species are usually inevitable components in the conservation strategy of threatened raptor species (Ontiveros & Pleguezuelos 2000, Palma *et al.* 2006, Bedrosian *et al.* 2017).

Although direct observations or remote camera systems can provide the most accurate datasets for studying the diet of raptors during the breeding season (Takeuchi *et al.* 2006, Sánchez *et al.* 2008), such investigations are expensive and they can only gather data from a very limited number of territories. Therefore, usually indirect methods are used for diet analyses, such as the collection and analysis of pellets is the most widespread method for the diet analyses of owls (Halliez *et al.* 2015, Hámori *et al.* 2017, Szép *et al.* 2017). In case of diurnal raptors, the data derived from pellets can be significantly completed with the analyses of other prey remains, such as bones, hairs and feathers found around nest sites and roosting trees (Watson *et al.* 1993, Balogh 1998, Preston *et al.* 2017).

The diet of the globally threatened Eastern Imperial Eagle *(Aquila heliaca)* predominantly consists of medium sized mammals, birds and reptiles in most parts of its range, although their relative frequencies vary considerably among regions (del Hoyo *et al.* 1995). In most of the range Sciuridae (especially Sousliks and Marmots) and Cricetinae (mostly Hamsters) were considered the main prey species of the Imperial Eagle (del Hoyo *et al.* 1995). Sousliks (*Spermophilus* sp.) are still the most important food items for the largest eastern populations of Russia and Kazakhstan (Belik *et al.* 2002, Karyakin *et al.* 2008). However, the severe decline of Souslik populations and available alternative food sources resulted remarkable changes of the diet composition of the species in the western part of the distribution area. Rook *(Corvus frugilegus)* was reported to be the main prey in Serbia (Vasic & Misirlic 2002), and in some regions of western Russia (Belik *et al.* 2002). The Brown Hare *(Lepus europaeus)* and Chicken *(Gallus gallus f. domestica)* were the main prey species in South Bulgaria (Marin *et al.* 2004), while Northern White-breasted Hedgehogs *(Erinaceus* *roumanicus)* and Yellow-legged Gulls *(Larus michahellis)* composed the largest part of the eagles' diet in the European part of Turkey (Demerdzhiev *et al.* 2014).

The westernmost isolated population of the species can be found in the Pannonian Basin of Central Europe, where most of the pairs breed in Hungary (Demerdzhiev *et al.* 2011). Early literature mentioned the European Souslik *(Spermophilus citellus)* as the main prey of Imperial Eagles in Hungary (Chernel 1899), but Common Hamster *(Cricetus cricetus)* and occasionally Brown Hare and poultry species were also noted (Szemere 1912, Vasvári 1938, Nagy 1943, Pátkay 1947). The first comprehensive survey on the diet of Imperial Eagles in Hungary was conducted between 1982 and 1991 (Haraszthy *et al.* 1996) and revealed that four species comprised more than 80% of the diet including the Common Hamster (51%), Brown Hare (12%), Common Pheasant *(Phasianus colchicus)* (12%) and European Souslik (7%). Chavko *et al.* (2007) studied the diet composition of the species in the Slovakian part of the Carpathian Basin between 1970 and 2005, where Brown Hare (35%) was the most frequent prey, followed by Common Hamsters (19%) and Common Pheasants (13%), and European Souslik reached only 4% of the identified prey items. The latest and largest dataset from Hungary from the period 1995–2004 revealed similar patterns for the most common species (Brown Hare 30%, Common Hamster, 21% Common Pheasant 15%), although the frequency of European Sousliks became less than 1% among the identified prey items (Horváth *et al.* 2010). Population surveys of the main prey species from the same period showed that Sousliks and Hamsters were present in the sampled eagle territories, but their relative frequencies were remarkably lower than of Hares and Pheasants (Kovács *et al.* 2008). All the four, previously mentioned main prey species of Imperial Eagles showed a severe decline in Hungary in the last 50 years (Bihari 2004, Báldi & Faragó 2007, Bihari *et al.* 2007). On the contrary, the Hungarian population of Imperial Eagles showed a significant increase and southern expansion towards the lowland plain areas in the same period (Horváth *et al.* 2011, Horváth *et al.* 2014).

In the present study we investigated if the diet composition of the expanding Imperial Eagle population had changed in long-term and large-scale. We hypothesized that the decrease of the traditional prey species (Common Hamster and European Souslik) continued in parallel to the retraction of their populations. Our aim was to investigate, which species and to what extent could substitute the traditional prey species and if those changes had any effect for future conservation strategies.

Materials and methods

Study area

The diet composition of breeding Imperial Eagles was analysed in the total distribution area of the species in Hungary. The regions covered by the study were categorized into ten geographical units *(Figure 2a)* in order to facilitate investigations of the regional differences in the diet composition *(Table 1)*. The units were defined in order to represent (1) coherent and similar-sized (2700–5700 km^2) parts of the distribution area, (2) similar foraging habitat structure, and (3) similar number of breeding territories (15–30 pairs, except the Kisalföld, Kiskunság and Duna-Ipoly areas, where less than 10 territories could be found over large areas). The units were named after the most representative part or National Park of the given area. Besides the Hungarian samples further 37 prey items were identified in neighboring countries within territories next to the Hungarian border, and they were joined to the nearest units of Zemplén (Southeast-Slovakia), Duna-Ipoly (Southwest-Slovakia), Kisalföld (East-Austria) and Körös-Maros (West-Romania).

Study period

A 36-years dataset (1982–2017) was used in the study, of which two subsets were partially published before. The first 10-years dataset from 1982 to 1991 was derived from Haraszthy *et al.* (1996), which included 627 prey specimens. The authors generously provided their raw data for this study, which enabled us to use them for regional comparisons as well. The next 13-years dataset from 1992 to 2004 was derived from Horváth *et al.* (2010), which included 1297 prey specimens, but it was completed with further 178 unpublished specimens from the same period (1475 specimens in total). The last 13-years part of the dataset from 2005 to 2017 comprised the majority of the data (6441 specimens), which have not yet been published before.

Sample collection

The breeding territories of Eastern Imperial Eagles were monitored and the active nests were searched by the members of the Hungarian Imperial Eagle Working Group in each year during the whole study period (Haraszthy *et al.* 1996, Horváth *et al.* 2010, Horváth *et al.* 2014). Data on prey remains were gathered unregularly between 1982 and 1997. From 1998 onwards the sampling became regular and the same protocol was applied for collecting data on food composition. The nesting sites were approached usually once or twice per year, when the ground below the nests and nearby roosting sites were checked thoroughly for food remains. The most comprehensive surveys were carried out in June, when most of the known nesting sites in Hungary were visited each year. This time the accessible nests were also climbed in the frame of the annual ringing of the chicks within the national Imperial Eagle monitoring protocol (Horváth *et al.* 2018a), when remains were collected directly from the nests as well. Those fresh preys, which included eatable parts for the chicks, were photographed and were not removed from the nests. The second visit to the nesting sites usually took place after fledging between July and October, when only the ground was checked for food remains. Besides these nest controls sporadic data on prey items (202 specimens) were also gathered in other months of the year.

The prey remains found around a nest site were collected together in the field and photographed with a scale and an ID label, including data on location, date and collector. Items, which could be identified unambiguously in the field were noted down on field datasheets. Food remains, which included significant amount of soft tissues and/or could be identified unambiguously in the field, were not collected in order to avoid contamination and putrefaction till the analyses. For the same reason, wet or fresh remains were dried out and treated with insecticides before long-term storage.

The following type of remains were not included in the data in order to reduce the bias of indirect sampling, even if they were found under the nest sites or roosting trees: (1) single feathers, which could be shed by alive birds; (2) full carcasses of large animals, which could not be brought there by the eagles; (3) old or deteriorated samples, which could derive from previous years.

Pellets, bones, feathers, hairs and dry skins of prey animals were collected and stored in plastic bags until further analyses. ID labels were placed in another plastic bag outside the original bag in order to keep them clean and readable.

Prey identification

The collected samples were identified by comparing them with museum reference materials from 0.5 to 3 years after the collection. The remains originated from the same nest site from the same year were ordered by species, sex (in case of species with clear sexual dimorphism), body size and body part. A remain was handled as a different prey specimen, if it (1) belonged to different species or sex, or (2) had a clearly different body size than the already listed specimens, or (3) included the same part of the body as another remain. The same minimal estimation methodology was applied when the field data (including both datasheets and photographs) and the laboratory data were merged together. Therefore, in some cases remains of different prey specimens could be handled as one, but the multiple counting of the same specimen was ruled out.

Data analyses

In order to investigate and visualize the main changes in the diet composition, the prey items were grouped into the following four main categories: (1) Traditional prey species (Common Hamster, European Souslik); (2) Small game species (Brown Hare, Common Pheasant); (3) Other bird species; (4) Other non-avian species. These groups were divided into 16 sub-categories according to *Table 1*.

As a first step we have compared the frequency of the four main prey categories among the geographical units in the three periods in order to investigate if there were any evident alteration in the diet composition in long-term. In the second part of the analyses we used the dataset of the last 20 years (1998–2017), when the annual number and coverage of samples enabled more detailed analyses.

Here we used linear regression model to detect linear trends of changes in the proportion of the prey sub-categories. The linear regression models were not carried out for the data on Souslik and ‘Other animals’ categories, as their frequency was under 1% and ‘0’ annual values appeared in at least 50% of the study years. The statistical analyses were done in R 3.4.4 (R Development Core Team 2018). We are aware that the used design cannot take into consideration that samples collected under the same or nearby nesting trees could be predated by the same individuals. On the other hand, it was not possible to distinguish the origin of samples and include this factor in the model due to three inevitable reasons. Firstly, the remains under a nest in a year include items predated by the male or the female of the given pair in an unknown proportion, therefore the data of two individuals are mixed in each sample. Secondly, the individuals breeding at a given nesting site could change from one year to another, therefore remains collected at the same nesting sites could derive from independent individuals. And finally, the grouping of nearby nesting locations in different years into "territories" is not evident and requires a more detailed analyses, which was out of the scope of this study. Anyway our aim was to detect robust and long-term changes in the diet composition, for which we believe that using the pooled data of the population is applicable if the sampling was representative.

Results

Coverage and distribution of the collected data

In the frame of the study altogether 6619 prey items were newly identified, which data was unified in the same database with the already published datasets of Haraszthy *et al.* (1996) and Horváth *et al.* (2010). This comprehensive 36-years dataset comprises 8543 prey items, which belongs to 126 different species and 29 other taxa, therefore it is the largest diet database of Eastern Imperial Eagles according to our knowledge. The distribution of different prey species in the three main study periods are summarized according to the defined categories and sub-categories in *Table 1*, while the total list of identified species and taxa is included in *Appendix 1*.

The sampling became regular and continuous between 1998 and 2017, when 7734 prey items (90.5% of all data) were gathered from 276 different breeding territories in the frame of 1517 field controls. The data covered an annually variable, but significant proportion (55% in average) of the national population *(Figure 1a)*. All together during this 20-years period 2872 (36.3%) items were identified only in the field, 4038 items (51.0%) were collected and identified later, and further 1006 (12.7%) items were detected by both methods *(Figure 1b)*. Unfortunately, the remains collected in 2009, 2010 and 2012 had been partially lost, therefore the items identified in the field composed largely the dataset for these years.

Data from the nest controls in June represented 70.4% of the last 20 years' dataset, and further 27.0% of the items were collected during the second nest controls between July and October. The sporadically collected items from November to May represented only 2.6% of the samples. Therefore, the presented dataset represents well the diet composition of territorial Imperial Eagles in the breeding season, but cannot be interpreted for the non-breeding period, neither for non-territorial, immature birds, whose diet can be considerably different (Sánchez *et al.* 2009, Bedrosian *et al.* 2017).

Table 1. Distribution of the main prey categories of Eastern Imperial Eagles in Hungary in the three study periods. The 'Waterbirds' sub-category included the families Anatidae, Podicipedidae, Rallidae, Gruidae, Ciconiidae, Threskiornithidae, Ardeidae, Recurvirostridae, Charadriidae, Scolopacidae and Laridae. The 'Poultry' sub-category included the Domestic Duck *(Anas platyrhynchos f. domestica)*, Domestic Goose *(Anser anser f. domestica)*, Chicken, Domestic Turkey *(Meleagris gallopavo f. domestica)* and Domestic Guineafowl *(Gallus gallus f. domestica)*. The 'Raptors and owls' sub-category included the families Tytonidae, Strigidae, Accipitridae and Falconidae

1. táblázat Parlagi sasok főbb táplálék-kategóriáinak eloszlása a három vizsgálati időszakban. A 'Waterbirds' alkategória az Anatidae, Podicipedidae, Rallidae, Gruidae, Ciconiidae, Threskiornithidae, Ardeidae, Recurvirostridae, Charadriidae, Scolopacidae és Laridae családokat fogalja magába. A 'Poultry' alkategória a házi kacsát *(Anas platyrhynchos f. domestica)*, házi ludat *(Anser anser f. domestica)*, házi tyúkot, házi pulykát *(Meleagris gallopavo f. domestica)* és a gyöngytyúkot *(Gallus gallus f. domestica)* foglalja magába. A 'Raptors and owls' alkategória a Tytonidae, Strigidae, Accipitridae és Falconidae családokat fogalja magába

Main prey categories	**1982–1991**		**1992–2004**		**2005–2017**		**Total (1982–2017)**	
	Number	***% N***	**Number**	***% N***	**Number**	***% N***	**Number**	**% N**
Cricetus cricetus	312	*49.76%*	296	*20.07%*	478	*7.42%*	1086	*12.71%*
Spermophilus citellus	44	*7.02%*	13	*0.88%*	2	*0.03%*	59	*0.69%*
Traditional prey species subtotal	**356**	***56.78%***	**309**	***20.95%***	**480**	***7.45%***	**1145**	***13.40%***
Lepus europaeus	77	*12.28%*	455	*30.85%*	1810	*28.10%*	2342	*27.41%*
Phasianus colchicus	75	*11.96%*	226	*15.32%*	723	*11.22%*	1024	*11.99%*
Small game species subtotal	**152**	***24.24%***	**681**	***46.17%***	**2533**	***39.33%***	**3366**	***39.40%***
Corvidae	8	*1.28%*	73	*4.95%*	844	*13.10%*	925	*10.83%*
Columbidae	22	*3.51%*	127	*8.61%*	573	*8.90%*	722	*8.45%*
Waterbirds	1	*0.16%*	56	*3.80%*	440	*6.83%*	497	*5.82%*
Raptors and owls	8	*1.28%*	53	*3.59%*	314	*4.88%*	375	*4.39%*
Poultry	22	*3.51%*	27	*1.83%*	120	*1.86%*	169	*1.98%*
Passeriformes (excl. Corvidae)	6	*0.96%*	19	*1.29%*	87	*1.35%*	112	*1.31%*
Other birds	2	*0.32%*	12	*0.81%*	50	*0.78%*	64	*0.75%*
Other bird species subtotal	**69**	***11.00%***	**367**	***24.88%***	**2428**	***37.70%***	**2864**	***33.52%***
Rodentia (excl. *Cricetus* and *Spermophilus*)	17	*2.71%*	38	*2.58%*	432	*6.71%*	487	*5.70%*
Capreolus capreolus	12	*1.91%*	38	*2.58%*	360	*5.59%*	410	*4.80%*
Carnivora	6	*0.96%*	18	*1.22%*	76	*1.18%*	100	*1.17%*
Other mammals	14	*2.23%*	23	*1.56%*	101	*1.57%*	138	*1.62%*
Other animals	1	*0.16%*	1	*0.07%*	31	*0.48%*	33	*0.39%*
Other non-avian species subtotal	**50**	***7.97%***	**118**	***8.00%***	**1000**	***15.53%***	**1168**	***13.67%***
Total	**627**	***100.00%***	**1475**	***100.00%***	**6441**	***100.00%***	**8543**	***100.00%***

Comparison of the three study periods

The four main prey-categories are summarized regionally according to the three main study periods in *Figure 2*. The ratio and the expansion of the sampling area of small game species (Brown Hare, Pheasant) showed a clear increase for the second period (24.24% vs. 46.17%), but slightly decreased for the last period (39.33%). Anyway Brown Hares still compose the largest part of the diet of Imperial Eagles in Hungary.

The ratio of the traditional prey species (Souslik, Hamster) decreased since the beginning of data collection (56.78% vs. 7.45%). The decrease was also evident in the Zemplén and Bükk regions, where sufficient data were available from all periods. The Souslik practically disappeared from the diet during the study period, while the Hamster was still important regionally, but its role became marginal in a national scale.

On the other hand, the ratio of other bird and mammal species showed a clear increase, therefore most probably they compensated the loss of traditional prey species.

Trend analyses of the main prey categories

The 20-years trend of the main prey categories and sub-categories are summarized in *Figure 3*. The results of the linear regression models are summarized in *Table 2* and *Figure 4*.

The Hamster showed the largest decrease during the study period, but the decrease of the Pheasant was also significant. The Brown Hare also showed an almost 4% decrease, but its trend was not significant according to the linear regression model. A significant increase was found among the Corvidae, mostly Hooded Crow *(Corvus cornix)* and Magpie *(Pica pica)* and waterbird species, and also in case of the Roe Deer *(Capreolus capreolus)*. The ratio of Common Voles *(Microtus arvalis)* was fluctuating and showing clear peaks in 2008, 2011 and 2014 according to their regional population cycles *(Figure 3d)*. Other prey categories did not show any significant trend.

Table 2. Results of the linear regression models carried out to analyse the trend of the main prey categories of Eastern Imperial Eagles in Hungary between 1998 and 2017. (Change: change in proportion of the main prey categories during 20 years)

2. táblázat A parlagi sasok főbb magyarországi táplálék-kategóriáinak trendjét vizsgáló lineáris regresszió modell eredménye 1998 és 2017 között. (Change: a főbb táplálék-kategóriák arányaiban történt változás a 20 év alatt), p-value: p-érték

Prey categories	Change	p-value
Corvidae	**+18.20%**	**<0.0001**
Waterbirds	**+6.25%**	**0.007**
Capreolus capreolus	**+5.39%**	**<0.001**
Rodentia (excluding *Cricetus* and *Spermophilus*)	+2.97%	0.479
Columbidae	+2.87%	0.160
Raptors and owls	+2.26%	0.270
Passeriformes (excluding Corvidae)	+0.47%	0.440
Poultry	+0.38%	0.688
Other birds	+0.13%	0.778
Other mammals	-0.13%	0.864
Carnivora	-0.14%	0.809
Lepus europaeus	-3.98%	0.293
Phasianus colchicus	**-6.38%**	**0.004**
Cricetus cricetus	**-27.79%**	**<0.001**
Spermophilus citellus	*n.a.*	*n.a.*
Other animals	*n.a.*	*n.a.*

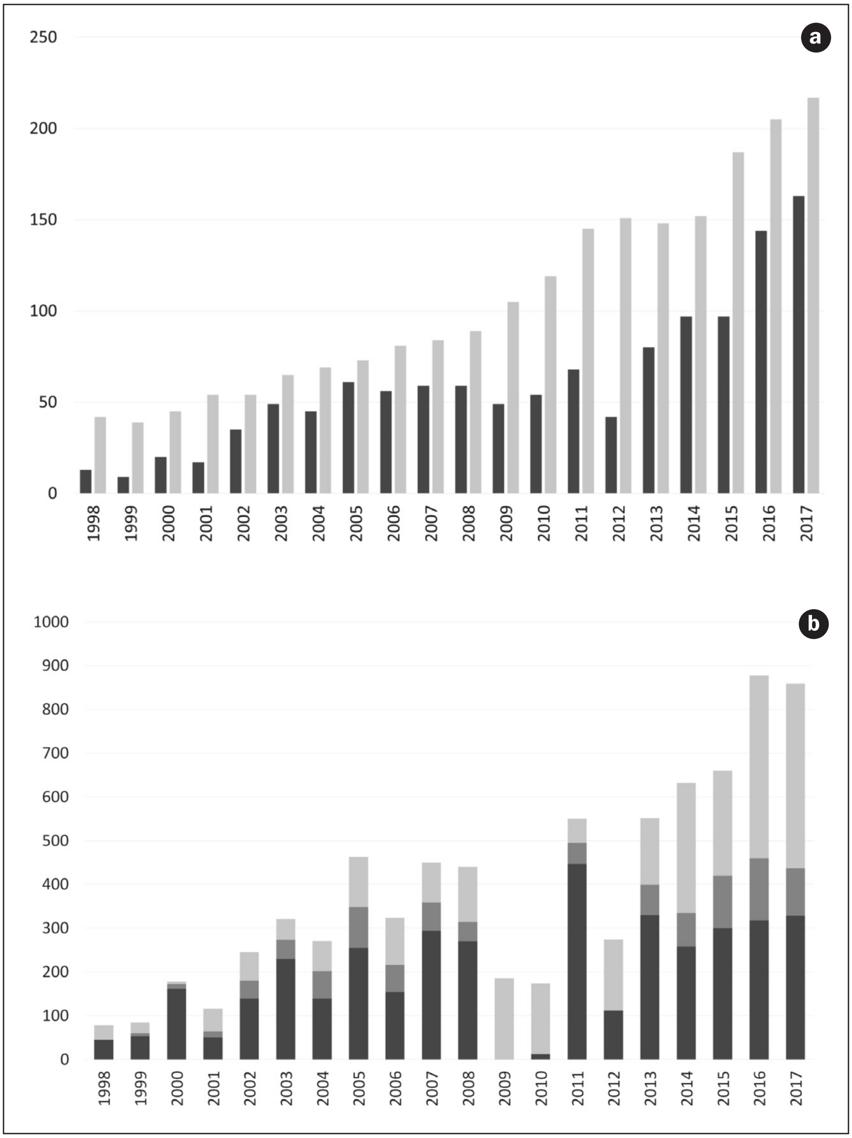


Figure 1. *a)* Annual coverage of collected prey samples of Eastern Imperial Eagles in relation to the total Hungarian nesting population between 1998 and 2017. Dark grey: number of sampled territories; Light grey: number of known Hungarian nesting territories. *b)* Annual number of identified prey items of Eastern Imperial Eagles in Hungary between 1998 and 2017. Dark grey: collected and later identified items; Light grey: items identified in the field; Medium grey: items detected by both methods

1. ábra *a)* A parlagi sas táplálékmaradványok lefedettsége a teljes magyarországi állománnyal összehasonlítva évenként 1998 és 2017 között. Sötétszürke: mintázott territóriumok száma; Világosszürke: ismert magyarországi fészkelő párok száma. *b)* A meghatározott parlagi sas táplálékmaradványok száma évenként 1998 és 2017 között. Sötétszürke: begyűjtött és később meghatározott minták; Világosszürke: terepen meghatározott minták; Középszürke: mindkét módszerrel kimutatott minták

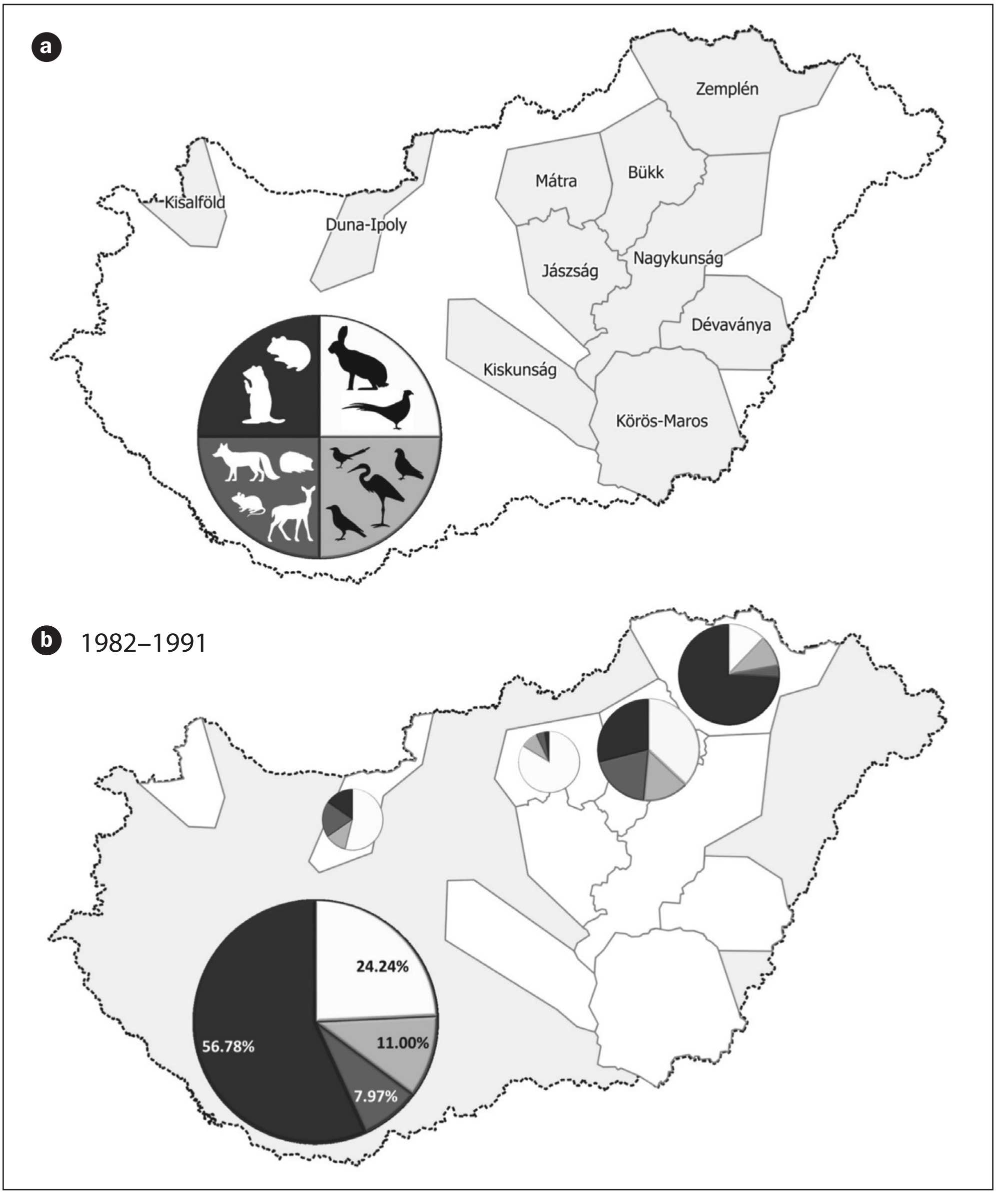
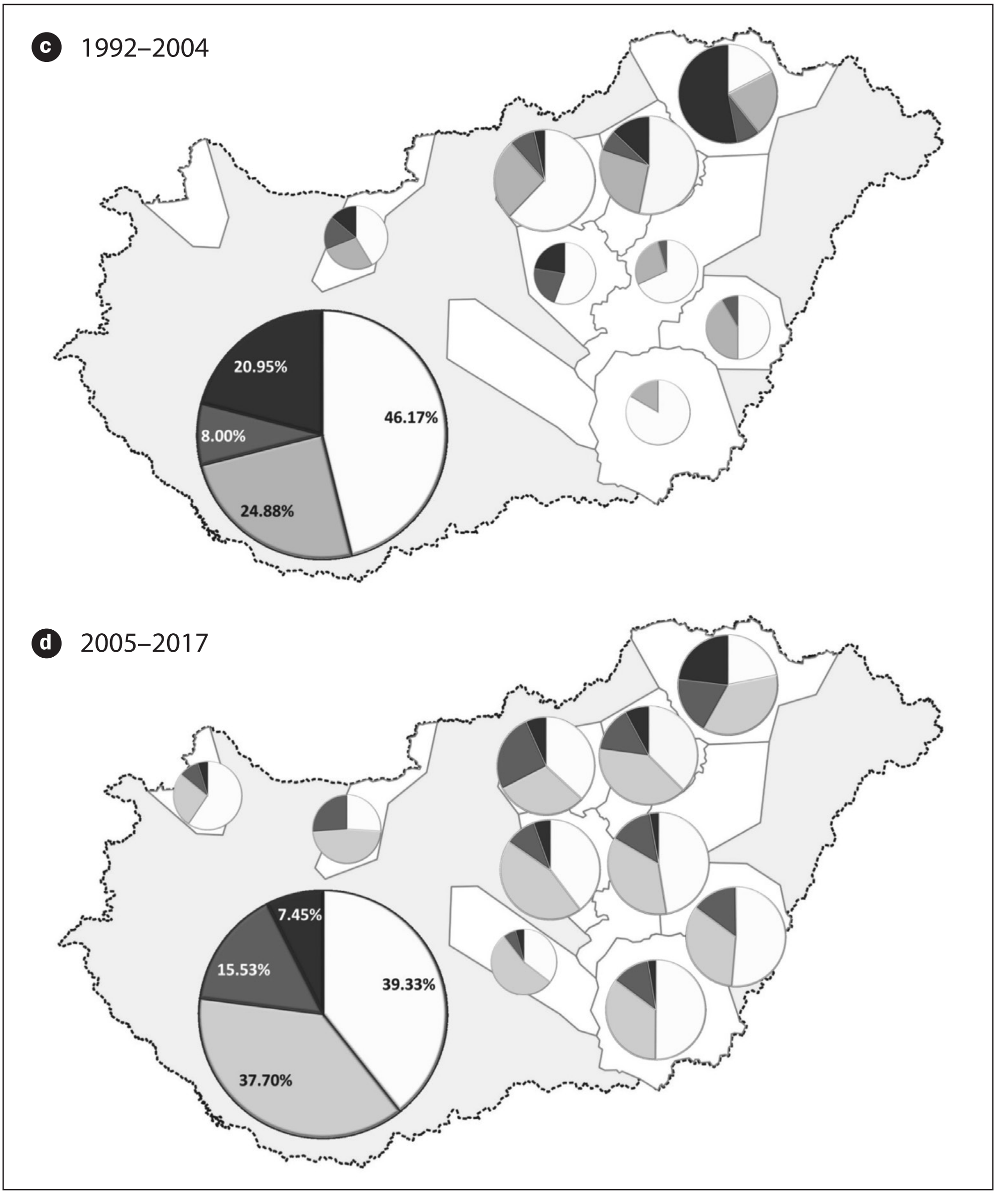


Figure 2. Proportion of the main prey categories of Eastern Imperial Eagles in the Hungarian study areas in the three study periods. a) Legend showing the location of the regions used in the study and the color codes of the main prey categories (see definitions at *Table 1*). b) Data for the period 1982–1991 are taken from Haraszthy *et al.* (1996) (*n* = 627). c) Data for the period 1992–2004 are taken from Horváth *et al.* (2010) and completed with unpublished data (*n*= 1475). d) Data for the period 2005–2017 (*n* = 6441). Black: traditional prey species; Dark Grey: other animals; Light grey: other birds; White: small game species. Large circle: national proportion of the main prey categories for the given period; Medium circle: regional proportion based on more than 100 items; Small circle: regional proportion based on less than 100 items



2. ábra A parlagi sasok főbb táplálék-kategóriáinak eloszlása a magyarországi régiókban a három vizsgálati időszakban. a) Az egyes régiók elhelyezkedését és a főbb táplálék-kategóriák szín jelölését mutató jelmagyarázat (definíciókat ld. az *1. táblázatban*). b) Az 1982–1991 közötti időszakra vonatkozó adatok Haraszthy *et al.* (1996) publikációjából származnak ($n = 627$). c) Az 1992–2004 közötti időszakra vonatkozó adatok Horváth *et al.* (2010) publikációjából származnak, kiegészítve publikálatlan adatokkal ($n = 1475$). d) A 2005–2017 közötti időszakra vonatkozó adatok ($n = 6441$). Fekete: hagyományos zsákmányfajok; Sötétszürke: egyéb állatok; Világos szürke: egyéb madarak; Fehér: apróvad-fajok. Nagy kör: a főbb táplálék-kategóriák országos aránya az adott időszakban; Közepes kör: regionális arány, amely több mint 100 meghatározott egyeden alapul; Kis kör: regionális arány, amely kevesebb, mint 100 meghatározott egyeden alapul

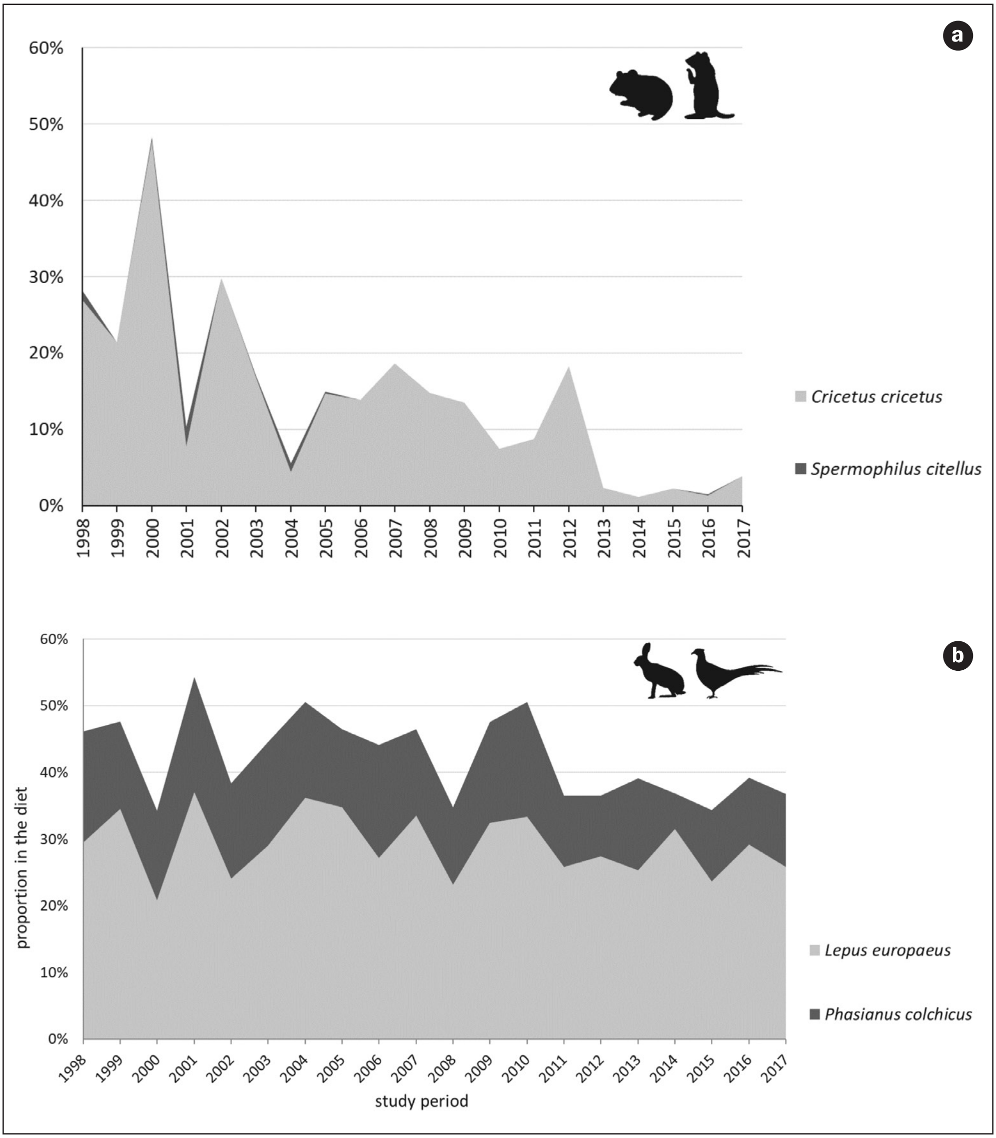
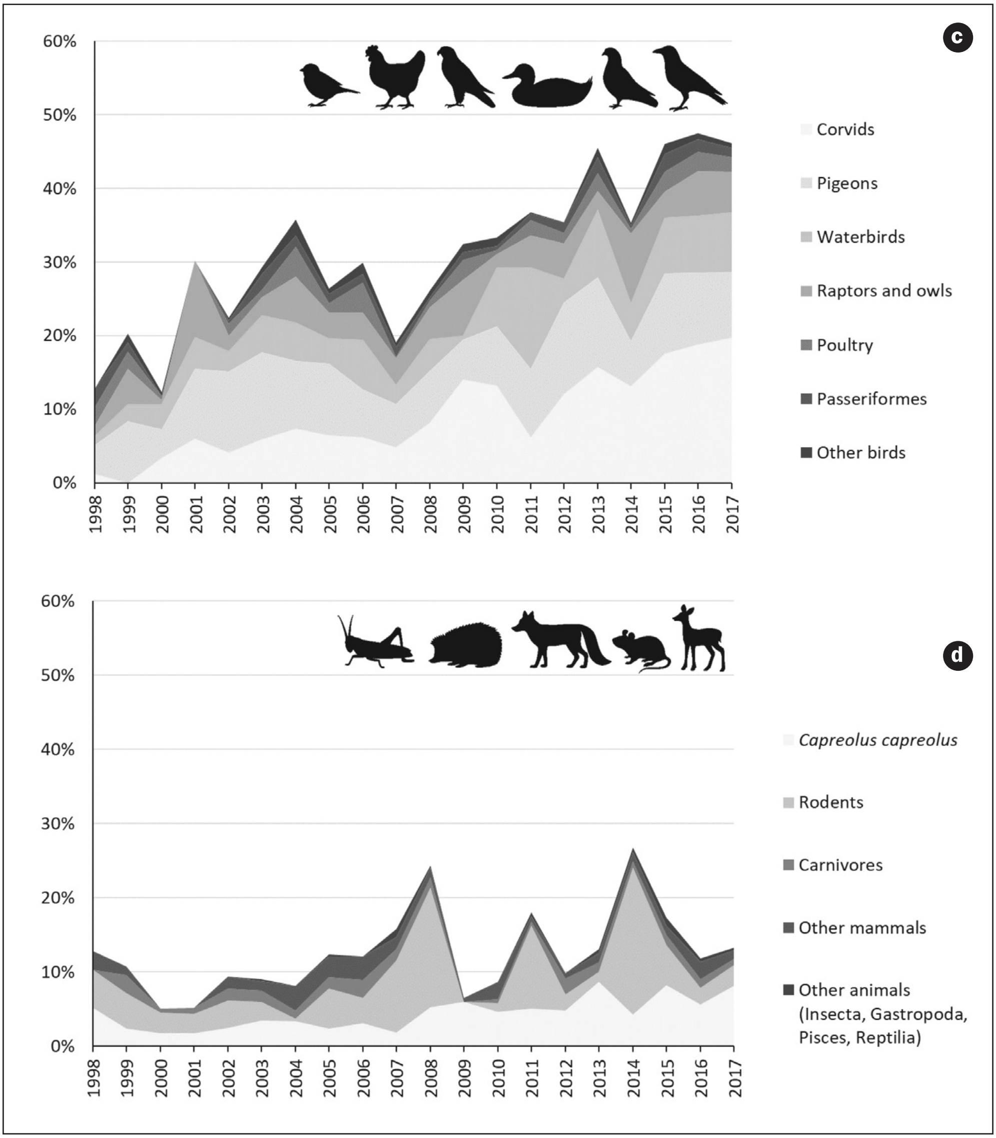


Figure 3. Annual proportion of the prey categories of Eastern Imperial Eagles in Hungary between 1998 and 2017 (see definitions at *Table 1*). a) Traditional prey species, b) Small game species. c) Other birds, d) Other animals



3. ábra A parlagi sasok táplálék-kategóriáinak évenkénti eloszlása 1998 és 2017 között Magyarországon (definíciókat ld. az *1. táblázatban*). a) Hagyományos zsákmányfajok, b) Apróvad-fajok, c) Egyéb madarak, d) Egyéb állatok

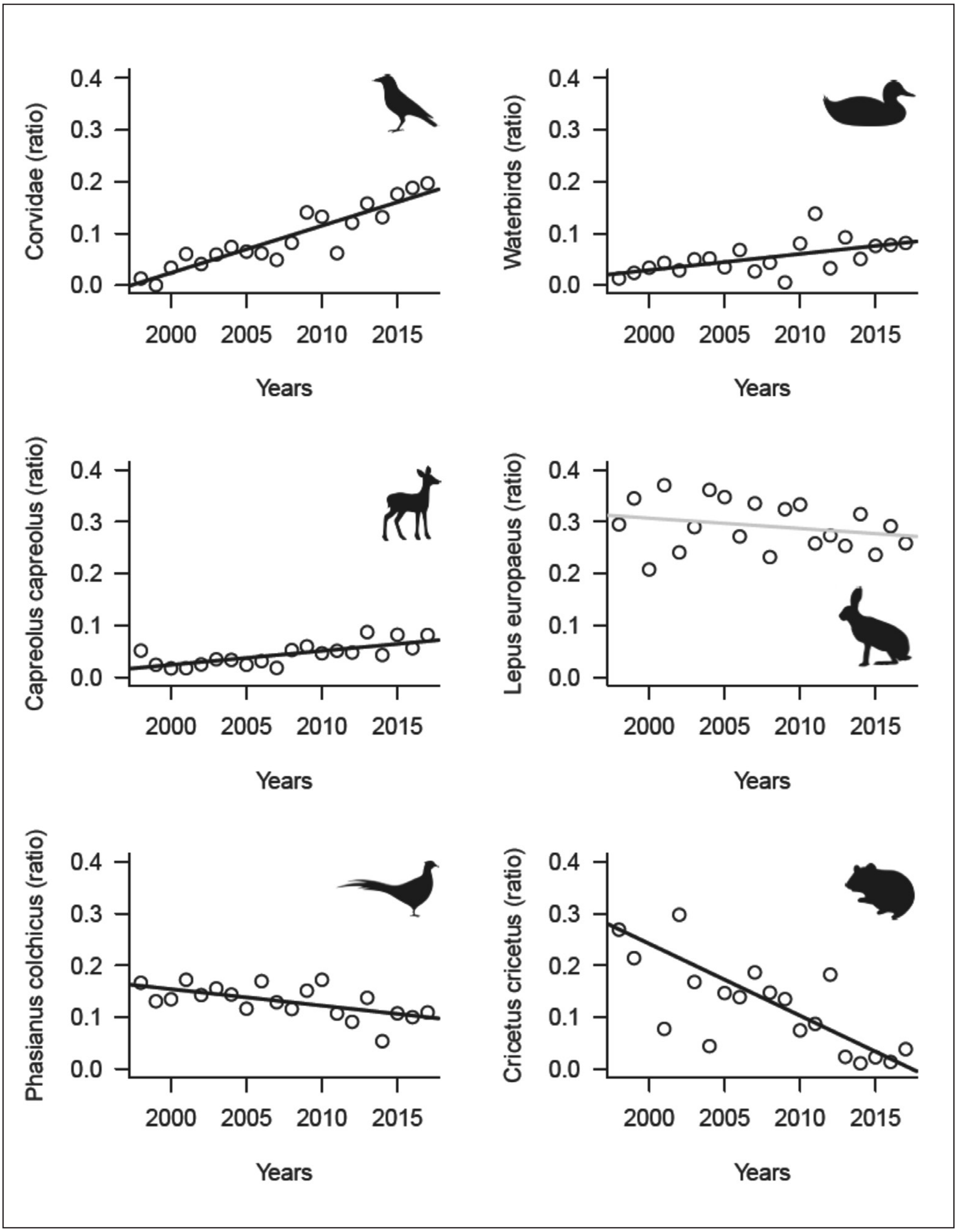


Figure 4. Results of the linear regression models carried out to analyse the trend of the main prey categories of Eastern Imperial Eagles in Hungary between 1998 and 2017. Black lines represent significant trends, while grey line represents non-significant trend. See detailed statistics at *Table 2*.

4. ábra A parlagi sasok főbb magyarországi táplálék-kategóriáinak trendjét vizsgáló lineáris regresszió modell eredménye 1998 és 2017 között. A fekete vonalak szignifikáns trendet, míg a szürke vonal nem szignifikáns trendet jelez. A részletes statisztikát ld. a *2. táblázatban*

Discussion

Foraging behavior and origin of prey items

Imperial Eagles are agile hunters, therefore a large proportion of the detected prey items were most probably actively hunted by the breeding pairs. However, based on the remains it was usually not possible to identify the source of the prey and it should be noted that some items were most probably not actively hunted by Imperial Eagles, but could be derived from three other sources as well.

First, eagles, like many other predators (e.g. Milchev & Spassov 2017), regularly bring carcasses to the nest, which died due to diseases, other predators or human activities. Agricultural activities – especially ploughing, harvesting or mowing machines – kill or wound a large amount of animals, especially Hares, Roe Deers and Pheasants. This extensive food source is largely utilized by eagles, as they are regularly seen to follow and forage after tractors in agricultural fields. Similarly, large mammal species were most probably exclusively taken from carcasses to the nest (i.e. Wild Boar *Sus scrofa*, Red Deer *Cervus elaphus* and Bovidae species).

Second, kleptoparasitism from other raptors and carnivores is also a common behaviour of Imperial Eagles (Danko & Mihók 2007). A part or all species of Pisces and small Passeriformes were probably taken this way, but a remarkable proportion of more common species could be also stolen from other predators.

Finally, some small species could also derive from the intestinal system of larger animals, which primarily predated those and later themselves became the prey of eagles. Probably a proportion of Insecta and Gastropoda species could be detected this way, although some observations were also reported on eagles, which were actively hunting on insects (Tóth 2006).

Interpretation of prey data

An inevitable limitation of our study is that the analysis of prey remains and/or pellets might estimate inaccurately the relative proportion of larger (e.g. Hare) and smaller (e.g. Vole) sized prey species in comparison to each other, caused by their different detectability (Redpath *et al.* 2001, Sánchez *et al.* 2008). Therefore, the exact frequency data of different taxa in the diet cannot be compared precisely to each other and the presented frequency data should be handled with caution. Anyway such large datasets well indicate the overall importance of key prey species within a region, as common preys must be detected regularly, while rare ones will be found only occasionally (Katzner *et al.* 2005, Bedrosian *et al.* 2017). Moreover, the frequency of a species or taxa can be analysed in a temporal scale, as their detectability do not change in time, therefore their detected frequency trends reflect real trends within the diet.

Flexibility in foraging behaviour

The presented results strengthened the notion that Imperial Eagles are able to change their diet and utilize the most available mammalian or avian prey sources within the preferred size range (250–2500 g). Katzner *et al.* (2005) found that dietary diversity of Eastern Imperial Eagles varied between regions in Kazakhstan, as eagles nesting near a high-density prey resource used that resource almost exclusively, while their diet was more diverse in locations with no single high-density prey species (Katzner *et al.* 2006). The closely related Spanish Imperial Eagle *(Aquila adalberti)* is highly dependent on its main prey species, the Rabbit *(Oryctolagus cuniculus)* (Ferrer & Negro 2004). However, Sánchez *et al.* (2009) also found variability in the diet of Spanish Imperial Eagles between different regions, and suggested that eagles were able to adapt to the habitat by utilizing alternative prey species, such as Pigeons (*Columba* spp.) or Hooded Crows, where their main prey was scarce.

Decrease of traditional rodent species

The observed flexibility in the foraging behaviour of Imperial Eagles greatly facilitate conservation efforts, as they proved to be able to utilize the most abundant prey sources, therefore they were not depending solely from the status of any single specific prey source. However, presumably eagles could only shift and survive in those regions, where their primary prey decreased, if alternative species were available for them. The enormous decrease of the Souslik in the eagles' diet was obviously caused by the remarkable retraction and isolation of their national populations, which raised serious conservational consequences even for Imperial Eagles regionally. In parallel with the decrease of Souslik populations, eagles also disappeared or decreased considerably at some parts of their former Hungarian breeding range (Bakony, Vértes, Gerecse, Börzsöny and Aggtelek mountains), where most probably other alternative prey species were not as abundant as in other parts of the distribution area (Horváth *et al.* 2011).

Similarly, the remarkable decrease of the Hamster populations was obviously visible from the prey analyses of eagles, but also caused decrease in the breeding density in some particular regions. E.g. the formerly abundant Hamster populations at the Northern section of the Hernád-valley provided foraging areas for six Imperial Eagle breeding pairs in the early 2000's (Bihari *et al.* 2008), but in parallel with the decrease of the Hamster population, three of these territories became vacant by the end the study period (Horváth *et al.*, unpubl. data).

The worrying decline of the Hamster and Souslik populations of Hungary urge specific and more efficient conservation actions in order to secure their presence in the Pannonian Basin, which holds the westernmost significant populations of both species. Moreover, these species are regionally still inevitable food sources for the Imperial Eagles and other specialised threatened predators, such as the Saker Falcon *(Falco cherrug)* or the Steppe Polecat *(Mustella eversmanni)* (Bihari *et al.* 2007, Horváth *et al.* 2010).

Possible effects on other species and conflicts with stakeholders

The high ratio of small game species (Hares, Pheasants), and the increasing frequency of Roe Deers among the prey remains found under eagle nests, raised a significant negative attitude among hunters towards the eagles (Kovács *et al.* 2016). This negative attitude in parallel with widespread illegal predator poisoning activities resulted in an enormously high mortality of Imperial Eagles in Hungary due to persecution (Horváth *et al.* 2018). In one hand it is crucial to communicate actively with and raise the conservational awareness of hunters. E.g. positive changes in the attitudes can be reached by emphasizing the importance of top predators in controlling mesopredators (e.g. Newsome *et al.* 2017), like the eagles predate on Corvids, raptors and carnivores, therefore indirectly they can also decrease the pressure on small games. The enhanced communication between conservationists and hunters was proved to be efficient in both decreasing persecution incidents, but also to recognize mutual interest in lobbying for nature-friendly agricultural land use practices (Fabók *et al.* 2015, Horváth *et al.* 2018).

The eagles' predation on Feral Pigeon *(Columba livia f. domestica)* and poultry species can also raise conflicts with pigeon fanciers and poultry keepers, which could also result on persecution incidents. Besides, the expanding eagle population and the occasional predation and disturbance on Great Bustards *(Otis tarda)* and Common Cranes *(Grus grus)* could also raise internal conflicts even within the conservation community. These kind of possible conflicts between predator and prey species are usually not proved by any scientific evidence on population-level effects, but based on single observations or beliefs. The clarification of these possible predator-prey interactions and the conflict management with the main stakeholder groups will be one of the most important future challenges for effective eagle conservation.

The recent study proved that the diet composition of Eastern Imperial Eagles had changed significantly during the last decades. We observed severe decrease of traditional prey species, like the Common Hamster and the European Souslik, which almost disappeared from the diet, while Corvids, waterbirds and Roe Deers increased. Brown Hare and Common Pheasant composed constantly the remarkable part of the diet, which emphasize that the conservation of this globally threatened raptor species is highly linked with small game management and agricultural land-use practices in Hungary.

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References

Báldi, A. & Faragó, S. 2007. Long-term changes of farmland game populations in a post-socialist country (Hungary). – Agriculture, Ecosystems & Environment 118: 307–311. DOI: 10.1016/j.agee.2006.05.021

Balogh, J. 1998. Adatok a szirti sas *(Aquila chrysaetos)* előfordulásához és táplálkozásához a Zempléni-hegységben [On the occurence and foraging of the Golden Eagle *(Aquila chrysaetos)* in the Zemplén-Mountains]. – Ornis Hungarica 8(Suppl. 1): 211–214. (in Hungarian with English Summary)

Bedrosian, G., Watson, J. W., Steenhof, K., Kochert, M. N., Preston, C. R., Woodbridge, B., Williams, G. E., Keller, K. R. & Crandall, R. H. 2017. Spatial and temporal patterns in Golden Eagle diets in the Western United States, with implications for conservation Planning. – Journal of Raptor Research 51(3): 347–367. DOI: 10.3356/JRR-16-38.1

Belik, V., Galushin, V. & Bogomolov, D. 2002. Results of the Imperial Eagle *(Aquila heliaca)* project in Russia during 1996 and 1997. – Aquila 107–108: 177–181.

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., Csorba, G. & Heltai, M. (eds.) 2007. Magyarország emlőseinek atlasza [Atlas of mammals of Hungary]. – Kossuth Kiadó Zrt., Budapest (in Hungarian)

Bihari, Z., Horváth, M., Lanszky, 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. – Biosystematics and Ecology Series No. 25., Austrian Academy of Sciences, Wien, pp. 61–68.

Chavko, J., Danko, Š., Obuch, J. & Mihók, J. 2007. The Food of the Imperial Eagle *(Aquila heliaca)* in Slovakia. – Slovak Raptor Journal 1: 1–18. DOI: 10.2478/v10262-012-0001-y

Chernel, I. 1899. Magyarország madarai – Különös tekintettel gazdasági jelentőségökre [Birds of Hungary – Considering their economical significance]. – Franklin-Társulat nyomdája, Budapest (in Hungarian)

Danko, Š. & Mihók, J. 2007. Kleptoparasitism by raptors, focusing on the Imperial Eagle *(Aquila heliaca)*. – Slovak Raptor Journal 1: 29–33. DOI: 10.2478/v10262-012-0004-8

del Hoyo, J., Elliot, A. & Sargatal, J. (eds.) 1995. Handbook of the Birds of the World, Vol. 2. Falconiformes to Galliformes. – Lynx Edicions, Barcelona

Demerdzhiev, D., Horváth, M., Kovács, A., Stoychev, S. & Karyakin, I. 2011. 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., Dobrev, D., Isfendiyaroglu, S., Boev, Z., Stoychev, S., Terziev, N. & Spasov, S. 2014. Distribution, abundance, breeding parameters, threats and prey preferences of the eastern Imperial Eagle *(Aquila heliaca)* in European Turkey. – Slovak Raptor Journal 8(1): 17–25. DOI: 10.2478/srj-2014-0004

Dövényi, Z. (ed.) 2010. Magyarország kistájainak katasztere [Inventory of microregions in Hungary] (2nd edition). – MTA Földrajztudományi Kutatóintézet, Budapest (in Hungarian)

Fabók, V., Kovács, E. & Kalóczkai, Á. 2015. Érintettek percepcióinak feltárása egy védett ragadozómadarakkal kapcsolatos konfliktusban a Jászság SPA részvételi tervezési folyamata során [Revealing stakeholder perceptions in a human – wildlife conflict during a public participation process in the Jászság SPA]. – Természetvédelmi Közlemények 21: 64–75. (in Hungarian with English Summary)

Ferrer, M. & Negro, J. J. 2004. The near extinction of two large European predators: super specialists pay a price. – Conservation Biology 18: 344–349. DOI: 10.1111/j.1523-1739.2004.00096.x

Gonzalez, L. M., Margalida, A., Sanchez, R. & Oria, J. 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish Imperial Eagle *(Aquila adalberti)*. – Biological Conservation 129: 477–486. DOI: 10.1016/j.biocon.2005.11.014

Halliez, G., Lucie Becel, C. M. & Canella, V. 2015. Eco-geographical variation in the diet of the Barn Owl *(Tyto alba)* in mountainous areas of France. – Ornis Hungarica 23(2): 39–48. DOI: 10.1515/orhu-2015-0013

Hámori, D., Szél, Gy. & Winkler, D. 2017. Food composition of the Little Owl *(Athene noctua)* in a farmland area of Central Hungary, with particular attention to arthropod diversity. – Ornis Hungarica 25(2): 34–50. DOI: 10.1515/orhu-2017-0014

Haraszthy, L., Bagyura, J., Szitta, T., Petrovics, Z. & Viszló, L. 1996. Biology, status and conservation of the Imperial Eagle *Aquila heliaca* in Hungary. – In: Meyburg, B-U. & Chancellor, R. D. (eds.) Eagle Studies. – World Working Group on Birds of Prey (WWGBP), Berlin, London & Paris, pp. 425–427.

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: 187–200.

Horváth, M., Szitta, T., Fatér, I., Kovács, A., Demeter, I., Firmánszky, G. & Bagyura, J. 2011. Population dynamics of the Eastern Imperial Eagle *(Aquila heliaca)* in Hungary between 2001 and 2009. – Acta Zoologica Bulgarica Suppl. 3: 61–70.

Horváth, M., Szitta, T., Bagyura, J., Fatér, I., Firmánszky, G. & Moskát, C. 2014. Simultaneous effect of habitat and age on reproductive success of Imperial Eagles *(Aquila heliaca)* in Hungary. – Ornis Hungarica 22(1): 57–68. DOI: 10.2478/orhu-2014-0011

Horváth, M., Fatér, I., Juhász, T., Deák, G., Bereczky, A. & Pásztory-Kovács, S. 2018a A Parlagisas-védelmi Munkacsoport 2016. évi beszámolója [Annual Report of Hungarian Imperial Eagle Working Groups 2016]. – Heliaca 14: 35–38. (in Hungarian with English Summary)

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 eagles between 2012 and 2016]. – Heliaca 14: 100–105. (in Hungarian with English Summary)

Karyakin, I. V., Nikolenko, E. N., Levin, A. S. & Kovalenko, A. V. 2008. Imperial Eagle in Russia and Kazakhstan: population status and trends. – Raptors Conservation 14: 18–27.

Katzner, T. E., Bragin, E. A., Knick, S. T. & Smith, A. T. 2005. Relationship between demographics and dietary specificity of Imperial Eagles in Kazakhstan. – Ibis 147: 576–586. DOI: 10.1111/j.1474-919X.2005.00443.x

Katzner, T. E., Bragin, E. A., Knick, S. T. & Smith, A. T. 2006. Spatial structure in the diet of Imperial Eagles *Aquila heliaca* in Kazakhstan. – Journal of Avian Biology 37: 594–600. DOI: 10.1111/j.2006.0908-8857.03617.x

Kovács, A., Demeter, I., Fatér, I., Bagyura, J., Nagy, K., Szitta, T., Firmánszky, G. & Horváth, M. 2008. Current efforts to monitor and conserve the Eastern Imperial Eagle *Aquila heliaca* in Hungary. – Ambio 37(6): 457–459. DOI: 10.1579/0044-7447(2008)37[460:CETMAC]2.0.CO;2

Kovács, E., Fabók, V., Kalóczkai, Á. & Hansend, H. P. 2016. Towards understanding and resolving the conflict related to the Eastern Imperial Eagle *(Aquila heliaca)* conservation with participatory management planning. – Land Use Policy 54: 158–168. DOI: 10.1016/j.landusepol.2016.02.011

Marin, S. A., Ivanov, I. I., Georgiev, D. G. & Boev, Z. N. 2004. On the food of the Imperial Eagle *Aquila heliaca* on Sakar Mountain and Dervent Heights, Bulgaria. – In: Chancellor, R. D. & Meyburg, B-U. (eds.) Raptors worldwide: Proceedings of the VI. Word Conference on Birds of Prey and Owls. – WWGBP/MME BirdLife Hungary, Budapest, pp. 589–592.

Milchev, B. & Spassov, N. 2017. First evidence for carrion–feeding of Eurasian Eagle-owl *(Bubo bubo)* in Bulgaria. – Ornis Hungarica 25(1): 58–69. DOI: 10.1515/orhu-2017-0005

Nagy, J. 1943. Európa ragadozómadarai [Raptors of Europe]. – Tiszai Madártani Egyesület (in Hungarian)

Newsome, T. M., Greenville, A. C., Cirovic, D., Dickman, C. R., Johnson, C. N., Krofel, M., Letnic, M., Ripple, W. J., Ritchie, E. G., Stoyanov, S. & Wirsing, A. J. 2017. Top predators constrain mesopredator distributions. – Nature Communications 8: 15469. DOI: 10.1038/ncomms15469

Newton, I. 1979 Population ecology of raptors. – T & AD Poyser, Berkhamsted

Ontiveros, D. & Pleguezuelos, J. M. 2000. Influence of prey densities in the distribution and breeding success of Bonelli's Eagle *(Hieraaetus fasciatus)*: management implications. – Biological Conservation 93(1): 19–25. DOI: 10.1016/S0006-3207(99)00117-2

Palma, L., Beja, P., Pais, M. & Da Fonseca, L. C. 2006. Why do raptors take domestic prey? The case of Bonelli's Eagles and Pigeons. – Journal of Applied Ecology 43: 1075–1086. DOI: 10.1111/j.1365-2664.2006.01213.x

Pátkai, I. 1947. Ragadozó madaraink [Our birds of prey]. – Nimród Kis Könyvtár, Budapest (in Hungarian)

Penteriani, V., Fortuna, M. A., Melián, C. J., Otalora, F. & Ferrer, M. 2006. Can prey behaviour induce spatially synchronic aggregation of solitary predators? – Oikos 113: 497–505. DOI: 10.1111/j.0030-1299.2006.14547.x

Preston, C. R., Jones, R. E. & Horton, N. S. 2017. Golden Eagle diet breadth and reproduction in relation to fluctuations in primary prey abundance in Wyoming's Bighorn Basin. – Journal of Raptor Research 51(3): 334–346. DOI: 10.3356/JRR-16-39.1

R Development Core Team 2018. R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, http://www.r-project.org/

Redpath, S. M., Clarke, R., Madders, M. & Thirgood, S. J. 2001. Assessing raptor diet: comparing pellets, prey remains, and observational data at Hen Harrier nests. – The Condor 103: 184–188. DOI: 10.1650/0010-5422(2001)103[0184:ARDCPP]2.0.CO;2

Sánchez, R., Margalida, A., González, L. M. & Oria, J. 2008. Biases in diet sampling methods in the Spanish Imperial Eagle *Aquila adalberti*. – Ornis Fennica 85: 82–89.

Sánchez, R., Margalida, A., González, L. M. & Oria, J. 2009. Temporal and spatial differences in the feeding ecology of the Spanish Imperial Eagle *Aquila adalberti* during the non-breeding season: effects of the Rabbit population crash. – Acta Ornithologica 44: 53–58. DOI: 10.3161/000164509X464885

Schweiger, A., Fünfstück, H. J. & Beierkuhnlein, C. 2015. Availability of optimal-sized prey affects global distribution patterns of the Golden Eagle *Aquila chrysaetos*. – Journal of Avian Biology 46: 81–88. DOI: 10.1111/jav.00396

Steenhof, K., Kochert, M. N. & McDonald, T. L. 1997. Interactive effects of prey and weather on Golden Eagle reproduction. – Journal of Animal Ecology 66: 350–362. DOI: 10.2307/5981

Szemere, L. 1912. A parlagi sas és kígyászölyv fészkénél. – Am horste von *Aquila melanaetus* Gm. und *Circaetus gallicus* Gm. [Beside the nest of Imperial Eagle and Short Toed Eagle]. – Aquila 19: 441–451. (in Hungarian and German)

Szép, Á., Klein, Á. & Purger, 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

Takeuchi, T., Shiraki, S., Nashimoto, M., Matsuki, R., Abe, S. & Yatake, H. 2006. Regional and temporal variations in prey selected by Golden Eagles *Aquila chrysaetos* during the nestling period in Japan. – Ibis 148: 79–87. DOI: 10.1111/j.1474-919X.2006.00495.x

Tóth I. 2006. A parlagi sas *(Aquila heliaca)* állomány helyzete és védelme Békés megyében 1989–2005 [The population status and conservation of Eastern Imperial Eagles *(Aquila heliaca)* in Békés County 1989–2005]. – Manuscript (in Hungarian)

Vasic, V. & Misirlic, R. 2002. The Eastern Imperial Eagle *(Aquila heliaca)* in Yugoslavia, with preference to F.Y.R. Macedonia. – Aquila 107–108: 145–168.

Vasvári, M. 1938. Der Verbreitung und Oekologie des Kaiseradlers (*Aquila heliaca* Sav.) [The distribution and ecology of Eastern Imperial Eagles (*Aquila heliacal* Sav.)]. – In: Festschrift zum 60. Geburtstage von Professor Dr. Embrik Strand. Riga, Vol. 5., pp. 290–317. (in German)

Watson, J., Leitch, A. F. & Rae, S. R. 1993. The diet of Golden Eagles *Aquila chrysaetos* in Scotland. – Ibis 135(4): 387–393. DOI: 10.1111/j.1474-919X.1993.tb02110.x

Appendix

Appendix Proportion of all identified prey taxa of Eastern Imperial Eagles in Hungary in the three study periods

Melléklet Valamennyi meghatározott taxon eloszlása a parlagi sasok magyarországi táplálékában a három vizsgálati időszakban

Taxa	**1982–1991**		**1992–2004**		**2005–2017**		**Total (1982–2017)**	
	Number	***% N***	**Number**	***% N***	**Number**	***% N***	**Number**	***% N***
Acridoidea indet.	–	–	–	–	1	0.02%	1	0.01%
Calosoma auropunctatum	–	–	–	–	1	0.02%	1	0.01%
Carabus cancellatus	–	–	–	–	1	0.02%	1	0.01%
Coleoptera indet.	–	–	–	–	5	0.08%	5	0.06%
Gryllotalpa gryllotalpa	–	–	–	–	2	0.03%	2	0.02%
Holochelus aequinoctialis	–	–	–	–	1	0.02%	1	0.01%
Lucanus cervus	–	–	–	–	1	0.02%	1	0.01%
Silpha carinata	–	–	–	–	1	0.02%	1	0.01%
Silpha obscura	–	–	–	–	1	0.02%	1	0.01%
Zabrus tenebrionides	–	–	–	–	1	0.02%	1	0.01%
Insecta indet.	–	–	–	–	5	0.08%	5	0.06%
INSECTA total	**–**	**–**	**–**	**–**	**20**	**0.63%**	**20**	**0.23%**
Cepaea sp.	–	–	–	–	1	0.02%	1	0.01%
Helix pomatia	–	–	–	–	1	0.02%	1	0.01%
GASTROPODA total	**–**	**–**	**–**	**–**	**2**	**0.06%**	**2**	**0.02%**
Carassius auratus	–	–	–	–	1	0.02%	1	0.01%
Cyprinus carpio	–	–	–	–	2	0.03%	2	0.02%
Pisces indet.	–	–	–	–	3	0.05%	3	0.04%
PISCES total	**–**	**–**	**–**	**–**	**6**	**0.19%**	**6**	**0.07%**
Elaphe longissima	–	–	–	–	1	0.02%	1	0.01%
Natrix natrix	–	–	–	–	1	0.02%	1	0.01%
Colubridae indet.	1	0.16%	1	0.07%	1	0.02%	3	0.04%
REPTILIA total	**1**	**0.16%**	**1**	**0.07%**	**3**	**0.10%**	**5**	**0.06%**
Coturnix coturnix	1	0.16%	–	–	23	0.36%	24	0.28%
Gallus gallus f. domestica	20	3.19%	19	1.29%	87	1.35%	126	1.47%
Meleagris gallopavo f. domestica	1	0.16%	–	–	5	0.08%	6	0.07%
Perdix perdix	1	0.16%	11	0.75%	13	0.20%	25	0.29%
Phasianus colchicus	75	11.96%	226	15.32%	723	11.22%	1024	11.99%
Phasianidae subtotal	**98**	**15.63%**	**256**	**17.36%**	**851**	**13.21%**	**1205**	**14.11%**
Numida meleagris	–	–	1	0.07%	11	0.17%	12	0.14%
Numididae subtotal	**–**	**–**	**1**	**0.07%**	**11**	**0.17%**	**12**	**0.14%**

Taxa	1982–1991		1992–2004		2005–2017		Total (1982–2017)	
	Number	*% N*	Number	*% N*	Number	*% N*	Number	*% N*
Anas acuta	–	–	–	–	1	0.02%	1	0.01%
Anas crecca	–	–	2	0.14%	1	0.02%	3	0.04%
Anas platyrhynchos	1	0.16%	22	1.49%	139	2.16%	162	1.90%
Anas platyrhynchos f. domestica	–	–	3	0.20%	4	0.06%	7	0.08%
Anas querquedula	–	–	2	0.14%	4	0.06%	6	0.07%
Anas sp.	–	–	1	0.07%	7	0.11%	8	0.09%
Anser albifrons	–	–	–	–	7	0.11%	7	0.08%
Anser anser	–	–	–	–	16	0.25%	16	0.19%
Anser anser f. domestica	1	0.16%	4	0.27%	13	0.20%	18	0.21%
Anser fabalis	–	–	–	–	2	0.03%	2	0.02%
Anser sp.	–	–	1	0.07%	6	0.09%	7	0.08%
Aythya nyroca	–	–	–	–	1	0.02%	1	0.01%
Cygnus olor	–	–	–	–	1	0.02%	1	0.01%
Anatidae indet.	–	–	–	–	8	0.12%	8	0.09%
Anatidae subtotal	**2**	**0.32%**	**35**	**2.37%**	**210**	**3.26%**	**247**	**2.89%**
Tachybaptus ruficollis	–	–	–	–	1	0.02%	1	0.01%
Podicipedidae subtotal	**–**	**–**	**–**	**–**	**1**	**0.02%**	**1**	**0.01%**
Columba livia f. domestica	10	1.59%	90	6.10%	311	4.83%	411	4.81%
Columba oenas	–	–	2	0.14%	6	0.09%	8	0.09%
Columba palumbus	9	1.44%	22	1.49%	108	1.68%	139	1.63%
Columba sp.	2	0.32%	12	0.81%	135	2.10%	149	1.74%
Streptopelia decaocto	1	0.16%	–	–	9	0.14%	10	0.12%
Streptopelia turtur	–	–	1	0.07%	4	0.06%	5	0.06%
Columbidae subtotal	**22**	**3.51%**	**127**	**8.61%**	**573**	**8.90%**	**722**	**8.45%**
Cuculus canorus	–	–	1	0.07%	2	0.03%	3	0.04%
Cuculidae subtotal	**–**	**–**	**1**	**0.07%**	**2**	**0.03%**	**3**	**0.04%**
Crex crex	–	–	–	–	1	0.02%	1	0.01%
Fulica atra	–	–	5	0.34%	24	0.37%	29	0.34%
Gallinula chloropus	–	–	–	–	4	0.06%	4	0.05%
Rallidae subtotal	**–**	**–**	**5**	**0.34%**	**29**	**0.45%**	**34**	**0.40%**
Grus grus	–	–	–	–	6	0.09%	6	0.07%
Gruidae subtotal	**–**	**–**	**–**	**–**	**6**	**0.09%**	**6**	**0.07%**
Otis tarda	–	–	–	–	3	0.05%	3	0.04%
Otidae subtotal	**–**	**–**	**–**	**–**	**3**	**0.05%**	**3**	**0.04%**
Ciconia ciconia	–	–	1	0.07%	1	0.02%	2	0.02%
Ciconia nigra	–	–	–	–	2	0.03%	2	0.02%
Ciconia sp. *(ciconia/ nigra)*	–	–	–	–	1	0.02%	1	0.01%
Ciconiidae subtotal	**–**	**–**	**1**	**0.07%**	**4**	**0.06%**	**5**	**0.06%**

Taxa	1982–1991		1992–2004		2005–2017		Total (1982–2017)	
	Number	% N	Number	% N	Number	% N	Number	% N
Platalea leucorodia	–	–	1	0.07%	1	0.02%	2	0.02%
Threskiornithidae subtotal	**–**	**–**	**1**	**0.07%**	**1**	**0.02%**	**2**	**0.02%**
Ardea alba	–	–	2	0.14%	27	0.42%	29	0.34%
Ardea cinerea	–	–	5	0.34%	33	0.51%	38	0.44%
Egretta garzetta	–	–	–	–	2	0.03%	2	0.02%
Ixobrychus minutus	–	–	–	–	1	0.02%	1	0.01%
Nycticorax nycticorax	–	–	–	–	11	0.17%	11	0.13%
Ardeidae subtotal	**–**	**–**	**7**	**0.47%**	**74**	**1.15%**	**81**	**0.95%**
Himantopus himantopus	–	–	–	–	1	0.02%	1	0.01%
Recurvirostridae subtotal	**–**	**–**	**–**	**–**	**1**	**0.02%**	**1**	**0.01%**
Vanellus vanellus	–	–	8	0.54%	94	1.46%	102	1.19%
Charadriidae subtotal	**–**	**–**	**8**	**0.54%**	**94**	**1.46%**	**102**	**1.19%**
Limosa limosa	–	–	1	0.07%	2	0.03%	3	0.04%
Philomachus pugnax	–	–	1	0.07%	1	0.02%	2	0.02%
Scolopacidae indet.	–	–	–	–	1	0.02%	1	0.01%
Scolopax rusticola	–	–	2	0.14%	1	0.02%	3	0.04%
Tringa totanus	–	–	–	–	2	0.03%	2	0.02%
Scolopacidae subtotal	**–**	**–**	**4**	**0.27%**	**7**	**0.11%**	**11**	**0.13%**
Chlidonias sp.	–	–	–	–	1	0.02%	1	0.01%
Chroicocephalus ridibundus	–	–	2	0.14%	16	0.25%	18	0.21%
Laridae indet.	–	–	–	–	3	0.05%	3	0.04%
Larus sp. *(cachinnans/ michahellis)*	–	–	–	–	10	0.16%	10	0.12%
Laridae subtotal	**–**	**–**	**2**	**0.14%**	**30**	**0.47%**	**32**	**0.37%**
Tyto alba	–	–	–	–	2	0.03%	2	0.02%
Tytonidae subtotal	**–**	**–**	**–**	**–**	**2**	**0.03%**	**2**	**0.02%**
Asio flammeus	–	–	2	0.14%	13	0.20%	15	0.18%
Asio otus	1	0.16%	24	1.63%	142	2.20%	167	1.95%
Asio sp. *(flammeus/ otus)*	–	–	–	–	4	0.06%	4	0.05%
Strigidae indet.	–	–	1	0.07%	2	0.03%	3	0.04%
Strix aluco	1	0.16%	2	0.14%	7	0.11%	10	0.12%
Strix uralensis	–	–	–	–	1	0.02%	1	0.01%
Strigidae subtotal	**2**	**0.32%**	**29**	**1.97%**	**169**	**2.62%**	**200**	**2.34%**
Accipiter nisus	–	–	–	–	2	0.03%	2	0.02%
Buteo buteo	4	0.64%	12	0.81%	67	1.04%	83	0.97%
Circus aeruginosus	–	–	1	0.07%	8	0.12%	9	0.11%
Pernis apivorus	1	0.16%	2	0.14%	–	–	3	0.04%
Accipitridae subtotal	**5**	**0.80%**	**15**	**1.02%**	**77**	**1.20%**	**97**	**1.14%**

Taxa	**1982–1991**		**1992–2004**		**2005–2017**		**Total (1982–2017)**	
	Number	***% N***	**Number**	***% N***	**Number**	***% N***	**Number**	***% N***
Upupa epops	–	–	–	–	1	0.02%	1	0.01%
Upupidae subtotal	**–**	**–**	**–**	**–**	**1**	**0.02%**	**1**	**0.01%**
Coracias garrulus	–	–	–	–	6	0.09%	6	0.07%
Coraciidae subtotal	**–**	**–**	**–**	**–**	**6**	**0.09%**	**6**	**0.07%**
Dendrocopos major	–	–	–	–	1	0.02%	1	0.01%
Dendrocopos sp.	–	–	–	–	1	0.02%	1	0.01%
Picus viridis	–	–	1	0.07%	2	0.03%	3	0.04%
Picidae subtotal	**–**	**–**	**1**	**0.07%**	**4**	**0.06%**	**5**	**0.06%**
Falco cherrug	–	–	–	–	2	0.03%	2	0.02%
Falco peregrinus	–	–	–	–	1	0.02%	1	0.01%
Falco subbuteo	–	–	–	–	1	0.02%	1	0.01%
Falco tinnunculus	1	0.16%	9	0.61%	60	0.93%	70	0.82%
Falco vespertinus	–	–	–	–	2	0.03%	2	0.02%
Falconidae subtotal	**1**	**0.16%**	**9**	**0.61%**	**66**	**1.02%**	**76**	**0.89%**
Corvus corax	–	–	10	0.68%	59	0.92%	69	0.81%
Corvus cornix	–	–	12	0.81%	216	3.35%	228	2.67%
Corvus frugilegus	5	0.80%	10	0.68%	67	1.04%	82	0.96%
Corvus monedula	–	–	2	0.14%	1	0.02%	3	0.04%
Corvus sp. *(cornix/ frugilegus)*	2	0.32%	13	0.88%	257	3.99%	272	3.18%
Garrulus glandarius	–	–	2	0.14%	7	0.11%	9	0.11%
Pica pica	1	0.16%	24	1.63%	237	3.68%	262	3.07%
Corvidae subtotal	**8**	**1.28%**	**73**	**4.95%**	**844**	**13.10%**	**925**	**10.83%**
Alauda arvensis	–	–	4	0.27%	18	0.28%	22	0.26%
Alaudidae indet. (Alauda arvensis/ Galerida cristata)	–	–	–	–	2	0.03%	2	0.02%
Galerida cristata	–	–	4	0.27%	–	–	4	0.05%
Alaudidae subtotal	**–**	**–**	**8**	**0.54%**	**20**	**0.31%**	**28**	**0.33%**
Acrocephalus arundinaceus	–	–	–	–	1	0.02%	1	0.01%
Acrocephalidae subtotal	**–**	**–**	**–**	**–**	**1**	**0.02%**	**1**	**0.01%**
Sturnus vulgaris	–	–	5	0.34%	49	0.76%	54	0.63%
Sturnidae subtotal	**–**	**–**	**5**	**0.34%**	**49**	**0.76%**	**54**	**0.63%**
Turdus merula	1	0.16%	1	0.07%	2	0.03%	4	0.05%
Turdus philomelos	–	–	–	–	3	0.05%	3	0.04%
Turdus pilaris	–	–	–	–	1	0.02%	1	0.01%
Turdus sp.	2	0.32%	–	–	1	0.02%	3	0.04%
Turdidae subtotal	**3**	**0.48%**	**1**	**0.07%**	**7**	**0.11%**	**11**	**0.13%**
Passer domesticus	–	–	–	–	1	0.02%	1	0.01%
Passer montanus	–	–	–	–	1	0.02%	1	0.01%
Passer sp. *(domesticus/ montanus)*	–	–	–	–	2	0.03%	2	0.02%
Passeridae subtotal	**–**	**–**	**–**	**–**	**4**	**0.06%**	**4**	**0.05%**

Taxa	**1982–1991**		**1992–2004**		**2005–2017**		**Total (1982–2017)**	
	Number	***% N***	**Number**	***% N***	**Number**	***% N***	**Number**	***% N***
Motacilla flava	–	–	–	–	1	0.02%	1	0.01%
Motacillidae subtotal	**–**	**–**	**–**	**–**	**1**	**0.02%**	**1**	**0.01%**
Emberiza calandra	–	–	1	0.07%	–	–	1	0.01%
Emberizidae subtotal	**–**	**–**	**1**	**0.07%**	**–**	**–**	**1**	**0.01%**
Passeriformes indet.	3	0.48%	3	0.20%	3	0.05%	9	0.11%
Passeriformes indet. subtotal	**3**	**0.48%**	**3**	**0.20%**	**3**	**0.05%**	**9**	**0.11%**
AVES total	**144**	**22.97%**	**593**	**40.20%**	**3151**	**100.00%**	**3888**	**45.51%**
Erinaceus roumanicus	11	1.75%	18	1.22%	67	1.04%	96	1.12%
Erinaceidae subtotal	**11**	**1.75%**	**18**	**1.22%**	**67**	**1.04%**	**96**	**1.12%**
Sorex araneus	–	–	–	–	1	0.02%	1	0.01%
Soricidae subtotal	**–**	**–**	**–**	**–**	**1**	**0.02%**	**1**	**0.01%**
Talpa europaea	–	–	–	–	15	0.23%	15	0.18%
Talpidae subtotal	**–**	**–**	**–**	**–**	**15**	**0.23%**	**15**	**0.18%**
Lepus europaeus	77	12.28%	455	30.85%	1810	28.10%	2342	27.41%
Oryctolagus cuniculus	1	0.16%	–	–	1	0.02%	2	0.02%
Leporidae subtotal	**78**	**12.44%**	**455**	**30.85%**	**1811**	**28.12%**	**2344**	**27.44%**
Sciurus vulgaris	–	–	1	0.07%	–	–	1	0.01%
Spermophilus citellus	44	7.02%	13	0.88%	2	0.03%	59	0.69%
Sciuridae subtotal	**44**	**7.02%**	**14**	**0.95%**	**2**	**0.03%**	**60**	**0.70%**
Glis glis	1	0.16%	–	–	–	–	1	0.01%
Gliridae subtotal	**1**	**0.16%**	**–**	**–**	**–**	**–**	**1**	**0.01%**
Arvicola amphibius	–	–	–	–	24	0.37%	24	0.28%
Arvicolinae indet.	2	0.32%	3	0.20%	6	0.09%	11	0.13%
Cricetus cricetus	312	49.76%	296	20.07%	478	7.42%	1086	12.71%
Microtus arvalis	4	0.64%	27	1.83%	363	5.64%	394	4.61%
Ondatra zibethicus	9	1.44%	1	0.07%	4	0.06%	14	0.16%
Cricetidae subtotal	**327**	**52.15%**	**327**	**22.17%**	**875**	**13.58%**	**1529**	**17.90%**
Apodemus agrarius	–	–	–	–	3	0.05%	3	0.04%
Apodemus sp.	–	–	–	–	1	0.02%	1	0.01%
Micromys minutus	–	–	–	–	1	0.02%	1	0.01%
Mus musculus	–	–	–	–	2	0.03%	2	0.02%
Mus sp. *(musculus/ spicilegus)*	–	–	–	–	2	0.03%	2	0.02%
Rattus norvegicus	1	0.16%	6	0.41%	26	0.40%	33	0.39%
Muridae subtotal	**1**	**0.16%**	**6**	**0.41%**	**35**	**0.54%**	**42**	**0.49%**
Felis sp. *(silvestris/ catus)*	1	0.16%	3	0.20%	3	0.05%	7	0.08%
Felis catus	2	0.32%	3	0.20%	26	0.40%	31	0.36%
Felis silvestris	–	–	–	–	1	0.02%	1	0.01%
Felidae subtotal	**3**	**0.48%**	**6**	**0.41%**	**30**	**0.47%**	**39**	**0.46%**

Taxa	1982–1991		1992–2004		2005–2017		Total (1982–2017)	
	Number	*% N*	Number	*% N*	Number	*% N*	Number	*% N*
Canis aureus	–	–	–	–	1	0.02%	1	0.01%
Canis familiaris	1	0.16%	1	0.07%	5	0.08%	7	0.08%
Vulpes vulpes	2	0.32%	9	0.61%	33	0.51%	44	0.52%
Canidae subtotal	**3**	**0.48%**	**10**	**0.68%**	**39**	**0.61%**	**52**	**0.61%**
Lutra lutra	–	–	1	0.07%	–	–	1	0.01%
Martes foina	–	–	–	–	1	0.02%	1	0.01%
Meles meles	–	–	–	–	1	0.02%	1	0.01%
Mustela eversmanii	–	–	–	–	1	0.02%	1	0.01%
Mustela nivalis	–	–	–	–	2	0.03%	2	0.02%
Mustela putorius	–	–	1	0.07%	–	–	1	0.01%
Mustela sp. *(erminea/ nivalis)*	–	–	–	–	1	0.02%	1	0.01%
Mustela sp. *(eversmanii/putorius)*	–	–	–	–	1	0.02%	1	0.01%
Mustelidae subtotal	**–**	**–**	**2**	**0.14%**	**7**	**0.11%**	**9**	**0.11%**
Sus scrofa	1	0.16%	4	0.27%	7	0.11%	12	0.14%
Sus domesticus	–	–	–	–	1	0.02%	1	0.01%
Suidae subtotal	**1**	**0.16%**	**4**	**0.27%**	**8**	**0.12%**	**13**	**0.15%**
Capreolus capreolus	12	1.91%	38	2.58%	360	5.59%	410	4.80%
Cervus elaphus	–	–	–	–	1	0.02%	1	0.01%
Cervidae subtotal	**12**	**1.91%**	**38**	**2.58%**	**361**	**5.60%**	**411**	**4.81%**
Bos taurus	–	–	–	–	1	0.02%	1	0.01%
Capra hircus	–	–	–	–	1	0.02%	1	0.01%
Ovis sp. *(aries/ orientalis)*	1	0.16%	1	0.07%	6	0.09%	8	0.09%
Bovidae subtotal	**1**	**0.16%**	**1**	**0.07%**	**8**	**0.12%**	**10**	**0.12%**
MAMMALIA total	**482**	**76.87%**	**881**	**59.73%**	**3259**	**50.60%**	**4622**	**54.10%**
TOTAL	**627**	**100.00%**	**1475**	**100.00%**	**6441**	**100.00%**	**8543**	**100.00%**

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Food-niche pattern of the Barn Owl *(Tyto alba)* in intensively cultivated agricultural landscape[×]

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Abstract This study investigated the dietary niche of the Barn Owl *(Tyto alba)* in an intensively farmed landscape, based on pellet samples from 12 nesting pairs containing 25 animal taxa and 1,994 prey items after the breeding season in 2016. Based on land use categories of the buffer area around each nest, three landscape types (agricultural, mosaic, urban) were considered, to analyse the diet composition and food-niche parameters. Niche breadth was calculated at the local and landscape level. Small mammals were the most frequent in the diet than other prey in each of the landscape types. The Common Vole *(Microtus arvalis)*, considered to be an important agricultural pest was the most numerous prey in all landscape groups. The trophic niche of Barn Owl varied between 0.69 – 0.86 at the local level, and the overall value of niche breadth was significantly higher in the urban than in the other two landscape types. Our results showed that the increase of Common Vole frequency lead to a decrease in niche breadth; significantly negative relationship was detected between these parameters. Despite differences in niche breadth, similarly high niche overlaps were detected by the randomisation test in the three landscapes. Our results suggest that the diet composition of Barn Owls, mainly their food-niche pattern, reflected prey availability in the comparison of the studied landscapes, which pointed out that it is necessary to examine the dietary difference of Barn Owls at the finer scale of land use.

Keywords: feeding ecology, niche breadth, pellet analysis, land use

Összefoglalás Jelen tanulmányban a gyöngybagoly *(Tyto alba)* táplálék-összetételét intenzíven művelt mezőgazdasági területen vizsgáltuk. A 2016-ban gyűjtött, 12 költőpártól származó köpetminta összesen 25 zsákmány taxon 1994 egyedét tartalmazta. Az egyes fészkelőhelyek körüli pufferterület tájhasználati kategóriái alapján három tájtípust (mezőgazdasági, mozaikos, urbán) különítettünk el, hogy vizsgáljuk a gyöngybagoly táplálék-összetételét és niche paramétereit. A niche szélességet a települések alapján lokális és tájszinten elemeztük. Minden egyes tájtípusban a kisemlősök domináltak a baglyok táplálék-összetételében, míg egyéb prédafajok alacsony gyakoriságban jelentek meg. Mindhárom településcsoport esetében a mezei pocok *(Microtus arvalis)*, mint jelentős mezőgazdasági kártevő volt a leggyakoribb zsákmány. A niche-szélesség lokális szinten 0,69 – 0,86 között változott, az összesített adatok alapján a niche-szélesség szignifikánsan nagyobb volt az agrárdominanciájú, mint a másik két településcsoport vonatkozásában. Eredményeink alapján a mezei pocok gyakoriságának növekedése a niche-szélesség csökkenéséhez vezetett, a két paraméter között szignifikáns negatív regressziót mutattunk ki. A niche-szélesség eltérésének ellenére, a randomizációs teszt alapján hasonlóan magas niche-átfedést mutattuk ki a három tájtípus összehasonlításában. Eredményeink azt sugallják, hogy a gyöngybaglyok táplálék-összetétele, főként a táplálék niche mintázat a vizsgált tájegységek összehasonlításában visszatükrözte a zsákmány-elérhetőséget, amely rámutatott arra, hogy a gyöngybagoly táplálék-összetétel különbségét a tájhasználat finomabb skáláján szükséges vizsgálni.

Kulcsszavak: táplálkozás ökológia, niche-szélesség, köpetanalízis, tájhasználat

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Introduction

Barn Owl *(Tyto alba)* as cosmopolitan nocturnal predator occurs worldwide in most open lands and farmlands (de Bruijn 1994, Taylor 1994, Charter *et al*. 2009, Frey *et al*. 2011) and its diet composition is influenced by the fluctuation of prey populations (Campbell *et al*. 1987, Taylor 1994, Bernard *et al*. 2010, Paspali *et al*. 2013), climatic factors (Clark & Bunck 1991, Avery 1999, Heisler *et al*. 2014), and change of land use and landscape composition (Rodríguez & Peris 2007, Milchev 2015, Veselovský *et al*. 2017).

Since the classical trophic niche studies of owls (Marti 1974, Herrera 1974, Herrera & Hiraldo 1976) the food-niche difference of Barn Owls has been investigated in several approaches such as through comparative intra- and interspecific feeding ecology (Herrera & Jaksić 1980, Capizzi & Luiselli 1998, Leader *et al*. 2010, Petrovici *et al*. 2013, Milchev 2016), trophic guild structure (Jaksić & Delibes 1987, Jaksić *et al*. 1993), long-term study of food composition (Marti 1988, 2010, Love *et al.* 2000), along different geographical regions (Jaksić *et al*. 1982, González-Fischer *et al.* 2011, Milana *et al.* 2016), and gradients (Leveau *et al.* 2006, Trejo & Lambertucci 2007, Hindmarch & Elliott 2015), as well as the impact of disturbances (Jaksić *et al.* 1997, Sahores & Trejo 2004) particularly dependence on growing agricultural activity and changes in farming practice (Love *et al.* 2000, de la Peña *et al.* 2003, Bontzorlos *et al.* 2005, Marti 2010).

Different results of Barn Owls' food-niche analyses have been demonstrated in agricultural ecosystems, and these depended on geographical regions and seasons. Niche breadth was different between seasons in Mediterranean areas (Pezzo & Morimando 1995, Bontzorlos *et al.* 2005), while the niche overlap was high in comparison between seasons (Pezzo & Morimando 1995), and between nest sites (Bosè & Guidali 2001). The food-niche breadth of Barn Owls varied significantly among the years but was not statistically different among seasons in a North American agricultural landscape (Marti 2010), although the seasonal difference of niche breadth was more detectable in temperate regions (Campbell *et al.* 1987, Taylor 1994, González-Fischer *et al.* 2011). Despite this seasonal variation, no correlation was observed between food niche breadth and latitude or longitude, but the prey selection of Barn Owls was associated with the rodent assemblages and responded to the abundance fluctuation of rodents along the gradients in South-America (Leveau *et al.* 2006, Trejo & Lambertucci 2007, González-Fischer *et al.* 2011). The relationship between density fluctuation of small mammals and diet composition was investigated in the Nearctic (Campbell *et al.* 1987, Marti 1988, 2010) and Palearctic range of the Barn Owl (Taylor 1994, Bernard *et al.* 2010). According to these studies, the variation of the Barn Owl's prey consumption was basically determined by high density open-field and agricultural pest rodents, such as species of *Microtus* in both distribution ranges of the Northern Hemisphere. The negative correlation between vole (*Microtus* spp.) frequency and food-niche breadth of the Barn Owl was demonstrated by long-term (Marti 1988, 2010) and other case studies (Milchev 2015, Hindmarch & Elliott 2015). Furthermore, the food-niche breadth of Barn Owl decreased significantly with the increase of mean prey weight (Marti 1988, Milchev 2015), and a significant positive regression was found between the sample size and niche breadth values (Milana *et al.* 2016).

Several studies suggested that the yearly and seasonal variations in the diet composition and thus the plasticity of the food-niche breadth of the Barn Owl reflected local resource conditions, especially the density fluctuation of small mammal preys and changes in the composition of the small mammal assemblages (Milana *et al.* 2016). The population and community attributes of this main prey groups of Barn Owls were determined by changes in the vegetation cover (Lovari *et al.* 1976, Marti 1988, Pezzo & Morimando 1995, Bontzorlos *et al.* 2005), land use and agricultural activity (crop rotation, frequency of mowing or harvesting) (Cooke *et al.* 1996, Askew *et al.* 2007).

In the present study we investigate the hypothesis that habitat variation at the local spatial scale influences the diet composition of Barn Owls, while according to alternative hypothesis, the prey consumption and niche breadth do not depend on the local environmental heterogeneity due to the dominance of intensively cultivated agricultural areas at the regional scale. Our objectives were: i) to evaluate the diet composition of Barn Owls and the relative abundance of small mammals, and ii) to investigate difference of food-niche breadth at the local and landscape scale and niche overlap between three distinguished landscape types within the intensively cultivated agricultural area.

Material and methods

Study area and sample collection

The study was conducted in the intensively cultivated south-eastern part of Transdanubian region in South Hungary (572.3 km^2) in Baranya county (45°53′ N, 18°20′ E) *(Figure 1)*. The climate of this region is characterising by the Mediterranean influence with the high number of sunny hours, the relative low fluctuations of temperatures and mild winters. In the present study pellets and prey remains were collected from 12 Barn Owl pairs from the sampling sites at the end of the breeding season in 2016. As a result of a successful artificial nest box program in this county the collection of pellet samples was implemented from active next boxes in each locality. Landscape compositions were assessed using Google Earth (2013) and landscape elements were analysed within a 1 km radius around each nest site because this corresponds to an area that approximates the home range (3 km^2) of a Barn Owl during the breeding season (e.g. Taylor 1994, Hindmarch *et al.* 2012, Kross *et al.* 2016). Three groups of the nesting sites (4 sampling localities/group) were distinguished based on landscape composition: 1) agricultural landscape (AL), 2) mosaic landscape (ML), and 3) urban landscape (UL). The following land-use types were identified and digitized, then the percentage of these categories were calculated: 1) agricultural field (annual and perennial crops); 2) extensive land use (grassland, pasture, orchards, vineyards); 3) wetland (including river banks, streams, artificial lakes, fishponds); 4) forest (all forest habitats), and 5) urban (all built-up surfaces) areas *(Table 1)*.

Pellets were processed by the dry technique when 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),

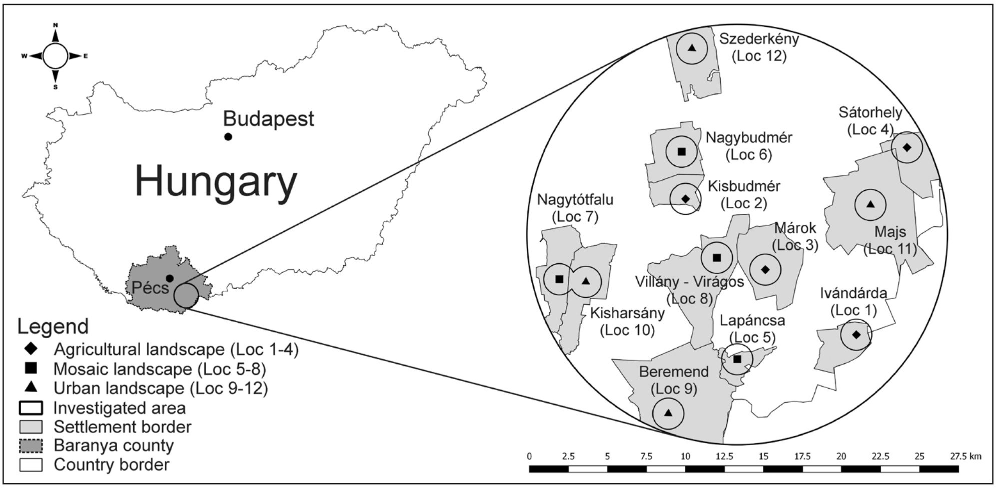


Figure 1. Study area in the South-Transdanubian region, Hungary, showing the location of Baranya county and 12 nesting pairs within the examined landscape. Code numbers (Loc1-12) besides settlement names correspond to those in Table 3.

1. ábra A vizsgált terület Dél-Dunántúlon, Magyarországon, feltűntetve Baranya megye és a 12 költőpár elhelyezkedését a vizsgált tájegységen belül. A településnevek melletti (Loc1-12) kódszámok a 3. táblázatban szereplő kódolásnak felelnek meg

following published literature (März 1972, Yalden 1977, Yalden & Morris 1990). Three different *Apodemus* species as the Wood Mouse *(Apodemus sylvaticus)*, the Yellow-necked Wood Mouse *(A. flavicollis)* and the Pygmy Field Mouse *(A. uralensis)* were categorized commonly as *Apodemus* spp. When the Striped Field Mouse *(A. agrarius)* was not separable from the *Sylvaemus* group (*Apodemus* spp.) the individuals were determined as 'unidentified *Apodemus*'. The sibling species of the genus *Mus* were determined according to Macholán (1996) and Kryštufek and Macholán (1998). In addition, birds were identified by their skulls, bills, feet, pelvises and feathers, and frog (Anura) by their skulls and bones of the postcranial skeleton. If major skeletal elements were missing, prey items were identified to genus (small mammals, birds), to order (frogs), and to class (birds) level.

Table 1. Mean proportions and value ranges (%) of land use categories in three distinct landscape types

1. táblázat A tájhasználati kategóriák átlagos aránya és érték-intervalluma (%) a három elkülönített tájtípusban

Landscape	**Agricultural**		**Mosaic**		**Urban**	
Land use	Mean ±SE	Range %	Mean ±SE	Range %	Mean ±SE	Range %
agricultural field	72.20 ±1.27	69.04-75.19	58.35 ±5.26	46.45-70.19	31.48 ±6.16	16.86-45.35
extensive land use	7.08 ±3.12	0.43-13.53	16.85 ±8.02	5.07-39.47	19.15 ±6.97	10.96-39.99
wetland	1.13 ±0.55	0.42-2.75	1.71 ±1.10	0-4.59	0.47 ±0.40	0-1.66
forest	7.85 ±3.84	1.67-18.95	13.99 ±3.15	4.91-18.77	13.20 ±2.97	4.33-16.87
urban areas	11.74 ±3.69	4.31-21.96	9.10 ±0.63	7.33-10.18	35.70 ±8.67	18.86-56.1

Prey numbers were estimated as the minimum number of individuals (MNI) which we determined according to the same anatomical parts of bones for small mammals (Klein & Cruz-Uribe 1984, McDowell & Medlin 2009, Torre *et al.* 2015, Tulis *et al.* 2015) and skulls, mandibles and long bones for birds. The percent frequency of occurrence (MNI%) was calculated for the total number of prey found in all the pellets at the three different landscape categories.

Statistical methods

First, we evaluated the difference of the relative abundance (MNI%) of small mammals among the separated landscape types. The arithmetic mean MNI% is presented with standard error. To test the hypothetic relationship between niche breadth and Common Vole *(Microtus arvalis)* frequency, linear regression method was used. These statistical analyses were performed using Statistica 8.0 software (StatSoft, Bedford, UK).

The food-niche breadth of Barn Owls was calculated by the Freeman-Tukey index (*FT*) from data of each nesting pair at the local scale and from the overall data of three different landscapes using the relative frequency of occurrence of food items which were identified in the pellets:

$$FT = \sum_{i=1}^{R} \sqrt{p_i a_i}$$

where *FT* is Smith's measure of niche breadth (Smith 1982), p_i is the proportion of individuals found using resource *i*, and a_i is the proportion of resource *i* of the total resources (*R*) found in a given summarized pellet sample. Smith's niche breadth is a standardized measure, as it takes resource availability into account (Devictor *et al.* 2010). The value of this index varies from 0 (minimal) to 1.0 (maximal) and it is relatively insensitive to selectivity for rare resources and to evaluate the significant difference of niche breadth, 95% confidence interval of *FT* values was calculated which measures the uncertainty of estimates (Krebs 1999).

To evaluate the food niche overlap of the Barn Owl among different landscapes, the Pianka overlap index ($O_{12,}$ Pianka 1974, Krebs 1999) was calculated:

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} p_{2i}\, p_{1i}}{\sqrt{\sum_{i=1}^{n}(p_{2i}^2)\sum_{i=1}^{n}(p_{1i}^2)}}$$

where p_i is the frequency of the i^{th} item in the diet. This index ranges between 0 (no overlap) and 1 (complete overlap). The significance of the overlap was tested using randomization procedures in R v. 3.3.2 (R Development Core Team 2016), using the "EcoSimR" packages (Gotelli *et al.* 2015). The statistical tests were considered significant at the level $P \leq 0.05$ as standard in all analyses (Sokal & Rohlf 1995).

Results

The diet composition and feeding range was analysed from a total of 890 pellets from which 258 whole pellets were collected in agricultural, 424 in mosaic and 208 in urban landscape. Based on all samples of 12 nesting Barn Owl pairs, 25 animal taxa and 1,994 prey items were identified from the pellets examined during the nesting period in 2016 *(Table 2)*. Small mammals were more frequent among Barn Owl food types (AL: 98.30% ±1.04, ML: 99.93% ± 0.07, UL: 99.40% ± 0.40) while the proportion of other prey categories was very low in each landscape type (AL: 1.70% ± 1.04, ML: 0.07% ± 0.04, UL: 0.60% ± 0.39). Rodents (AL: 90.98% ±2.73, ML: 88.27% ±1.88, UL: 91.76% ±1.43) were more represented within the small mammals than shrews (AL: 7.31% ± 3.04, ML: 11.66% ± 1.82, UL: 7.36% ± 1.73) in the case of each landscape. The proportion of rodents was quite the same in the landscapes while this value of shrews was higher in mosaic than in the other two landscapes *(Table 2)*.

The Common Vole *(M. arvalis)* was the most abundant prey in each of the localities of the three landscape types (AL: 55.95% ± 9.49, ML: 45.72% ± 4.67, UL: 43.30% ± 6.09). Despite the predominance of the Common Vole which basically determined the percent frequency of voles (Arvicolinae), the amount of mice (Murinae) as an important alternative prey group was higher in the case of some sampling localities within rodents. At the species level, the percent distribution of the Striped Field Mouse was higher in the area dominated by built-up surfaces (8.63% ± 0.81) than in the agricultural land (3.75% ± 1.71) but the abundance of this species was similar between the urban and mosaic landscapes (7.53% ± 0.77) *(Table 2)*.

The calculated Freeman-Tukey index (*FT*) indicated that the niche breadth of the Barn Owl varied in different intervals within each separated landscape *(Table 3)*. The range of niche breadth of nesting pairs (localities) was greater in the agricultural land while narrower in the mosaic and urban landscapes which were confirmed by the 95% confidence interval of minimum and maximum values of *FT* index. The lack of overlap indicated a significant difference between the minimal and maximal values of niche breadth in the case of the agricultural landscape. In contrast, the same narrower range of food-niche breadth was showed by the overlap of 95% confidence interval of terminal values in the case of other two landscapes *(Table 3)*. Based on results of each nesting pair, a significant negative linear regression was detected between the local abundance of common vole and food-niche breadth ($R^2 = 0.659$, $F = 19.39$, $P < 0.01$) *(Figure 2)*.

The value of overall niche breadth at the landscape level was significantly higher in the urban than in the agricultural and mosaic landscapes while there was no significant difference between agricultural and mosaic landscapes due to an overlap of 95% confidence interval *(Figure 3)*.

Despite the difference of overall niche breadth values which was observed between urban and another two landscapes, significantly higher food-niche overlap indices were presented by the randomization procedure in the comparison of all the considered landscapes than the obtained mean values from simulations *(Table 4)*.

Table 2. Diet composition of the Barn Owl in the three considered landscapes (MNI: minimum number of individuals, MNI%: percentage frequency of occurrence)

2. táblázat A gyöngybagoly táplálék-összetétele a három figyelembe vett tájegységben (MNI: minimum ismert egyedszám, MNI%: az előfordulási frekvencia százalékos értéke)

Landscape	**Agricultural**		**Mosaic**		**Urban**		**Total**	
Taxa	MNI	MNI%	MNI	MNI%	MNI	MNI%	MNI	MNI%
Soricidae	40	8.03	118	12.25	52	9.76	210	10.53
Sorex araneus	1	0.20	11	1.14	6	1.13	18	0.90
Sorex minutus	1	0.20	2	0.21	2	0.38	5	0.25
Neomys fodiens	2	0.40	14	1.45	4	0.75	20	1.00
Neomys anomalus	3	0.60	13	1.35	8	1.50	24	1.20
Neomys sp.	3	0.60	2	0.21	3	0.56	8	0.40
Crocidura suaveolens	14	2.81	47	4.88	14	2.63	75	3.76
Crocidura leucodon	16	3.21	29	3.01	15	2.81	60	3.01
Arvicolinae	314	63.05	476	49.43	233	43.71	1023	51.30
Myodes glareolus	0	0.00	6	0.62	3	0.56	9	0.45
Microtus agrestis	2	0.40	1	0.10	0	0.00	3	0.15
Microtus arvalis	301	60.44	456	47.35	216	40.53	973	48.80
Microtus subterraneus	6	1.20	3	0.31	8	1.50	17	0.85
Arvicola amphibius	5	1.00	10	1.04	6	1.13	21	1.05
Murinae	142	28.51	364	37.80	236	44.28	742	37.21
Rattus norvegicus	0	0.00	0	0.00	3	0.56	3	0.15
Rattus sp.	4	0.80	12	1.25	22	4.13	38	1.91
Apodemus agrarius	16	3.21	74	7.68	48	9.01	138	6.92
Apodemus spp.	65	13.05	150	15.58	109	20.45	324	16.25
Apodemus indet	26	5.22	59	6.13	20	3.75	105	5.27
Micromys minutus	6	1.20	18	1.87	1	0.19	25	1.25
Mus spicilegus	10	2.01	20	2.08	13	2.44	43	2.16
Mus musculus	2	0.40	13	1.35	10	1.88	25	1.25
Mus sp.	13	2.61	18	1.87	10	1.88	41	2.06
Gliridae	0	0.00	3	0.31	4	0.75	7	0.35
Muscardinus avellanarius	0	0.00	3	0.31	4	0.75	7	0.35
Other prey	2	0.40	2	0.21	8	1.50	12	0.60
Birds	2	0.40	0	0.00	7	1.31	9	0.45
Amphibians	0	0.00	1	0.10	1	0.19	2	0.10
Insects	0	0.00	1	0.10	0	0.00	1	0.05

Table 3. Freeman-Tukey index of niche breadth of Barn Owls at a local scale (for each considered nesting pair)

3. táblázat A gyöngybagoly niche szélességének Freeman-Tukey index értékei lokális skálán (minden figyelembe vett költőpár esetén)

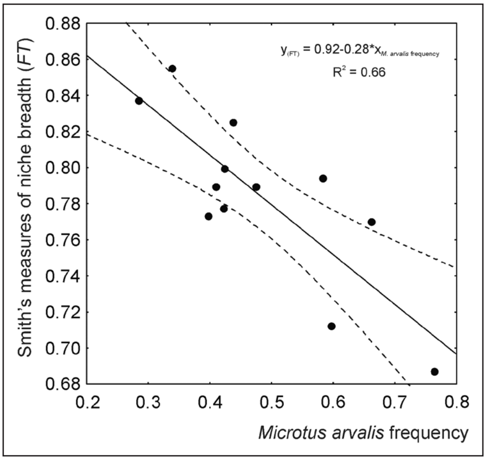
Landscape	**Agricultural**		**Mosaic**			**Urban**		
Code/nest	*FT*	95% CI	Code	*FT*	95% CI	Code	*FT*	95% CI
Loc1	0.789	0.730 – 0.841	Loc5	0.777	0.744 – 0.808	Loc9	0.837	0.797 – 0.872
Loc2	0.687	0.621 – 0.749	Loc6	0.712	0.672 – 0.750	Loc10	0.794	0.733 – 0.848
Loc3	0.855	0.782 – 0.914	Loc7	0.773	0.720 – 0.822	Loc11	0.825	0.766 – 0.877
Loc4	0.770	0.724 – 0.812	Loc8	0.789	0.735 – 0.838	Loc12	0.799	0.742 – 0.850

CI: Confidence Interval

Table 4. Pianka's food niche overlap (O) (below the diagonal) of Barn Owls among landscapes. Above the diagonal are the type I errors of each comparison, obtained by 1000 random permutations in EcoSim R

4. táblázat A gyöngybaglyok tájegységek közötti Pianka-féle niche átfedés (O) értékei (az átló alatt). Az átló felett az EcoSim R-ben 1000 random permutáció alapján kapott I. típusú hiba értékei minden összehasonlításban

Landscape	**Agricultural**	**Mosaic**	**Urban**
Agricultural	1.000	< 0.001	< 0.001
Mosaic	0.987	1.000	< 0.001
Urban	0.954	0.983	1.000



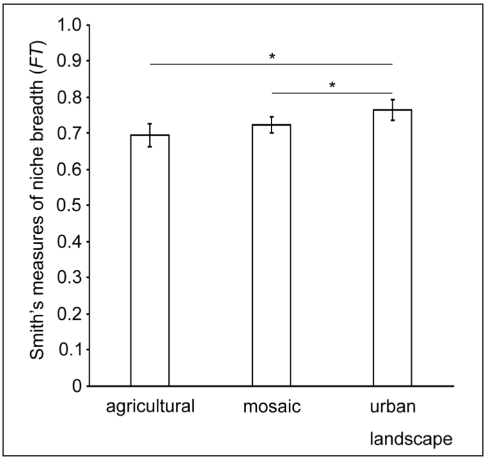


Figure 2. Linear regression between common vole frequency and niche breadth

2. ábra A mezei pocok gyakoriság és a niche szélesség közötti lineáris regresszió

Figure 3. Values of Smith's measures of niche breadth (±95% confidence interval) at landscape level

3. ábra A Smith-féle niche szélesség értéke (±95% konfidencia intervallum) táj szinten

Discussion

The feeding habit analysis of Barn Owls from regurgitated pellets is an appropriate method to understand the impact of land use and agricultural practice on the diet composition (Love *et al.* 2000, Burel *et al.* 2004), especially on the change of small mammal assemblages in areas dominated by different human activity and land use (de la Peña *et al.* 2003, González-Fischer *et al.* 2011, Massa *et al.* 2014, Torre *et al.* 2015). The results of the present study demonstrated that the prey consumption of the Barn Owl showed less variation within the boundaries of the larger and intensively cultivated agricultural area. Similar low variability of Barn Owls' diet was reported by some studies in different habitats (González-Fischer *et al.* 2011) or during long-term study periods (Marti 2010) in agro-ecosystems, as opposing the greater seasonal variability of food compositions (Bontzorolos *et al.* 2005, González-Fischer *et al.* 2011, Paspali *et al.* 2013). Similar to other studies, our result confirmed that small mammals are the dominant prey group in the diet of the Barn Owl, and this owl species is characterized as a typical small mammal specialist (Bosè & Guidali 2001, Trejo & Lambertucci 2007, Milchev 2015, Torre *et al.* 2015). The percent frequency of Striped Field Mouse as a generalist species was significantly higher in the urban landscape. With respect to the relative proportion of this species, our results are consistent with other studies which described the Striped Field Mouse as a permanent but non-dominant prey in the Barn Owl's food composition in the southern part of the Transdanubian region (Horváth *et al.* 2005, Purger 2014, Szép *et al.* 2017). Some studies have also pointed out that this rodent species is rather a supplementary component than a crucial or important alternative prey in the diet of Barn Owls (Ruprecht 1979, Milchev 2015). Moreover it is known that Striped Field Mouse is a well spreading species due to its mobility (Spitzenberger & Engelberger 2014), thus its distribution range has expanded north in the Transdanubian region of Hungary over the last forty years (Bihari 2007) and it was detected in some parts of Austria and Slovakia (Herzig-Straschil 2004, Obuch *et al.* 2016, Tulis *et al.* 2016). Despite the distribution of this species in Slovakia, it did not occur in the diet of the Barn Owl in an intensively used farmland (Veselovský *et al.* 2017). The Striped Field Mouse prefers fields, meadows, wastelands and it is also found in different forests, woodlots patches, in urban and suburban mosaic habitats (Andrzejewski *et al.* 1978, Gliwicz 1980, Liro & Szacki 1987, Kozakiewicz *et al.* 1999, Łopucki *et al*. 2013, Pieniążek *et al*. 2017) and it is well adapted to heterogeneous agricultural landscapes (Gentili *et al*. 2014). Its frequency of occurrence is associated with landscape complexity (Fischer *et al*. 2011). According to our results the greatest proportion of Striped Field Mouse in pellet samples of urban land reflected the relatedness of this species with urban and suburban habitat patches.

We found that the Common Vole was the most abundant prey in each of the landscape types considered, the same predominance having been reported by other studies in central Europe (Goszczyński 1977, Horváth *et al.* 2005, Kitowski 2013, Petrovici *et al.* 2013, Purger 2014, Veselovský *et al.* 2017). Despite this general predominance, the significant heterogeneity of overall proportion values proved that the consumption frequency of common voles was higher in the agricultural than in the urban landscape. As shown by the heterogeneous percent frequency distribution of common voles and total *Microtus* genus among different landscapes, and the higher relative frequency of both prey categories in agricultural lands, our results agree with those reported in other studies conducted in different geographical regions of Europe (Taylor 1994, de la Peña *et al.* 2003, Milchev *et al.* 2006, Milchev 2015, Obuch *et al.* 2016), and in North-America (Smith *et al.* 1972, Colvin & MacLean 1986, Marti 1998, 2010, Hindmarch & Elliott 2015). In contrast, the higher frequency of mice (*Apodemus* or *Mus*) as an alternative prey type was detected principally in European Mediterranean regions (Pezzo & Morimando 1995, Bontzorolos *et al.* 2005, Rodrígez & Peris 2007) while in other studies, the predominance was detected in case of either mice or *Microtus* voles which was the consequence of different prey availability depending on landscape composition and farming practice (Love *et al.* 2000, Bosè & Guidali 2001, Bontzorolos *et al.* 2005). In North-America, Lyman (2012) reported that mice *(Peromyscus)* dominated the agricultural prey fauna, whilst voles (*Microtus* spp.) were the dominant prey group in the pellet samples of non-agricultural lands which was related with the conversion of land use. In addition, Kross *et al.* (2016) found that mice *(Mus, Reithrodontomys)* were the most frequently consumed prey item in the Barn Owl's diet, although voles were consumed by the greatest proportion of nesting pairs. This study pointed out the importance of land use gradient both for pest control and for the breeding success of Barn Owls.

The analysis of the Barn Owl's niche breadth showed that its value at the landscape level was significantly higher in the urban than in the agricultural and mosaic landscapes. Our results are in accordance with other studies conducted in Europe (e.g. Milchev 2015, Veselovský *et al.* 2017), in South-America (Leveau *et al.* 2006, Gonzalez-Fischer *et al.* 2011, Teta *et al.* 2012), and in North-America (Marti *et al.* 1988, 2010) which reported that the dominance of small mammals, particularly the high frequency of an available and profitable prey in the diet, explained the low values of niche breadth. Our results confirmed that the food niche breadth of Barn Owls was significantly higher in an urban landscape, caused by the decrease of predominant *Microtus* voles as main prey items (Hindmarch & Elliott 2015) and by the increase of commensal rodents (rats, house mice) as alternative prey which are associated with human activities (Salvati *et al.* 2002, Teta *et al.* 2012, Hindmarch & Elliott 2015). Hindmarch and Elliott (2015) found that the consumption of predominantly smaller rats increased significantly with increased urbanization within the hunting area of the Barn Owl. Clark and Bunck (1991) pointed out that the increase of these commensal or exotic species' frequency over time indicate the impact of human landscape transformation on the environment of Barn Owls. Despite the different overall niche breadth, based on randomization procedure we detected larger niche overlap between the landscapes considered. This result is consistent with other studies which described very high niche overlap in a comparison of seasons (Pezzo & Morimando 1995), nest sites (Marti 1988, Bosè & Guidali 2001), and subsequent years at the same site (Marti 1988, 2010).

According to our results, the regression analysis between percent frequency of Common Voles and niche breadth proved a significant negative relationship. This result is consistent with other studies according to which the higher frequency of voles (*Microtus* spp.) in the diet affects the evenness component of food-niche, that is, the increase in the frequency of voles leads to a reduction of prey evenness hence to a narrowing of the niche breadth (Marti 1988, 2010, Hindmarch & Elliott 2015, Milchev 2015).

Our findings suggest that the diet composition of Barn Owls, mainly their food-niche pattern, reflected prey availability in the comparison of the studied landscapes, which pointed out that it is necessary to examine the dietary difference of Barn Owls at the finer scale of land use.

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References

Andrzejewski, R., Babińska-Werka, J., Gliwicz, J. & Goszczyński, J. 1978. Synurbization processes in population of *Apodemus agrarius*. I. Characteristics of populations in an urbanization gradient. – Acta Theriologica 23(20): 341–358.

Askew, N. P., Searle, J. B. & Moore, N. P. 2007. Agri-environment schemes and foraging of Barn Owls *Tyto alba*. – Agriculture, Ecosystems & Environment 118(1): 109–114. DOI: 10.1016/j.agee.2006.05.003

Avery, D. M. 1999. A preliminary assessment of the relationship between trophic variability in southern African Barn Owls *Tyto alba* and climate. – Ostrich 70(3–4): 179–186. DOI: 10.1080/00306525.1999.9634232

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

Bihari, Z. 2007. Pirók erdeiegér (*Apodemus agrarius* Pallas, 1771) [Striped Field Mouse *Apodemus agrarius* (Pall.)]. – In: Bihari, Z., Csorba, G. & Heltai, M. (eds.) Magyarország emlőseinek atlasza [Atlas of mammals in Hungary]. – Kossuth Kiadó, Budapest, pp. 179–180.

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): 99–100.

Bosé, M. & Guidali, F. 2001. Seasonal and geographic differences in the diet of the Barn Owl in an agro-ecosystem in northern Italy. – Journal of Raptor Research 35(3): 240–246.

Burel, F., Butet, A., Delettre, Y. R. & de La Peña, N. M. 2004. Differential response of selected taxa to landscape context and agricultural intensification. – Landscape and Urban Planning 67(1–4): 195–204. DOI: 10.1016/S0169-2046(03)00039-2

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

Capizzi, D. & Luiselli, L. 1998. A comparative study of the variability of owl diets in three localities of central Italy. – Revue d'Ecologie (La Terre et la Vie) 53: 367–385.

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

Clark, D. R. & Bunck, C. M. 1991. Trends in North American small mammals found in Common Barn Owl dietary studies. – Canadian Journal of Zoology 69: 3093–3102. DOI: 10.1139/z91-435

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.

Cooke, D., Nagle, A., Smiddy, P., Fairley, J. & Ó Muircheartaigh, I. 1996. The diet of the Barn Owl *Tyto alba* in County Cork in relation to land use. – Biology and Environment 96(2): 97–111.

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

de la Peña, N. M., Butet, A., Delettre, Y., Paillat, G., Morant, P., Le Du, L. & Burel, F. 2003. Response of the small mammal community to changes in western French agricultural landscapes. – Landscape Ecology 18(3): 265–278.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. & Mouquet, N. 2010. Defining and measuring ecological specialization. – Journal of Applied Ecology 47(1): 15–25. DOI: 10.1111/j.1365-2664.2009.01744.x

Fischer, C., Thies, C. & Tscharntke, T. 2011. Small mammals in agricultural landscapes: opposing responses to farming practices and landscape complexity. – Biological Conservation 144(3): 1130–1136. DOI: 10.1016/j.biocon.2010.12.032

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

Gentili, S., Sigura, M. & Bonesi, L. 2014. Decreased small mammals species diversity and increased population abundance along a gradient of agricultural intensification. – Hystrix, the Italian Journal of Mammalogy 25(1): 39–44. DOI: 10.4404/hystrix-25.1-9246

Gliwicz, J. 1980. Ecological aspects of synurbization of Striped Field Mouse *Apodemus agrarius* (Pall.) – Wiadomosci Ekologiczne 26: 185–196.

González-Fischer, C. M., Codesido, M., Teta, P. & Bilenca, D. 2011. Seasonal and geographic variation in the diet of Barn Owls *(Tyto alba)* in temperate agroecosystems of Argentina. – Ornitología Neotropical 22: 295–305.

Goszczyński, J. 1977. Connections between predatory birds and mammals and their prey. – Acta Theriologica 22(30): 399–430.

Gotelli, N. J., Hart, E. M. & Ellison, A. M. 2015. EcoSimR: Null model analysis for ecological data. R Package Version 0.1.0. Available at github. com/gotellilab/EcoSimR. Accessed August, 29, 2017

Heisler, L. M., Somers, C. M. & Poulin, R. G. 2014. Rodent populations on the northern Great Plains respond to weather variation at a landscape scale. – Journal of Mammalogy 95(1): 82–90. DOI: 10.1644/13-MAMM-A-115.1

Herrera, C. M. 1974. Trophic diversity of the Barn Owl *Tyto alba* in continental Western Europe. – Ornis Scandinavica 5(2): 181–191. DOI: 10.2307/3676061

Herrera, C. M. & Hiraldo, F. 1976. Food-niche and trophic relationships among European owls. – Ornis Scandinavica 7(1): 29–41. DOI: 10.2307/3676172

Herrera, C. M. & Jaksić, F. M. 1980. Feeding ecology of the Barn Owl in central Chile and southern Spain: a comparative study. – The Auk 97(4): 760–767.

Herzig-Straschil, B., Bihari, Z. & Spitzenberger, F. 2003. Recent changes in the distribution of the Field Mouse *(Apodemus agrarius)* in the western part of the Carpathian basin. – Annalen des Naturhistorischen Museums in Wien 105B: 421–428.

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

Hindmarch, S., Krebs, E. A., Elliott, J. E. & Green, D. J. 2012. Do landscape features predict the presence of Barn Owls in a changing agricultural landscape? – Landscape and Urban Planning 107(3): 255–262. DOI: 10.1016/j.landurbplan.2012.06.010

Horváth, G. F., 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.

Jaksić, F. M., Seib, R. L. & Herrera, C. M. 1982. Predation by the Barn Owl *(Tyto alba)* in Mediterranean habitats of Chile, Spain and California: A comparative approach. – American Midland Naturalist 107: 151–162. DOI: 10.2307/2425196

Jaksić, F. M. & Delibes, M. 1987. A comparative analysis of food-niche relationships and trophic guild structure in two assemblages of vertebrate predators differing in species richness: causes, correlations, and consequences. – Oecologia 71(3): 461–472. DOI: 10.1007/BF00378722

Jaksić, F. M., Feinsinger, P. & Jiménez, J. E. 1993. A long-term study on the dynamics of guild structure among predatory vertebrates at a semi-arid Neotropical site. – Oikos 67: 87–96. DOI: 10.2307/3545099

Jaksić, F. M., Silva, S. I., Meserve, P. L. & Gutierrez, J. R. 1997. A long-term study of vertebrate predator responses to an El Nino (ENSO) disturbance in western South America. – Oikos 78: 341–354. DOI: 10.2307/3546302

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.

Klein, R. G. & Cruz-Uribe, K. 1984. The analysis of animal bones from archeological sites. – University of Chicago Press, Chicago, IL.

Krebs, C. J. 1999. Ecological Methodology. – Addison Wesley Educational Publishers Inc. Menlo Park, CA.

Kozakiewicz, M., Gortat, T., Kozakiewicz, A. & Barkowska, M. 1999. Effects of habitat fragmentation on four rodent species in a Polish farm landscape. – Landscape Ecology 14(4): 391–400.

Kross, S. M., Bourbour, R. P. & Martinico, B. L. 2016. Agricultural land use, barn owl diet, and vertebrate pest control implications. – Agriculture, Ecosystems & Environment 223: 167–174. DOI: 10.1016/j.agee.2016.03.002

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

Leader, Z., Yom-Tov, Y. & Motro, U. 2010. Diet comparison between two sympatric owls – *Tyto alba* and *Asio Otus* – in the Negev Desert, Israel. – Israel Journal of Ecology & Evolution 56(2): 207–216. DOI: 10.1560/IJEE.56.2.207

Leveau, L. M., Teta, P., Bogdaschewsky, R. & Pardiñas, U. F. 2006. Feeding habits of the Barn Owl *(Tyto alba)* along a longitudinal-latitudinal gradient in central Argentina. – Ornitología Neotropical 17(3): 353–362.

Liro, A., & Szacki, J. 1987. Movements of Field Mice *Apodemus agrarius* (Pallas) in a suburban mosaic of habitats. – Oecologia 74(3): 438–440. DOI: 10.1007/BF00378942

Łopucki, R., Mróz, I., Berliński, Ł. & Burzych, M. 2013. Effects of urbanization on small-mammal communities and the population structure of synurbic species: an example of a medium-sized city. – Canadian Journal of Zoology 91(8): 554–561. DOI: 10.1139/cjz-2012-0168

Lovari, S., Renzoni, A. & R. Fondi 1976. The predatory habits of the Barn Owl (*Tyto alba* Scopoli) in relation to vegetation cover. – Bollettino di Zoologia Italiana 43: 173–191. DOI: 10.1080/11250007609434894

Love, R. A., Webon, C., Glue, D. E. & Harris, S. 2000. Changes in the food of British Barn Owls *(Tyto alba)* between 1974 and 1997. – Mammal Review 30(2): 107–129. DOI: 10.1046/j.1365-2907.2000.00060.x

Lyman, R. L. 2012. Rodent-prey content in long-term samples of Barn Owl *(Tyto alba)* pellets from the northwestern United States reflects local agricultural change. – The American Midland Naturalist 167(1): 150–163. DOI: 10.1674/0003-0031-167.1.150

Macholán, M. 1996. Morphometric analysis of European house mice. – Acta Theriologica 41(3): 255–275.

Marti, C. D. 1974. Feeding ecology of four sympatric owls. – The Condor 76(1): 45–61. DOI: 10.2307/1365983

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. 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

März, R. 1972. Gewöll- und Rupfungskunde [The science of pellets and pluck]. – Akademie Verlag, Berlin (in German)

Massa, C., Teta, P. & Cueto, G. R. 2014. Effects of regional context and landscape composition on diversity and composition of small rodent assemblages in Argentinian temperate grasslands and wetlands. – Mammalia 78(3): 371–382. DOI: 10.1071/AM08115

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

Milana, G., Lai, M., Maiorano, L., Luiselli, L. & Amori, G. 2016. Geographic patterns of predator niche breadth and prey species richness. – Ecological Research 31(1): 111–115. DOI 10.1007/s11284-015-1319-6

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.

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. 2016. Dietary comparison of coexisting Barn Owl *(Tyto alba)* and Eagle Owl *(Bubo bubo)* during consecutive breeding seasons. – Animal Biology 66(2): 219–228. DOI: 10.1163/15707563-00002499

Obuch, J., Danko, Š. & Noga, M. 2016. Recent and subrecent diet of the Barn Owl *(Tyto alba)* in Slovakia. – Slovak Raptor Journal 10(1): 1–50. DOI: 10.1515/srj-2016-0003

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

Petrovici, M., Molnar, 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

Pianka, E. R. 1974. Niche overlap and diffuse competition. – Proceedings of the National Academy of Sciences 71(5): 2141–2145.

Pieniążek, A., Sokół, M. & Kozakiewicz, M. 2017. Ecological characteristics of two closely related rodent species in urban environment –Permanent inhabitant vs newcomer. – Natural Resources 8(2): 69–80. DOI: 10.4236/nr.2017.82005

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.

R Development Core Team 2016. R: A Language and Environment for Statistical Computing. – R Foundation for Statistical Computing, Vienna

Rodríguez, C. & Peris, S. J. 2007. Habitat associations of small mammals in farmed landscapes: implications for agri-environmental schemes. – Animal Biology 57(3): 301–314. DOI: 10.1163/157075607781753092

Ruprecht, A. L. 1979. Food of the Barn Owl, *Tyto alba guttata* (CL Br.) from Kujawy. – Acta Ornithologica 16(19): 493–511.

Sahores, M. & Trejo, A. 2004. Diet shift of Barn Owls *(Tyto alba)* after natural fires in Patagonia, Argentina. – Journal of Raptor Research 38: 174–177. DOI: 10.3356/0892-1016(2007)41[277:FHOBOA]2.0.CO;2

Salvati, L., Manganaro, A. & Ranazzi, L. 2002. Aspects of the ecology of the Barn Owl *Tyto alba* breeding in a Mediterranean area. – Bird Study 49(2): 186–189. DOI: 10.1080/00063650209461264

Smith, D. G., Wilson, C. R. & Frost, H. H. 1972. Seasonal food habits of Barn Owls in Utah. – The Great Basin Naturalist 32: 229–234.

Smith, E. P. 1982. Niche breadth, resource availability, and inference. – Ecology 63(6): 1675–1681.

Sokal, R. R. & Rohlf, F. J. 1995. The principles and practice of statistics in biological research. – W. H. Freeman and Company, New York, NY.

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

Spitzenberger, F. & Engelberger, S. 2014. A new look at the dynamic western distribution border of *Apodemus agrarius* in Central Europe (Rodentia: Muridae). – Lynx Nova 45: 69–79.

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

Teta, P., Hercolini, C. & Cueto, G. 2012. Variation in the diet of Western Barn Owls *(Tyto alba)* along an urban-rural gradient. – The Wilson Journal of Ornithology 124(3): 589–596. DOI: 10.1676/11-173.1

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

Trejo, A. & Lambertucci, S. 2007. Feeding habits of Barn Owls along a vegetative gradient in northern Patagonia. – Journal of Raptor Research 41(4): 277–287. DOI: 10.3356/0892-1016(2007)41[277:FHOBOA]2.0.CO;2

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-2015-00

Tulis, F., Ambros, M., Baláz, I., Ziak, D., Sládkovicová, V. H., Miklós, P., Dudich, A., Stollmann, A., Klimant, P., Somogyi, B. & Horváth, G. 2016. Expansion of the Striped field Mouse *(Apodemus agrarius)* in the south-western Slovakia during 2010–2015. – Folia Oecologica 43(1): 64–72.

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

Yalden, D. W. & Morris, P. A. 1990. Owl pellet analysis. – The Mammal Society, London

Yalden, D. W. 1977. Identification of remains in owl pellets. – The Mammal Society, London

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Analysis of skull morphometric characters in Owls (Strigiformes)

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Abstract Owls (Strigiformes) are small to large birds, mostly solitary and nocturnal predators. They can be found all around the Earth except Antarctica and some remote islands. The species differ in size, diet and habitat, which led to different morphological adaptations of the skull. The main differences are in the *orbital* and the *otical* region, which are connected to the visual and hearing capabilities. The aim of the recent study is to increase our knowledge of the relationship between skull shape and foraging habits and tried to find those characters that are related to diet. A geometric morphometric approach was used to analyse two-dimensional cranial landmarks. We used principal component (PC) analyses on measurements that may be related to visual and hearing abilities. The PCs are resulted in the robusticity of the skull and the asymmetry of the *otical* region. There are differences in position and shape of postorbital processes (POP) and *tympanic* wings (TW). Species with symmetrical skull shape are basically crepuscular or diurnal predators and species with more asymmetrical skulls are mostly nocturnal hunters and have better hearing capabilities.

Keywords: cranial morphology, morphometrics, anatomy, nocturnal predator, prey preference

Összefoglalás A baglyok közé (Strigiformes) kis- és nagytestű fajok egyaránt tartoznak. Többnyire magányos éjszakai ragadozók. Világszerte megtalálhatóak az Antarktisz és néhány távoli sziget kivételével. A fajok különböznek méretüket, táplálékbázisukat és táplálékszerzésüket tekintve, mindezek a koponyán is morfológiai adaptációt mutatnak. A legfőbb különbségek az orbitalis és oticalis régióhoz köthetők, amelyek elsősorban látással és hallással kapcsolatos képességekkel mutatnak összefüggést. Jelen cikkben a baglyok cranialis jegyeinek elemzésével a táplálékpreferencia, a táplálékszerzés és a morfológiai jellemzők közötti lehetséges kapcsolatokat kerestük. A craniomorfometriai vizsgálat során kétdimenziós landmarkok használatával főkomponens-analíziseket végeztünk. A főkomponensek a koponya robuszticitásával és a koponya oticalis régiójának aszimmetriájával hozhatók kapcsolatba. Különbségek vannak a *processus postorbitalis*ok (POP) és halántékcsont *tympanicus* nyúlványainak (TW) helyzetében és alakjában. Azok a fajok, amelyek szimmetrikus koponyával rendelkeznek, többnyire nappali vagy alkonyati ragadozók, szemben az aszimmetrikus koponyájú fajokkal, amelyek leginkább éjszaka aktívak és jobb hallási képességekkel rendelkeznek.

Kulcsszavak: koponya-sajátosságok, morfometria, anatómia, éjszakai ragadozó, táplálék-összetétel, táplálékpreferencia

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Introduction

Owls are small to large predators; mostly solitary and nocturnal or crepuscular. The group is globally distributed, except the Antarctica and some remote islands. The order Strigiformes is divided into 2 families, Tytonidae (barn owls and allies) and Strigidae (true owls) (Cramp 1978). Owls are sharing similar anatomical characteristics with the diurnal raptors like sharp hooked beak and talons. Due to these similarities owls were closely related to falcons (Cracraft 1981), but some authors supported the view, that these birds are closer relatives of nightjars (Caprimulgiformes) (Mayr & Amadon 1951, Sibley & Ahlquist 1990). Recent studies have provided good evidence, that diurnal raptors are closer relatives of owls than nightjars (Ericson *et al.* 2006, Hackett *et al.* 2008, Wink *et al.* 2009, Brusatte *et al.* 2015). The anatomical similarities between owls and nightjars are probably influenced by convergence (Feduccia 1996).

The barn owls (Tytonidae) comprise 2 extant genera around 20 species (Aliabadian *et al.* 2016, Uva *et al.* 2018), the true owls (Strigidae) comprise around 190 species in 25 genera (Wink *et al.* 2008).

Features are common to both families. Eyes directed forwards. Bills hooked as in Falconiformes, but directed more downwards. Base of bill with soft cere is similar to Falconiformes, but covered by bristles projecting laterally from base of bill. Outer toe is reversible, but directed laterally at rest. In some species, erectile ear-like tufts of feathers are visible on forehead (Cramp 1978). Owls are generally active at night and have a highly developed auditory system. The ears are covered by the feathers of the facial disc. Some species have asymmetrically set ear openings and a very pronounced facial disc, guiding sounds into the ear openings. The shape of the disc can be modulated with special facial muscles. The bill is pointed downward, increasing the surface area over which the soundwaves are collected by the facial disc (Nishikawa 2002). The translation of left, right, up and down signals are combined in the brain, and create an image of the space where the sound source is located. Studies of owl brains have revealed that the *medulla* is more complex than in other birds (Dyson *et al.* 1998). These factors have strong effect on the skeletal structure of the head.

In most avian lineages, male-male competition for females has led to an increase in male size due to sexual selection, therefore the males are larger than females (Andersson 1994, Colwell 2000). However, in some groups like raptors and owls, reversed size dimorphism exists, which means that females are the larger sex (Mueller 1990, Owens & Hartley 1998). In owls, the results showed clear parallels. Reversed sexual dimorphism (RSD) increases with prey size, consistent with the small-male hypothesis. Evolutionary pathway analysis suggests that RSD in owls has most likely evolved before specialisation on large prey, so a small and more agile male might be advantageous even when hunting small prey. These results suggest that RSD in owls evolved due to natural-selection pressures rather than sexual-selection pressures (Krüger 2005). The intrasexual dimorphism is visible in the case of number of vertebrate taxa. However, morphological differences in shape between males and females are undetectable (Verwaijen *et al.* 2002).

In the recent study, our objective was to increase our knowledge on the relationship between skull shape and foraging habits, and to find those characters that are related to diet.

Materials and methods

Specimens

This study is based on 42 skulls of 25 species *(Table 1)*. All skulls are from adult specimens and belonging to the collection of Eötvös Loránd University (Budapest, Hungary), the collection of the Hungarian Natural History Museum and the digital archive of Wageningen University (Wageningen, Netherlands). No birds has been killed to get its skull, all birds died of natural causes or accidental or died in captivity.

Table 1. List of owl species examined in this study
1. táblázat A vizsgálatban szereplő bagolyfajok

Scientific name	Common name	n	Abbrevation
Aegolius funereus	Tengmalm's Owl	1	aegfun
Asio capensis	African Marsh Owl	1	asicap
Asio flammeus	Short-eared Owl	3	asifla
Asio otus	Long-eared Owl	3	asiotu
Athene brama	Spotted Owlet	1	athbra
Athene cunicularia	Burrowing Owl	1	athcun
Athene noctua	Little Owl	4	athnoc
Bubo africanus	Spotted Eagle Owl	1	bubafr
Bubo bubo	Eagle Owl	3	bubbub
Bubo virginianus	Great Horned Owl	1	bubvir
Glaucidium brasilianum	Ferruginous Pygmy Owl	1	glabra
Glaucidium passerinum	Eurasian Pygmy Owl	1	glapas
Glaucidium perlatum	Pearl-spotted Owlet	1	glaper
Bubo scandiaca	Snowy Owl	2	bubsca
Otus asio	Eastern Screech Owl	1	otuasi
Otus brucei	Striated Scops Owl	1	otubru
Otus kennikottii	Western Screech Owl	1	otuken
Otus leucotis	White-faced Scops Owl	1	otuleu
Otus scops	Eurasian Scops Owl	3	otusco
Strix aluco	Tawny Owl	4	stralu
Strix nebulosa	Great Grey Owl	1	strneb
Strix uralensis	Ural Owl	3	strura
Strix varia	Barred Owl	1	strvar
Surnia ulula	Northern Hawk Owl	1	surulu
Tyto alba	Barn Owl	2	tytalb

Groups and diet

Before the analyses, we created three groups, which represent the following diet categories (Earhart & Johnson 1970). The present study seeks to test also that the different prey preference may have effect on skull morphology.

- A: feeds primarily on arthropods, for example Eurasian Scops Owl *(Otus scops)* (Kadochnikov 1963, Galeotti & Sacchi 2001, Lee & Severinghaus 2004)
- B: species feed on arthropods and vertebrates, for example Little Owl *(Athene noctua)* (Glue & Scott 1980, Laursen 1981, Hounsome *et al.* 2004, Šálek *et al.* 2013, Hámori *et al.* 2017), Northern Hawk Owl *(Surnia ulula)* (Nybo & Sonerud 1990, Sonerud 1986, 1992).
- C: feeds exclusively on vertebrates, for example Great Eagle Owl *(Bubo bubo)* (Papageorgiou *et al.* 1993, Penteriani *et al.* 2002, Milchev & Spassov 2017), Barn Owl *(Tyto alba)* (Milchev 2015, Horváth *et al.* 2018)

Landmarks and procedures

The variation of strigiform cranial morphology is analysed using landmark-based geometric morphometry. In our former study, we used conventional morphometric variables which were selected *a priori* (Pecsics *et al.* 2017), however in this case (although the landmarks) the meaningful variables are discovered by the analysis. We do not need to decide among them before the analysis. We tried to choose the landmarks for this analysis to cover the geometric form of the skull. The landmarks should provide a comprehensive sampling of morphology that the features of biological significance can be discovered. The discrete and obvious anatomical characters are ideal landmarks, do not alter their topological positions relative to other landmarks, provide adequate coverage of the morphology and can be found repeatedly and reliably (Zelditch *et al.* 2004). The landmarks were taken from high resolution (1200×1600 pixels) photos. We took 2 photographs from each specimen (lateral and dorsal) with closed jaws. Images were standardised for the *foramen magnum occipitale* and the

Table 2. Number and description of landmarks. Terminology according to (Baumel *et al.* 1993)

2. táblázat Az egyes landmarkok száma és leírása. Terminológia Baumel *et al.* (1993) alapján

Number of landmark	Description of landmark
1	tip of the maxilla
2	upper point of the left nostril
3	upper point of the right nostril
4	connection of maxilla and frontale
5	upper point of the right orbital margin
6	upper point of the left orbital margin
7	tip of the right postorbital process
8	tip of the left postorbital process
9	inner point of the right postorbital process
10	inner point of the left postorbital process
11	tip of right tympanic wing
12	tip of left tympanic wing
13	basal point of the right tympanic wing
14	basal point of the left tympanic wing
15	lowest point of the occipital bone

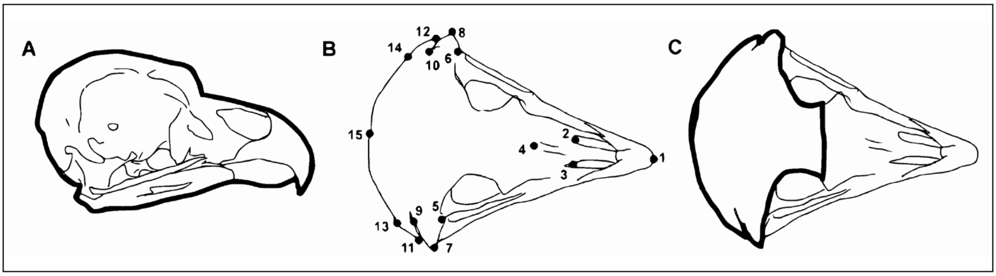

Figure 1. Position and number of landmarks. A: whole skull shape in lateral view, B: fixed landmarks in dorsal view (numbers correspond to *Table 2*), C: the shape of the neurocranium behind the lacrimal bones in lateral view

1. ábra A vizsgálatban használt landmarkok száma és pozíciója. A: a teljes koponya oldalnézetből, B: fix landmarkok felülnézetből (a számok megnevezését lásd a 2. táblázatban), C: az agykoponya könnycsontok mögötti része felülnézetből

tip of the beak. We investigated the repeatability of the measurements by Speraman's correlation. The test was between two separate digital measures performed on skull photos (n = 20). For each specimen 15 fixed landmarks *(Table 2)* were recorded in dorsal view and we used 1000 sliding landmarks to examine the shape of the neurocranium in dorsal view and the shape of the whole skull in lateral view *(Figure 1)*. These landmarks were allowed to slide along their corresponding curve, which is necessary in the case of the minimalisation of the bending energy. The coordinates of the landmarks were digitised using TpsDig 2.16 software (Rohlf 2010). The coordinates were transformed using the Procrustes superimposition method. The consensus configurations and relative warps were conducted. Variability in shape was assessed using the scores obtained for each individual on the first two relative warps. We conducted principal component analyses (PCA) on these morphological variables. The relative warps are corresponding to the principal components (PCs) and define the shape space in which individuals are replaced. We used PAST v.1.7 software (Hammer *et al.* 2001) for principal component analysis and to extract deformation grids. We only considered those PCs which are explaining individually >10% of the variance.

Results

Our measures were highly significant irrespective of measuring mode (all $r > 0.98$, all $P < 0.00001$).

The first analysis focused on the whole skull from lateral view *(Figure 2)*. We used sliding landmarks (1000) to describe the shape. The first two PCs explained 49% and 15% of the variance in skull shape. The first PC axis described the relative height of the skull and the roundness of the frontal bone (PC1). The second PC axis described the relative highness of the beak (PC2). The shape of the skull of Barn Owl was found different from that species.

During the second analysis we used 15 fixed landmarks recorded in dorsal view. The first three PCs explained 44%, 15%, and 10% of the variance in shape *(Figure 3)*. The first and second PC axes described variation in the relative distances of the temporal wing (PC1), and

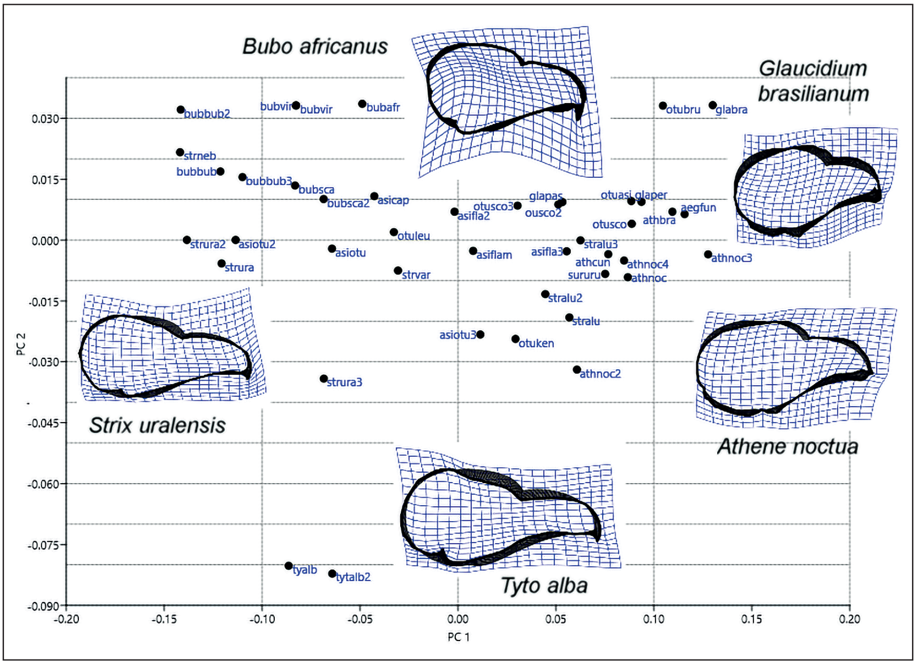

Figure 2. Graphical output of PCA performed on the two-dimensional landmark data (lateral view). PC1–PC2 biplot. The first PC axis described the relative height of the skull and the roundness of the frontal bone (PC1). The second PC axis described the relative highness of the beak (PC2). Thick black areas are showing the differences compared to the computer generated mean shape

2. ábra A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (oldalnézet). Az első főtengely a koponya relatív magasságát és a homlokcsont domborúságát magyarázza (PC1). A második főtengely a csőr relatív magasságával hozható kapcsolatba (PC2). A fekete vastagított terület a komputergenerált átlagformától való eltérést mutatja

the relative orientation at the tip (PC2) compared to the *postorbital processes*. The third PC axis described differences in the distance of the tip of the beak (results not shown). In dorsal view, the Little Owl and the Northern Hawk-Owl showed symmetrical shape. Species like Short-eared Owl and Tawny Owl have moderate, the Boreal Owl has extremely asymmetrical shape *(Figure 3, 4)*.

The third analysis tried to describe the shape of the *neurocranium* in dorsal view. The first three PCs explained 49%, 24% and 12% of the variance in shape. The first PC axis described variation in the relative size and position (PC1) and the second reflected to the asymmetry of the otical region (PC2). The third PC axis described differences in the curvature of the occipital region (results not shown) *(Figure 4)*. The analysis showed that *Strix* species differ considerably in their degree of asymmetry *(Figure 6)*.

We tried to identify the differences between the diet categories *(Figure 5)*. Larger species *(Bubo bubo, Strix uralensis)* are usually feeding primarily on vertebrates and having bigger beaks, lesser species *(Athene noctua, Otus kennikotti)* with smaller beaks feed more on smaller prey.

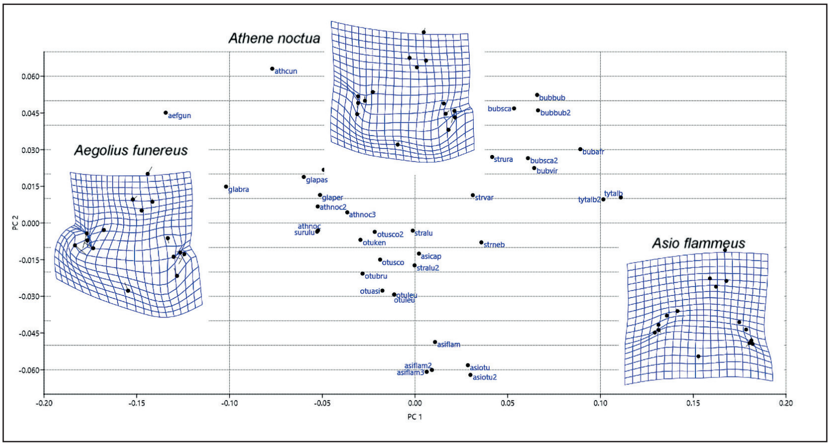

Figure 3. Graphical output of PCA performed on the two-dimensional landmark data (dorsal view). PC1–PC2 biplot. PC axes described variation in the relative distances of the temporal wing (PC1), and the relative orientation at the tip (PC2) compared to the postorbital processes

3. ábra A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (felülnézet). Az első főtengely (PC1) a halántékcsont *tympanicus* nyúlványainak (TW) relatív távolságát, a második főtengely a *processus postorbitalis*ok (POP) végeinek relatív helyzetét magyarázza

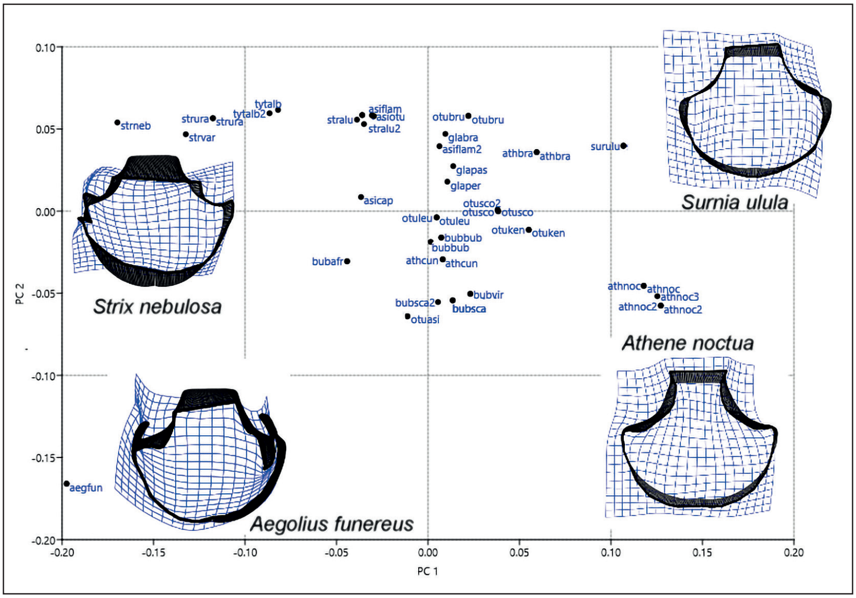

Figure 4. Graphical output of PCA performed on the two-dimensional landmark data (dorsal view). PC1–PC2 biplot. This analysis tried to describe the shape of the neurocranium in dorsal view. PC axes described the variation in the relative size and position (PC1) and reflected to the asymmetry of the *otical* region (PC2). Thick black areas are showing the differences compared to the computer generated mean shape

4. ábra A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (felülnézet). A PC tengelyek az *oticalis* régió relatív nagyságát és helyzetét (PC1) valamint annak aszimmetriája mértékét (PC2) mutatják. A fekete vastagított terület a komputergenerált átlagformától való eltérést mutatja

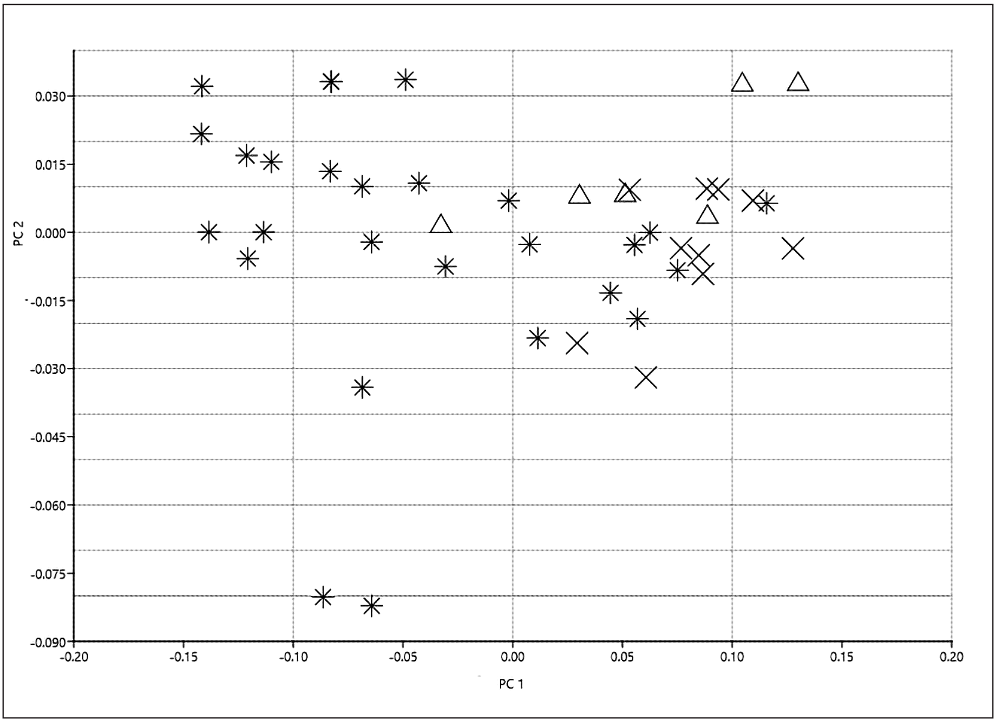

Figure 5. The species of different diet categories combined with the cranial shape in lateral view. X: feeds primarily on arthropods, Δ: species feed on arthropods and vertebrates, *: feeds exclusively on vertebrates

5. ábra Kombinált ábra az egyes fajok oldalnézeti koponyaalakja és a táplálékbázisa alapján. X: elsődlegesen ízeltlábúakat fogyasztók, Δ: ízeltlábúakat és gerinceseket is fogyasztók, *: gerinceseket fogyasztók

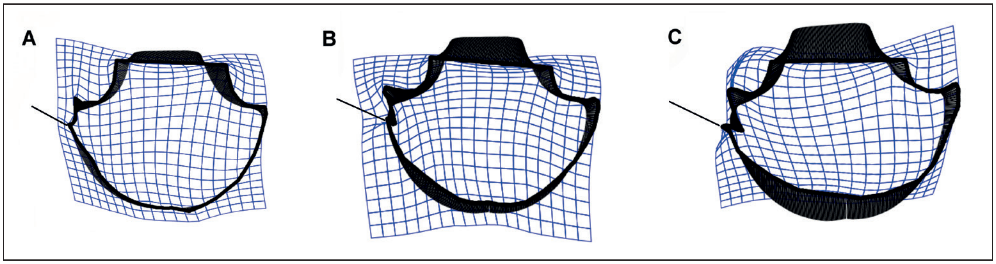

Figure 6. Various *Strix* species differ considerably in their degree of asymmetry. A: Tawny Owl *(Strix aluco)*, B: Ural Owl *(Strix uralensis)*, C: Great Grey Owl *(Strix nebulosa)*

6. ábra Az egyes *Strix* fajok különböznek az aszimmetria mértékében. A: Macskabagoly *(Strix aluco)*, B: Uráli bagoly *(Strix uralensis)*, C: Szakállas bagoly *(Strix nebulosa)*

Discussion

We found that in the lateral view there are differences in the shape of the frontal and the occipital bone. The shape of the skull of Barn Owl was found to be markedly different from that other owl species, probably due to the phylogenetic distance. The main differences are in the relative height of the skull and the curvature of the frontal bone and the relative height and length of the beak. Owls swallow the prey animal whole but larger prey size demands stronger beaks and use their feet to tear apart their prey, then they swallow the pieces bit by bit. Larger species have longer beaks compared to the *neurocranium*. The allometric head growth reflected in variation in head length can explain some of the observed differences between various species because the smaller species usually have more paedomorphic attributes. Allometric patterns within populations do not necessarily parallel interspecific allometry (Grant *et al.* 1985). The skull of the owls is *desmognathous* and *holorhinal,* which means that the maxilla-palatine bones united and the anterior border of the nasal bones not deeply cleft. The occipital condyle is sessile and the plane of the occipital foramen looks directly downwards, forming a very oblique angle with the *basicranial* axis. In some species of eagle owls *(Bubo)* the crest folded back upon itself into a narrow loop. The lambdoidal ridge well presented in eared owls *(Asio),* and the roof of the skull in most of the owls differs from the eared owls due to the excessive development of spongy pneumatic tissue (Pycraft 1902). The species of *Asio* have a very distinctive cranial morphology owing primarily to the large, semi-vertical, flattened surfaces of the cranium above and behind the orbits (Olson 1995). Possibly the dimensions of the lower jaw are showing that there are differences in bite performance between the species. Owls with symmetric skull structure may have stronger adductor muscles. Larger species are usually feeding exclusively or primarily on vertebrates, lesser species with smaller beaks feed more or only on arthropods. We found exceptions like the Boreal Owl *(Aegolius funereus)* and the Eurasian Pygmy Owl *(Gaucidium passerinum)*.

The owls have generally good eyesight, which allows detecting the prey in low light and poor sighting conditions but these creatures are the most specialized birds for hearing. Many species are remarkable for the bilateral asymmetry of the ears. These attributes are linked to a highly developed sense of directional hearing (Coles *et al.* 1989). However, the differences are represented by different tissues of the head (feathers, earflaps, ear holes, etc.), ear asymmetry basically caused by cranial structures only, confined here the entirely to the different positions and orientations of the *squamoso-occipital* wing on both sides. Ear morphology is rather uniform among species but different in structure and geometry between groups. It is possible that the ear asymmetry has evolved independently at few times among owls (Norberg 1977). The symmetrical ears are representing a most basal form and cranial structure (Nishikawa 2002). Owls with asymmetrical ears can determine the horizontal and vertical direction of a sound, separately, since the time of arrival of the sound differ compare to the ears. This attribute allows localising the sound without head tilting (Newton 2002). A comparative study of location abilities between species with asymmetrical ears *(Asio otus, Tyto alba)* and symmetrical ears *(Athene cunicularia, Bubo virginianus)* has shown that the latter species accurate locate sources of sound in the horizontal plane only, while species with asymmetrical ears also localise sound vertically (Volman & Konishi 1990). Symmetrical and relatively narrow earholes are present in *Otus scops*, *Surnia ulula* and *Athene noctua* (Voous 1988) and the asymmetry well presented by the species *Tyto alba* and *Aegolis funereus* (Norberg 1978, Nishikawa 2002). The great hearing abilities led the birds to be acoustic hunters. The birds with less sensitive hearing are using usually their eyes as visual hunters (Mikkola 2014).

Species with northern distribution should spend more time in darkness both daily and yearly, e.g. the Tawny Owl *(Strix aluco)*, Ural Owl *(Strix uralensis)* (Goffette *et al*. 2016) and the Great Gray Owl *(Strix nebulosa)* (Del Hoyo *et al*. 1999, Mysterud 2016). Various *Strix* species differ considerably in their degree of asymmetry (Derlink *et al.* 2018). This suggests that selection pressure may differ among species, or may target different aspects of the hearing system. Modification of the tympanic wing affects the configuration of the temporal portion of the adductor muscles. The morphological change in the external ear and adductor muscle of owls are lesser known. Changes in the adductor muscle may be non-adaptive, and explainable mainly as side effects of evolutionary experimentation in the external ear (Holland 1993).

Species with large distribution, such as Barn Owl, have similar diet composition and similar preference in prey size in different regions. It was investigated in the Nearctic (Marti 1988, 2010) and Palearctic range (Bernard *et al.* 2010). Due to the similar prey consumption, differences in cranial morphology are not presented.

Future studies should further examine which proximate factors determine intraspecific and intersexual differences on skull (Tornberg *et al.* 2016). We can have the question, why species and subspecies differ in the degree of sexual dimorphism in different environments (McGillivray 1989). Due to the RSD, the females are usually larger than males, therefore their head is larger. Head size alone does not explain the sexual dimorphism in possibly different prey preference, assuming that other factors may be involved. Results suggest once more that foraging habits deserves closer attention. The dietary data also suggest strong implications for different prey preference in males. Male owls possibly eat smaller, softer, and less evasive prey than do females, and the electivity analyses implicate that they achieve this by actively selecting such prey types, and may thus potentially avoid competition of the males and females (Pérez-Camacho *et al.* 2015). In some cases, the similarities in the skull shape reflect the phylogenetic connection. In this study, we did not investigate the effect of phylogeny and the similarities due to phylogeny. The phylogenetic control would be necessary in further analyses.

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References

Andersson, M. 1994. Sexual Selection. – Princeton University Press, Princeton, NJ.

Baumel, J. J. 1993. Handbook of avian anatomy: Nomina Anatomica Avium. – Publications of the Nuttall Ornithological Club (USA). no. 23.

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

Brusatte, S. L., O'Connor, J. K. & Jarvis, E. D. 2015. The origin and diversification of birds. – Current Biology 25(19): R888–R898. DOI: 10.1016/j.cub.2015.08.003

Cramp, S. 1978. The Birds of the Western Palearctic, Vol. 1. Ostrich to Ducks. – Oxford University Press, Oxford

Coles, R. B., Guppy, A., Anderson, M. E. & Schlegel, P. 1989. Frequency sensitivity and directional hearing in the Gleaning Bat, *Plecotus auritus* (Linnaeus 1758). – Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 165(2): 269–280.

Colwell, R. K. 2000. Rensch's rule crosses the line: convergent allometry of sexual size dimorphism in hummingbirds and flower mites. – American Naturalist 156: 495–510. DOI: 10.1086/303406

Cracraft, J. 1981. Towards a phylogenetic classification of recent birds of the world (class Aves). – Auk 98: 681–714.

del Hoyo, J., Elliott, A. & Sargatal, J. (eds.) 1999. Handbook of the Birds of the World, Vol. 5. Barn-owls to Hummingbirds. – Lynx Edicions, Barcelona

Derlink, M., Wernham, C., Bertoncelj, I., Kovács, A., Saurola, P., Duke, G. & Vrezec, A. 2018. A review of raptor and owl monitoring activity across Europe: its implications for capacity building towards pan-European monitoring. – Bird Study DOI: 10.1080/00063657.2018.1447546

Dyson, M. L., Klump, G. M. & Gauger, B. 1998. Absolute hearing thresholds and critical masking ratios in the European Barn Owl: a comparison with other owls. – Journal of Comparative Physiology A 182(5): 695–702.

Ericson, P. G. P., Anderson, C. L., Britton, T., Elzanowski, A., Johansson, U., Källersjö, M., Ohlson, J. I., Parsons, T. J., Zuccon, D. & Mayr, G. 2006. Diversification of neoaves: integration of molecular sequence data and fossils. – Biological Letters 2: 543–547. DOI: 10.1098/rsbl.2006.0523

Feduccia, A. 1996. The origins and evolution of birds. – Yale University Press, New Haven

Galeotti, P. & Sacchi, R. 2001. Turnover of territorial Scops Owls *Otus scops* as estimated by spectrographic analyses of male hoots. – Journal of Avian Biology 32(3): 256–262. DOI: 10.1111/j.0908-8857.2001.320308.x

Glue, D. & Scott, D. 1980. Breeding biology of the Little Owl. – British Birds 73(1): 167–180.

Goffette, Q., Denis, M., Pöllath, N. & Van Neer, W. 2016. Change in historical range of the Ural Owl in Europe. – Belgian Journal of Zoology 146(1): 33–43.

Grant, P. R., Abbott, I., Schluter, D., Curry, R. L. & Abbott, L. K. 1985. Variation in the size and shape of Darwin's finches. – Biological Journal of the Linnean Society 25(1): 1–39. DOI: 10.1111/j.1095-8312.1985.tb00384.x

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

Hámori, D., Winkler, D. & Vadász, Cs. 2017. Demographic data on the Little Owl *(Athene noctua)* in Upper-Kiskunság (Hungary). – Ornis Hungarica 25(2): 11–22. DOI: 10.1515/orhu-2017-0012

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K-L., Harshman, J., Huddleston, Ch. J., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W., Witt, Ch. C. & Yuri, T. 2008. A phylogenomic study of birds reveals their evolutionary history. – Science 320: 1763–1768. DOI: 10.1126/science.1157704

Holland, P. W. 1993. Avian skull. – In: Hanken, J. & Hall, B. K. (eds.) The Skull, Vol. 2. Patterns of Structural and Systematic Diversity. – University of Chicago Press, Chicago

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

Hounsome, T., O'Mahony, D. & Delahay, R. 2004. The diet of Little Owls *Athene noctua* in Gloucestershire, England. – Bird Study 51(3): 282–284. DOI: 10.1080/00063650409461366

Kadochnikov, N. 1963. On the breeding biology of the Scops Owl in the Voronezh province. – Ornitologia 6: 104–110.

Krüger, O. 2005. The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. – Evolutionary Ecology 19(5): 467–486. DOI: 10.1007/s10682-005-0293-9

Laursen, J. T. 1981. Prey of the Little Owl *(Athene noctua),* East Jutland (Denmark). – Danish Ornithological Society Magazine 75(3–4): 105–110.

Lee, Y. F. & Severinghaus, L. L. 2004. Sexual and seasonal differences in the diet of Lanyu Scops Owls based on fecal analysis. – Journal of Wildlife Management 68(2): 299–306. DOI: 10.2193/0022-541X(2004)068[0299:SASDIT]2.0.CO;2

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. 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

Mayr, E. & Amadon, D. 1951. A classification of recent birds. – American Museum Novitates, American Museum of Natural History City of New York

McGillivray, W. B. 1989. Geographic variation in size and reverse size dimorphism of the Great Horned Owl in North America. – Condor 91(4): 777–786. DOI: 10.2307/1368060

Mikkola, H. 2014. Owls of the World – A Photographic Guide, 2nd edition. – Firefly Books Ltd., Buffalo, New York

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. & Spassov, N. 2017. First evidence for carrion-feeding of Eurasian Eagle-owl *(Bubo bubo)* in Bulgaria. – Ornis Hungarica 25(1): 58–69. DOI: 10.1515/orhu-2017-0005

Mueller, H. C. 1990. The evolution of reversed sexual dimorphism in size in monogamous species of birds. – Biological Reviews 65: 553–585. DOI: 10.1111/j.1469-185X.1990.tb01238.x

Mysterud, I. 2016. Range extensions of some boreal owl species: comments on snow cover, ice crusts, and climate change. – Arctic, Antarctic, and Alpine Research 48(1): 213–219. DOI: 10.1657/AAAR0015-041

Newton, I. (ed.) 2002. Ecology and conservation of owls. – Csiro Publishing, Collingwood, Victoria, Australia

Nishikawa, K. C. 2002. Evolutionary convergence in nervous systems: insights from comparative phylogenetic studies. – Brain, Behavior and Evolution 59(5–6): 240–249. DOI: 10.1159/000063561

Norberg, R. Å. 1977. Occurrence and independent evolution of bilateral ear asymmetry in owls and implications on owl taxonomy. – Philosophical Transactions of the Royal Society of London B: Biological Sciences 280(973): 375–408. DOI: 10.1098/rstb.1977.0116

Norberg, R. Å. 1978. Skull asymmetry, ear structure and function, and auditory localization in Tengmalm's Owl, *Aegolius funereus* (Linné). – Philosophical Transactions of the Royal Society of London B: Biological Sciences 282(991): 325–410. DOI: 10.1098/rstb.1978.0014

Nybo, J. O. & Sonerud, G. A. 1990. Seasonal changes in diet of Hawk Owls *Surnia ulula*: importance of snow cover. – Ornis Fennica 67: 45–51.

Olson, S. L. 1995. The genera of owls in the Asioninae. – Bulletin of the British Ornithologists' Club 115(1): 35–39.

Owens, I. P. F. & Hartley, I. R. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? – Proceedings of the Royal Society B 265: 397–407. DOI: 10.1098/rspb.1998.0308

Papageorgiou, N. K., Vlachos, C. G. & Bakaloudis, D. E. 1993. Diet and nest site characteristics of Eagle Owl *(Bubo bubo)* breeding in two different habitats in north-eastern Greece. – Avocetta 17(1): 49–54.

Pecsics, T., Laczi, M., Nagy, G. & Csörgő, T. 2017. The cranial morphometrics of the wildfowl (Anatidae). – Ornis Hungarica 25(1): 44–57. DOI: 10.1515/orhu-2017-0004

Penteriani, V., Gallardo, M. & Roche, P. 2002. Landscape structure and food supply affect Eagle Owl *(Bubo bubo)* density and breeding performance: a case of intra-population heterogeneity. – Journal of Zoology 257(3): 365–372. DOI: 10.1017/S0952836902000961

Pérez-Camacho, L., García-Salgado, G., Rebollo, S., Martínez-Hesterkamp, S. & Fernández-Pereira, J. M. 2015. Higher reproductive success of small males and greater recruitment of large females may explain strong reversed sexual dimorphism (RSD) in the Northern Goshawk. – Oecologia 177(2): 379–387. DOI: 10.1007/s00442-014-3146-9

Pycraft, W. P. 1902. Contributions to the osteology of birds. Part II. Strigiiformes. – Proceedings of the Zoological Society of London 20:1–46.

Rohlf, F. J. 2010. TpsDig, version 2.16. – Department of Ecology and Evolution, State University of New York, Stony Brook, USA

Šálek, M., Chrenkova, M. & Kipson, M. 2013. High population density of Little Owl *(Athene noctua)* in Hortobagy National Park, Hungary, Central Europe. – Polish Journal of Ecology 61(1): 165–169.

Sibley, C. G. & Ahlquist, J. E. 1990. Phylogeny and classification of birds: a study in molecular evolution. – Yale University Press

Sonerud, G. A. 1986. Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. – Ecography 9(1): 33–47. DOI: 10.1111/j.1600-0587.1986.tb01189.x

Sonerud, G. A. 1992. Search tactics of a pause-travel predator: adaptive adjustments of perching times and move distances by Hawk Owls *(Surnia ulula)*. – Behavioral Ecology and Sociobiology 30(3–4): 207–217.

Tornberg, R., Mikkola, H. & Rytkönen, S. 2016. Morphometric sex determination of Great Grey Owls *Strix nebulosa*. – Ornis Norvegica 39: 6–10. DOI: 10.15845/on.v39i0.991

Uva, V., Päckert, M., Cibois, A., Fumagalli, L. & Roulin, A. 2018. Comprehensive molecular phylogeny of barn owls and relatives (Family: Tytonidae), and their six major Pleistocene radiations. – Molecular Phylogenetics and Evolution 125: 127–137. DOI: 10.1016/j.ympev.2018.03.013

Verwaijen, D., Van Damme, R. & Herrel, A. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. – Functional Ecology 16(6): 842–850. DOI: 10.1046/j.1365-2435.2002.00696.x

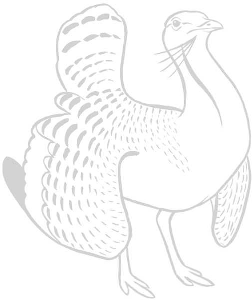
Volman, S. F. & Konishi, M. 1990. Comparative physiology of sound localization in four species of owls (Part 1 of 2). – Brain, Behavior and Evolution 36(4): 196–205. DOI: 10.1159/000115307

Voous, K. H. 1988. Owls of the Northern Hemisphere. – MIT Press, Cambridge, Massachusetts

Wink, M., Heidrich, P., Sauer-Gürth, H., El-Sayed, A-A. & Gonzalez, J. M. 2008. Molecular phylogeny and systematics of owls (Strigiformes). – In: König, C. & Weick, F. (eds.) Owls of the world, 2nd edition. – Christopher Helm, London, pp. 42–63.

Wink, M., El-Sayed, A. A., Sauer-Gürth, H. & Gonzalez, J. 2009. Molecular phylogeny of owls (Strigiformes) inferred from DNA sequences of the mitochondrial cytochrome b and the nuclear RAG-1 gene. – Ardea 97(4): 581–591. DOI: 10.5253/078.097.0425

Zelditch, M., Swiderski, D., Sheets, D. H. & Fink, W. 2004. Geometric Morphometrics for Biologists: A primer: Elsevier Academic Press, Waltham, MA.



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Preliminary study on the tolerance to human disturbance of Eagle Owl *(Bubo bubo)* in an active quarry in NW Hungary

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Abstract Population of the Eagle Owl *(Bubo bubo)* has been increasing in Europe including Hungary. The species occupy new habitats beside its ancient territories including quarries and buildings. This may result in conflicting conservation and economic interests in active quarries. Because eagle owls are strictly protected in Hungary, human activities around known nest sites require environmental permits. We aimed to obtain information on Eagle Owl behaviour in an operating quarry by tracking an adult female to base a future species-specific guideline to issue environmental permits for mining in quarries. We used a combined GPS-GSM and VHF telemetry. We found that the tracked female did not breed in the study year but remained in her home range during the study period. By studying her seasonal and daily patterns of movements, we found that she was not disturbed by regular human activities under the nesting cliff, but she was more sensitive to unexpected non-regular disturbance. Based on the satellite-tracking data, this specimen used an approximately 18 km^2 home range during the study period.

Keywords: telemetry, tracking, human activity, environmental permit, species-specific guideline

Összefoglalás Az uhu *(Bubo bubo)* állománya emelkedőben van Európában, ahogy Magyarországon is. A faj egykori élőhelyei visszafoglalása mellett új élőhelyeket is birtokba vesz, beleértve kőbányákat és épületeket is. Ennek eredményeképpen a működő kőbányákban konfliktusok alakulhatnak ki a természetvédelmi és gazdasági érdekek között. Mivel a faj Magyarországon védett, a revírben történő emberi tevékenységekhez környezetvédelmi engedély szükséges. Célunk az volt, hogy nyomkövetés segítségével információkat gyűjtsünk egy öreg tojó uhu viselkedéséről egy működő kőbányában, hogy megalapozzunk egy, a későbbiekben elkészítendő, fajspecifikus útmutatót a kőbányák működésére vonatkozó környezetvédelmi engedélyek kiadásához. Egy kombinált GPS-GSM és VHF alapú eszközt használtunk. Utóbbi jeleit egy automata vevőegység rögzítette folyamatosan, a nap 24 órájában. A VHF adó jeleit kézi vevőegységgel is lehetett fogni. A pár nem költött a vizsgált évben, de a vizsgált időszakban folyamatosan a revírben volt. A szezonális és a napi mozgásmintázatok elemzése azt mutatta, hogy a fészek alatt végzett rendszeres emberi tevékenység nem zavarta, azonban sokkal érzékenyebben reagált a nem várt, nem rendszeres zavarásra. A műholdas nyomkövetés adatai alapján az uhu egy megközelítőleg 18 km^2 kiterjedésű területet használt a vizsgált időszakban.

Kulcsszavak: telemetria, emberi tevékenység, környezetvédelmi engedély, fajspecifikus útmutató

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Introduction

Although global population of Eagle Owl (*Bubo bubo* Linnaeus, 1758) appears to be declining, the European population has undergone a continuous increase in the last decades (BirdLife 2018). Accordingly, population of Eagle Owl has increased in Hungary *(Figure 1)* gradually re-occupying the former habitats of the species (Firmánszky *et al.* 2004, 2005, Petrovics 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015). The increase of the European population is not without conflicts. As an apex avian predator, almost all bird and mammal species are on the diet of Eagle Owls including rare and protected ones (Lourenço *et al.* 2011). Accordingly, Eagle Owls regulate also population sizes and distribution patterns of other birds of prey species through intraguild predation (Mikkola 1976, Gainzarain *et al.* 2000, Sergio *et al.* 2004, 2007, 2008, Brambilla *et al.* 2006, 2010, Martínez *et al.* 2008, Lourenço *et al.* 2011).

Eagle Owls generally prefers habitats at lower altitude with open space in proximity of nest. They do not build nest, they usually lay eggs on cliff ledges or in stick nests of other bird species. Therefore, their most favoured nests sites are natural rock formations and quarries, but they may also breed in riparian forests, as well as on loess ledges (Firmánszky *et al*. 2004, Petrovics 2007). The Eagle Owl is known to tolerate human presence and nests not only near human settlements (Marchesi *et al.* 2002, Martínez *et al.* 2003, Cochet 2006, Petrovics 2007), but also started to colonize buildings in cities (Harms 2016). Quarries play an important role in this respect. For example, in Germany, quarries – both actively mined as well as inactive quarries used for leisure activities – are the most important breeding sites for Eagle Owls (Lindner 2005).

Human – Eagle Owl conflicts arises especially in active quarries, where conservation and economic interests meet, and disturbance resulted from human activities may jeopardize

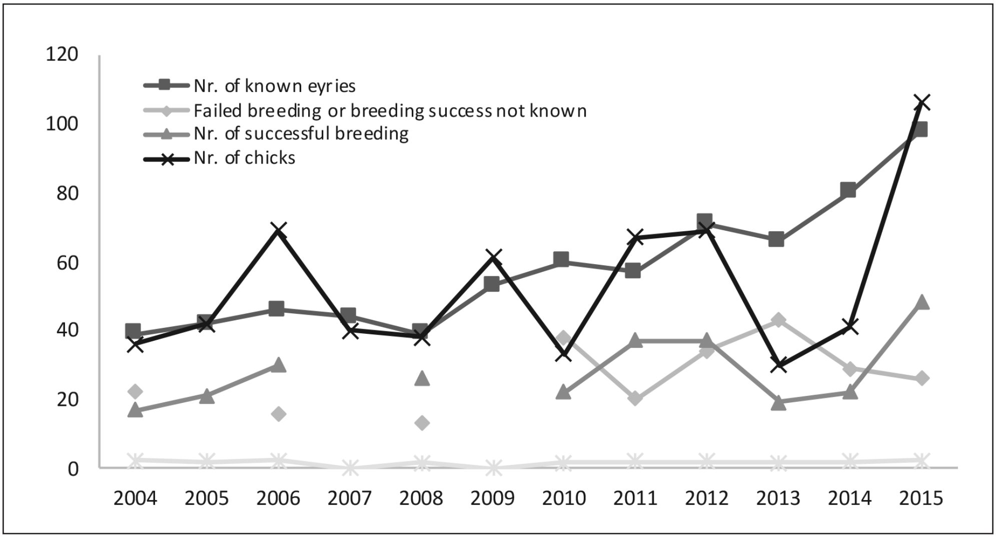

Figure 1. Population trend of the Eagle Owl in Hungary
1. ábra Az uhu állományának alakulása Magyarországon

breeding success. Disturbance caused by human activities can be manifold from economic activities (e.g. mining operations like extraction and crushing), through road or air traffic, hiking, rock climbing, walking dog, as well as targeted disturbance like birdwatching. It is desirable therefore to take preventive measures to support breeding success of this protected bird of prey species.

The international conservation status of the Eagle Owl is "*Least concern*" (BirdLife 2018). It is listed in CITES Appendix II., Bern Convention Appendix II and European Union's Birds Directive Annex I. and protected also by national legislation in most countries within its range (BirdLife 2018). In Hungary, Eagle Owl falls in the "*strictly protected*" category as defined in general by the Law 1996. LIII. "*on the conservation of nature*" and specified in the annex 3. of the decree 13/2001 (V.9.) listing the species under legal protection. It is necessary therefore, to obtain environmental permits for any activity including economic ones that can have potentially negative effect on the life activities of Eagle Owls. As for mining in quarries, permits usually define seasonal restrictions to prevent disturbance of breeding pairs. There is however, no guidelines for regional authorities, on how to set the restrictions to reach a mutually beneficial compromise between successful breeding and economic activities. As a result, different regional authorities in Hungary prescribe different restrictions ranging from fairly weak to unnecessary strict ones. None of those extremes will be beneficial for the owls on long term. Well-designed restrictions however, will result in conservation benefit for the species.

The main goal of the study was to evaluate the response of Eagle Owls to human disturbance in an active quarry in Hungary by radiotracking an adult female Eagle Owl with a combined GPS-GSM and VHF device. We also aimed to map her home range. The hypothesis was that the tracked Eagle Owl nesting in the quarry would tolerate disturbance resulted from everyday mining activities, also remaining in their nest or cliff perch in the quarry even during the day. However, she will respond negatively to unusual or targeted disturbances. We also assumed that the bird will be in the home range throughout the year and her movements likely remain within a few kilometres.

Material and methods

The first phase of the study was carried out near Esztergom, Hungary in a limestone quarry owned and managed by COLAS Északkő Ltd. The quarry has been used by Eagle Owls since 2004. The quarry is about 3.8 ha and an approximately 50 m high cliff closes the northeast side of the yard. The border of Pilis-Visegrádi Mountains Natura 2000 site runs on the top of the quarry. The cliff itself has not been permitted to be mined in the last two decades partly due to conservation considerations. The main cliff of the quarry faces to southwest offering a good view on an open landscape with a mosaic of grasslands, arable lands, vineyards, gardens and patches of bushes and wood. Extensive forests from northeast reach the top of the cliff and cover the top of the range to which the quarry belongs. The village of Kesztölc is located southeast of the quarry within only a kilometre. A major road, a lake and a covered landfill site can be found west – southwest of the quarry within only 3 kilometres.

The ownership of the quarry changed several times through the years and mining activities were ceased in some years. In 2016, when the field work was done, the quarry was active. Limestone extraction was done in the yard under the cliff but crushing and classifying was done further away, outside of the yard. The equipment and the yard were guarded permanently. Outside of working hours, guards on duty had to walk around the yard and check the equipment once in every hour also in the night. All work activities or extraordinary events occurred in the mine was registered in a book, which was our source of background information to compare against data from the owl's VHF transmitter.

In 2016, we trapped the adult female of the pair before the start of the breeding season to mount her with tracking devices. We used bow net for trapping as described in other studies (Leditznig 1992, Hull & Bloom 2001, Barclay 2008). After successful trapping, we mounted the Eagle Owl with a combined GPS-GSM and VHF device by using Teflon ribbon harness similarly to other studies (Delgado *et al.* 2009). The tracking equipment formed a rucksack on the bird, not preventing her from activities like hunting or mating.

The devices consisted of two attached, but otherwise separately functioning units. The GPS-GSM unit was a 45 gram, solar powered "*Crane*" type logger manufactured by Ecotone Telemetry. Crane loggers were designed with large backup batteries for birds mostly active in poor light conditions or with extreme large feathers (covering the solar panel). The unit can be programmed via an online panel and capable to locate the bird in every half an hour in good light conditions. Data is transmitted to the online panel via GSM network after every fourth successful GPS localization. Supplementary data as battery status, temperature, activity, and GSM network level are also recorded and transmitted. The accuracy of built-in GPS is a few metres in open areas, but worse in covered places. In our study, we set the localization frequency to one GPS record per night to save battery.

We attached a 10-gram VHF unit to the logger to complement a low frequency data service with a high frequency data provider unit, thus the combined device with the harness weighted approximately 60 grams, which was about 2.7% of the Eagle Owl's weight (2230 gram). The proportion was lower than the internationally accepted 3% rule. The VHF transmitter emitted a signal in every ten second and the estimated lifetime was four years. We deployed a full automatic receiver station in the guards' container in the mine yard that worked 24/7 and we recorded signal strength with a laptop. Data recorded by the automatic receiver station did not give information about the exact location of the bird, as it is not possible to detect direction of the transmitter with a single, fixed receiver. Signal strength however, indicated very accurately the presence/absence of the bird on the nesting cliff. According to previous tests, when the signal was strong, reaching the maximum value on the scale, we could be sure that the bird was on the cliff. As soon as the bird left the cliff, signal strength dropped significantly. There was not any radio signal emitting device in the area that could have distorted the signals of our VHF transmitter deployed on the bird. In addition to the automatic receiver station, VHF signals could be received also with a regular hand-held VHF receiver and a Yagi-antenna, thus Eagle Owl's roost sites during the day could be located. The VHF system including the transmitter and the receiver units and software was manufactured by Richard Wohlfart. Combining data received through the automatic receiver station and the hand-held receiver with the GPS-GSM data and visual observations (also with night-vision binoculars), we could make a good assessment of the bird's movements.

For technical reasons, we received comparable data between late February and early November, thus we evaluated data and present results from the period between 1 March and 31 October 2016.

GPS data showed the approximate range within the bird was moving during night that we put on a map (Minimum Convex Polygon) to visualize the home range of the Eagle Owl. The map was informative about the territory used by the bird, however information resulted from high-frequency VHF data were more important considering the aim of the study. We did not consider exact time of sunset and sunrise to keep processing simple. As a result, we received a very good visualization of owl's movements against circadian periods indicating the presence or absence of the bird on the nesting cliff. In addition, based on the quarry activity results, we showed (with a hypothetical value) every relevant human activity (disturbance) on the chart referring them to the date and time they happened. As a result, visual identification of disturbance events was straightforward.

All activities in the study was licensed by the environmental authority and requirements prescribed in the permit were strictly followed.

Results

We found that the Eagle Owl used intensively the nesting cliff throughout the year from the beginning of the year until early December, when she perished for unknown reason within the city limits of Kesztölc, the nearest settlement (the carcass was recovered with help of the tracking device). The female (and probably also the male) used the nesting cliff intensively especially during nights. The main resting area during daytime was not on the cliff, but over the top on the other side of the hill. The female perched on 15–20 metres tall, older trees covered with common ivy *(Hedera helix)*.

Although the pair did not start breeding, Eagle Owls' presence was gradually becoming more explicit towards May and June, spending more days on the cliff and being present every night. In July and August, the Eagle Owl avoided the cliff even in night, while in September, her presence was more explicit again, followed by a lower presence in October.

Circadian activities of owls usually followed the seasonally changing timing of sunset and sunrise. In many cases, the male and the tracked female (as visual observations confirmed) left the day roost and appeared on the cliff already at dusk. Usually the male arrived first and perched on his favourite rock or tree branch. The female usually showed up shortly after the male and she was less conspicuous, often we learnt about her approach only through the intensifying VHF signals. In some cases, she appeared much later than the male. In the night, she was away from the cliff mostly in the beginning or middle of the night period, when we suppose she was out hunting. In March, for example, she frequently left about two hours after sunset – around 8:00 pm CET – and returned only after midnight. However, we have records for earlier or later absence from the cliff and occasionally she left the cliff for hours twice a night. Oppositely, a few times she spent most of the night on the cliff. She always left the cliff only shortly before dawn every time, when she did not spend the daytime there. Vocalization was more intensive during the breeding period, but it occurred in every season.

We identified fifty days during the 245 days of the study period, when the tracked owl spent the entire daytime on the nesting cliff in the quarry. For forty nights the owl did not visit the cliff at all *(Figure 2)*. There were two occasions, when the owl spent the day in the quarry and the crusher was operating – the owl did not leave the cliff *(Figure 3)*. Human presence was continuous in the quarry, as the guards were always walking around regularly in the quarry in every hour according to their protocol.

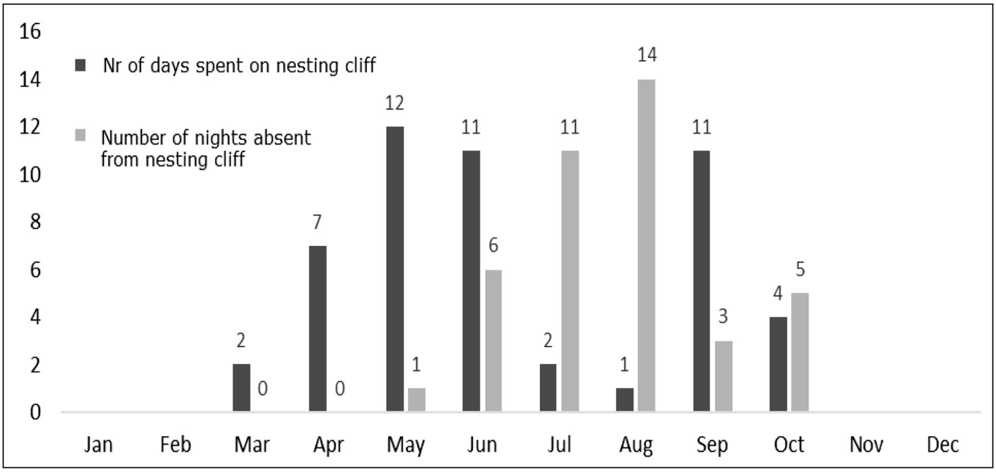

Figure 2. Number of days of diurnal presence and nocturnal absence on and from the nesting cliff
2. ábra A fészkelőfalon eltöltött nappalok és a faltól távol eltöltött éjszakák számának alakulása

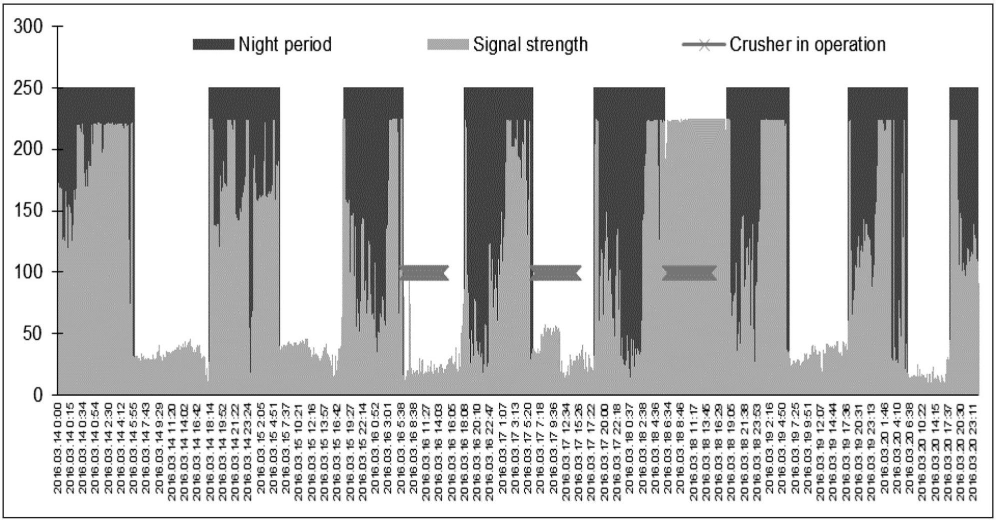

Figure 3. Diurnal and nocturnal presence of the tagged Eagle Owl on the nesting cliff in the period 14.03.2016 – 20.03.2016 indicated by VHF signal strength. On 18.03.2016 diurnal presence can be observed; the crusher was in operation on the same day
3. ábra A jeladós uhu nappali és éjszakai jelenlétének alakulása a fészkelőfalon 2016.03.14. és 2016.03.20. között, a VHF jelek erőssége alapján. Nappali jelenlét figyelhető meg 2016.03.18-án, amikor a törőgép üzemelt a bányaudvarban

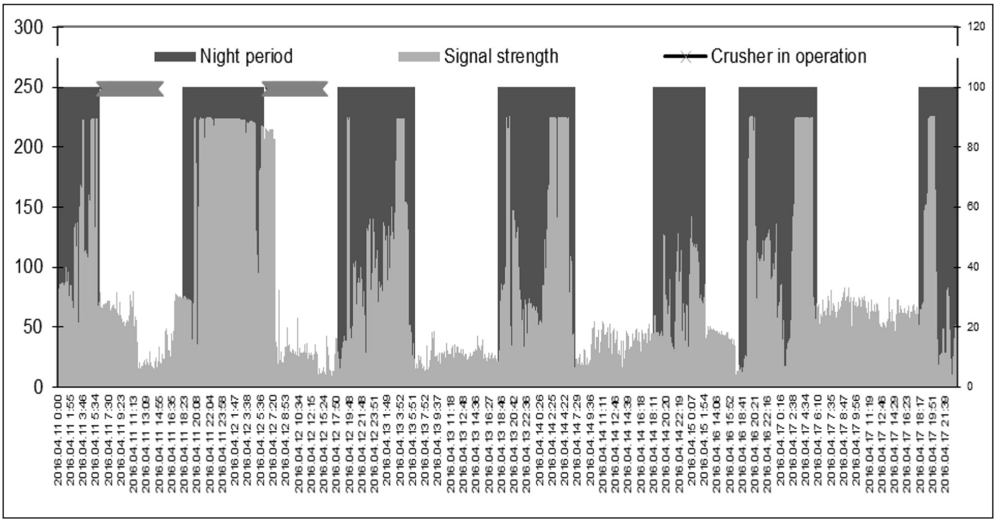

Figure 4. Diurnal and nocturnal presence of the tagged Eagle Owl on the nesting cliff in the period 11.04.2016 – 17.04.2016 indicated by VHF signal strength. The signal pattern indicates a disturbance event in the morning on 12.04.2016.

4. ábra. A jeladós uhu nappali és éjszakai jelenlétének alakulása a fészkelőfalon 2016.04.11. és 2016.04.17. között, a VHF jelek erőssége alapján. A jelek mintázata 2016.04.12-én zavarást jelez

When spending the daytime on the cliff, we found that she did not leave the roosting ledge during the day except for two cases (in April and June) that we identified as possible disturbance events *(Figure 4)*. According to the register book, on one of those days a heavy machine was doing earthwork on an upper terrace of the quarry close to the daytime roost of the owl.

Data from that device showed first the regular day roost area roughly 300 metres northeast from the cliff in straight line, where we found the Eagle Owl with the hand-held VHF receiver. The logger also confirmed our hypothesis that the adult female Eagle Owl remained within a few kilometres from the nesting site and regular roosting area. We found that the home range of the owl was about 18 km^2 including open and semi-open habitats with arable land bordered with patches of wood and abandoned vineyards. She visited two different manors of farmers' cooperatives, three and six kilometres from the cliff, to south and northwest, respectively *(Figure 5)*. The female Eagle Owl crossed linear infrastructures and even industrial zone on her revealed routes. It is likely that she flew over the village of Kesztölc regularly, as she hunted in its immediate vicinity. According GPS-GSM and VHF data, longer distance flights occurred in July and August, when she spent less time in the nesting cliff. The owl did not visit the closed forest areas in the mountains northeast of the cliff.

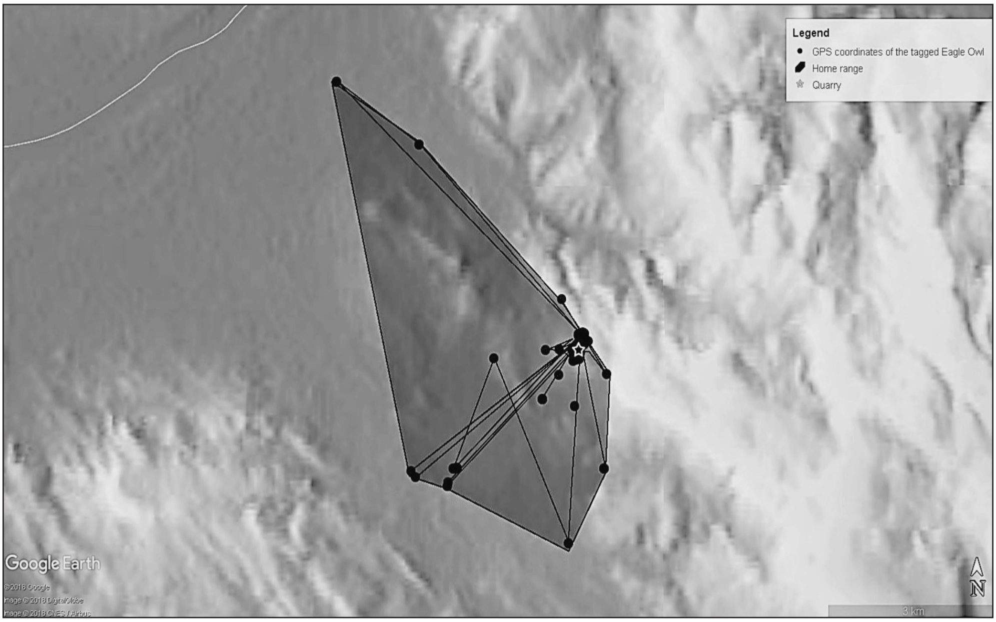

Figure 5. Area (minimum convex polygon) used by the tagged Eagle Owl based on GPS-GSM data
5. ábra A jelölt uhu által használt terület (minimum konvex poligon) a GPS-GSM adatok alapján

Discussion

The tracked female Eagle Owl spent considerable time – mostly at night, but also in daytime – on the cliff, even so that the pair did not breed in 2016.

Our study showed that the Eagle Owl tolerated repeated, non-targeted activities that occurred regularly and that was outside of a certain safety zone regardless if they were resulted from machines or men. Irregular operations, on an irregular place, closer than usual to the day roost of the owl however, can be classified as disturbance that may endanger breeding, if they often occur.

Studies focussed on owls' response to human disturbance (Delaney *et al.* 1999, Dalbeck & Breuer 2001) seem to be contradictory, but different types of disturbance must be evaluated separately. Regular "non-human" disturbance like quarry operations (Petrovics 2007), military helicopter practicing at low altitude (Delaney *et al.* 1999) has less impact on owls' behaviour, than seasonal direct human activities like rock climbing on the breeding cliff (Dalbeck & Breuer 2001). While owls can breed successfully in first case, in case of latter even breeding pairs can disappear, if the activity is not banned totally. Disturbance after all thus effects habitat quality. Quality of available habitats and individual choices has an impact on population density and breeding success (Penteriani *et al.* 2004). High tolerance of non-targeted disturbance had been reported from Germany, adding that Eagle Owls were even protected from targeted disturbance in actively used quarries (Harms 2015). The most important consideration is that no work or other human activity should be carried out in the immediate vicinity of the breeding site (Lindner 2005). In East-Westphalia-Lippe, in Germany high percentage of breeding pairs were found in industrial areas including quarries (Lödige *et al.* 2008). Apparently, owls can get use to repeated, non-targeted, intense human disturbance (e.g. mechanical noise, traffic, mining activities etc.), while they are sensitive to targeted disturbance (e.g. rock climbing, dog walking, bird watching etc.) even if it happens on a significantly smaller scale compared to previous activities.

The avoidance of the cliff in the summer was not related to any human activity in the quarry. Apart from the fact that no nestlings bonded her to the cliff, one possible explanation is that in the summer period the cool forest roosts offer better microclimate than the sun-heated bare rock, which stores the heat also for the night. Additionally, also in other parts of the territory fully developed foliage provides good cover during the day. As an opportunistic predator, she hunted not only in natural and agricultural areas, but also very close to settlements and even in the immediate vicinity of buildings (manors). Other authors also found that Eagle Owls regularly spent daytime further away from the nesting cliff (Dalbeck *et al.* 1998).

In summary, the tracked Eagle Owl tolerated "business-as-usual" activities in the quarry, but she was sensitive to activities she had not been used to. This result is in accordance with the literature describing co-existence of Eagle Owl breeding and industrial activities in quarries. Findings suggest that full ban on mining activities in quarries, where Eagle Owls breed is not always necessary. Activities (e.g. explosion, opening new yards or terraces, doing occasional earthworks close to nest etc.) however, that go beyond normal operation in the breeding season must be carefully evaluated and restricted if they endanger breeding.

It is important to note that sensitivity to disturbance varies among individuals, as well as breeding season may shift within years depending on weather conditions, and there are differences also in geographical features of quarries. Thus, spatial-temporal restrictions of mining must be adjusted to the individual quarries and owls annually.

Our study did not detail possible schedules for restrictions, as the tracked female and her mate did not start breeding in 2016. Another weakness of the study is the limited number of tracked individuals. For that we plan to continue the research in the coming years to complete the study and have a broader base for conclusions.

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References

Barclay, J. H. 2008. A technique for nighttime trapping of Burrowing Owls with a bow net. – Journal of Raptor Research 42(2): 142–148. DOI: 10.3356/JRR-07-34.1

BirdLife International 2018. Species factsheet: *Bubo bubo.* – Downloaded from http://www.birdlife.org on 08/02/2018

Brambilla, M., Bassi, E., Ceci, C. & Rubolini, D. 2010. Environmental factors affecting patterns of distribution and co-occurrence of two competing raptor species. – Ibis 152(2): 310–322. DOI:10.1111/j.1474-919X.2009.00997.x

Brambilla, M., Rubolini, D. & Guidali, F. 2006. Eagle Owl *Bubo bubo* proximity can lower productivity of cliff-nesting Peregrines *Falco peregrinus*. – Ornis Fennica 83: 20–26.

Cochet, G. 2006. Le grand-duc d'Europe [The Eagle Owl]. – Delachaux et Niestlé, Paris (in French)

Dalbeck, L., Bergerhausen, W. & Krischer, O. 1998. Telemetriestudie zur Orts- und Partnertreue beim Uhu *Bubo bubo* [Telemetry studies for Eagle Owl's *Bubo bubo* site and partner fidelity]. – Vogelwelt 119: 337–344. (in German with English Summary)

Dalbeck, L. & Breuer, W. 2001. Der Konflikt zwischen Klettersport und Naturschutz am Beispiel der Habitatansprüche des Uhus *(Bubo bubo)* [Conflict between rock climbing and nature conservation through an example of Eagle Owls' *(Bubo bubo)* habitat requirements]. – Natur und Landschaft 76(1): 1–7. (in German)

Delaney, D. K., Grubb, T. G., Beier, P., Pater, L. L. & Reiser, M. H. 1999. Effects of helicopter noise on Mexican Spotted Owls. – The Journal of Wildlife Management 63(1): 60–76. DOI: 10.2307/3802487

Delgado, M. M., Penteriani, V. & Nams, V. O. 2009. How fledglings explore surroundings from fledging to dispersal. A case study with Eagle Owls *Bubo bubo*. – Ardea 97(1): 7–15. DOI: 10.5253/078.097.0102

Firmánszky, G., Petrovics, Z., Szitta, T., Solti, B., Váczi, M., Molnár, I. L., Kovács, A., Kleszó, A., Harmos, K., Kazi, R. & Bagyura, J. 2004. Uhu költési adatok – 2004 [Eagle Owl breeding data – 2004]. – Heliaca 2004: 35–36. (in Hungarian with English Summary)

Firmánszky, G., Petrovics, Z., Szitta, T., Solti, B., Váczi, M., Molnár, I. L., Kovács, A., Kleszó, A., Harmos, K., Kazi, R. & Bagyura, J. 2005. Uhu költési adatok – 2005 [Eagle Owl breeding data – 2005]. – Heliaca 2005: 50–51. (in Hungarian with English Summary)

Gainzarain, J. A., Arambarri, R. & Rodríguez, A. F. 2000. Breeding density, habitat selection and reproductive rates of the Peregrine Falcon *Falco peregrinus* in Álava (northern Spain). – Bird Study 47(2): 225–231. DOI: 10.1080/00063650009461177

Harms, Ch. T. 2015. Der Uhu *(Bubo bubo)* am Südlichen Oberrhein – Bestand und Gefährdung [The Eagle Owl *(Bubo bubo)* in south Oberrhein – Population and threats]. – Naturschutz südlichen Oberrhein 8: 25–40 (in German with English Summary)

Harms, Ch. 2016. Bauwerkbruten des Uhus *(Bubo bubo)* – Fallbeispiele zu Konflikten und Problemlösungen [Eagle Owl nesting on buildings *(Bubo bubo)* – Case studies for conflicts and problem solutions]. – Naturschutz südlichen Oberrhein 8: 231–246. (in German with English Summary)

Hull, B. & Bloom, P. 2001. The North American banders' manual for raptor banding techniques. – North American Banding Council

Leditznig, C. 1992. Telemetriestudie am Uhu *(Bubo bubo)* im niederösterreichischen Alpenvorland – Methodik und erste Ergebnisse [Eagle Owl *(Bubo bubo)* telemetry studies on alpine foothills in Lower Austria – Method and first results]. – Egretta 35: 69–72. (in German)

Lindner, M. 2005: Reproduktion des Uhus *(Bubo bubo)* in stillgelegten und betriebenen Steinbrüchen im Sauerland [Breeding of Eagle Owl *(Bubo bubo)* in disused and active quarries in Sauerland]. – Artenschutzreport (Sonderheft) 17: 15–19. (in German)

Lourenço, R., Santos, S. M., Rabaça, J. E. & Penteriani, V. 2011. Superpredation patterns in four large European raptors. – Population Ecology (53): 175–185. DOI: 10.1007/s10144-010-0199-4

Lödige, C., Vor, T. & Büttner, G. 2008. Populationsdichte und Bestandesentwicklung des Uhus (*Bubo bubo* L.) in Ostwestfalen-Lippe von 1996 bis 2005 [Population density and dynamics of Eagle Owl (*Bubo bubo* L) in Eastern Westphalia-Lippe from 1996 to 2005]. – Forstarchiv 79: 179–186. DOI: 10.23760300-4112-79-179 (in German with English Summary)

Marchesi, L., Sergio, F. & Pedrini, P. 2002. Costs and benefits of breeding in human-altered landscapes for the Eagle Owl *Bubo bubo*. – Ibis 144(4): 164–177. DOI: 10.1046/j.1474-919X.2002.t01-2-00094_2.x

Martínez, J. A., Serrano, D. & Zuberogoitia, I. 2003. Predictive models of habitat preferences for the Eurasian Eagle Owl *Bubo bubo*: a multiscale approach. – Ecography 26: 21–28. DOI: 10.1034/j.1600-0587.2003.03368.x

Martínez, J. E., Martínez, J. A., Zuberogoitia, I., Zabala, J., Redpath, S. M. & Calvo, J. F. 2008. The effect of intra- and interspecific interactions on the large-scale distribution of cliff-nesting raptors. – Ornis Fennica 85: 13–21.

Mikkola, H. 1976. Owls killing and killed by other owls and raptors in Europe. – British Birds 69: 144–154.

Penteriani, V., Delgado, M. M., Gallardo, M. & Ferrer, M. 2004. Spatial heterogeneity and structure of bird populations: a case example with the Eagle Owl. – Population Ecology 46: 185–192. DOI: 10.1007/s10144-004-0178-8

Petrovics, Z. 2006. Az uhu országos állományfelmérése – 2006 [National survey of the breeding population of Eagle Owl, in 2006]. – Heliaca 2006: 36–38 (in Hungarian with English Summary)

Petrovics, Z. 2007. Uhu *(Bubo bubo)* állomány adatok – 2007 [Eagle Owl (*Bubo bubo*) population data – 2007]. – Heliaca 2007: 69–71 (in Hungarian with English Summary)

Petrovics, Z. 2008. Uhu *(Bubo bubo)* állomány adatok – 2008 [Eagle Owl (*Bubo bubo*) population data – 2008]. – Heliaca 2008: 46–47. (in Hungarian with English Summary)

Petrovics, Z. 2009. Uhu *(Bubo bubo)* állomány adatok – 2009 [Eagle Owl (*Bubo bubo*) population data – 2009]. – Heliaca 2009: 76–77. (in Hungarian with English Summary)

Petrovics, Z. 2010. Uhu *(Bubo bubo)* állomány adatok – 2010 [Eagle Owl (*Bubo bubo*) population data – 2010]. – Heliaca 2010: 50–51. (in Hungarian with English Summary)

Petrovics, Z. 2011. Uhu *(Bubo bubo)* állomány adatok – 2011 [Eagle Owl (*Bubo bubo*) population data – 2011]. – Heliaca 2011: 39. (in Hungarian with English Summary)

Petrovics, Z. 2012. Uhu *(Bubo bubo)* állomány adatok – 2012 [Eagle Owl (*Bubo bubo*) population data – 2012]. – Heliaca 2012: 37. [in Hungarian with English Summary)

Petrovics, Z. 2013. Uhu *(Bubo bubo)* állomány adatok – 2013 [Eagle Owl (*Bubo bubo*) population data – 2013]. – Heliaca 2013: 37. (in Hungarian with English Summary)

Petrovics, Z. 2014. Uhu *(Bubo bubo)* állomány adatok – 2014 [Eagle Owl *(Bubo bubo)* population data – 2014]. – Heliaca 2014: 48–49. (in Hungarian with English Summary)

Petrovics, Z. 2015. Uhu *(Bubo bubo)* állományadatok – 2015 [Eagle Owl *(Bubo bubo)* population data in 2015]. – Heliaca 2015: 16–17 (in Hungarian with English Summary)

Sergio, F. & Hiraldo, F. 2008. Intraguild predation in raptor assemblages: a review. – Ibis 150 (Suppl. 1.): 132–145. DOI: 10.1111/j.1474-919X. 2008.00786.x

Sergio, F., Marchesi, L., Pedrini, P. & Penteriani, V. 2007. Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? – Animal Behaviour 74(6): 1607–1616. DOI: 10.1016/j.anbehav.2006.10.022

Ornis Hungarica 2018. 26(1): 65–88.
DOI: 10.1515/orhu-2018-0005

Changes in the nest sites of White Stork *(Ciconia ciconia)* in Hungary

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Abstract The breeding strategies of the White Stork changed drastically during the past decades: a decreasing number of individuals nest on traditional nest sites – trees, roofs, chimneys, whereas electricity poles are increasingly selected. Here we analysed long-term breeding data of White Storks breeding in six Hungarian counties to detect patterns in nest site preferences in Hungary. According to our results, the shift to preference for electricity poles was shown at the same rate in every county, independently from the proportion of original nest sites. After 2000, although electricity poles dominated everywhere, the proportion of nest on poles without platform increased, despite the abundance of available empty platforms. To explain this pattern, we propose that White Storks show a preference for viewpoints, thus choosing to breed as near as possible to optimal habitats, regardless of nest site types. Therefore, conservation measures concerning the nest sites of this species should include preliminary habitat analysis.

Keywords: nest site selection, population dynamics, species conservation, rural area, habitat selection, Hungary

Összefoglalás A fehér gólya fészkelési szokásai látványosan megváltoztak az elmúlt évtizedekben: egyre kevesebb egyed költ hagyományos fészkelőhelyeken – fákon, háztetőkön, kéményeken – és egyre több villanyoszlopokon. Hat megye hosszú távú fészkelési adatsorait elemeztünk annak megválaszolására, hogy Magyarország különböző tájain hogyan zajlott le a fészkelőhely-váltás. Eredményeink alapján mindegyik megyében azonos időben és ütemben kezdődött meg az áttelepülés a villanyoszlopokra, függetlenül a fészekhely-típusok eredeti összetételétől. A 2000-es években már a villanyoszlopok domináltak mindenhol, azonban a tartó nélküli villanyoszlopon fészkelő gólyák aránya nőtt annak ellenére, hogy nagy számban voltak elérhetőek üres fészektartók. Ez azzal magyarázható, hogy a gólyák számára a fészek térbeli elhelyezkedése az elsődleges: a jó táplálkozóterületekhez közelieket preferálják a fészekalap típusától függetlenül. A fehér gólya fészkelésével kapcsolatos természetvédelmi intézkedésekhez, műfészkek helyének optimális kiválasztásához elengedhetetlen az élőhelyek minőségének előzetes felmérése.

Kulcsszavak: fészkelőhely-választás, populációdinamika, fajvédelem, élőhelyválasztás, vidéki térség, habitat-szelekció, Magyarország

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Introduction

The White Stork *(Ciconia ciconia)* originally built nest on trees, but since the extent of natural habitats (wetlands, floodplains, steppes with scattered trees) decreased because of human activities and in parallel, extensive agriculture created alternative habitats, White Storks started to show a preference for nest sites in human settlements. Buildings, as artificial nest sites, facilitated the urbanisation of Storks (Cramp & Simmons 1977).

The most drastic change of the past decades is represented by a process including White Storks starting to use electricity poles as nest sites as a dominant strategy. Since environmental and sociological changes occurred at different rates in Europe, this transition in nest sites was also spatially uneven. For instance, in Wielkopolska region of Poland, preference for nesting on electricity poles started and predominantly increased in the western areas, in accordance with the direction of rural electrification (Boguczki & Ożgo 1999). In the former area of Yugoslavia, the dominant nest sites – haystacks – disappeared in a few years due to economical changes. This sudden and compulsory transition impacted the population negatively as breeding success dropped by 50% during the following decade (Pelle 1999). Further, in Vojvodina region, Serbia, the most abundant nest sites are located on electricity poles (Tucakov 2006). In Estonia, significant amounts of nesting events on electricity poles were registered in 1984, and became dominant in 20 years (Ots 2009). The contribution of electricity poles in nest sites grew sixfold in Bulgaria between 1979 and 1994, in paralleel, the contribution of trees dropped by 50%, possibly because suitable trees disappeared (Petrov *et al.* 1999). In Turkey, electricity pole was also the most abundant type in the latest census, whereas nest site types were distributed unevenly in regions (Omnuş *et al.* 2016). For example, in the Kızılırmak delta, tree remained the dominant nest site, attributed to the natural stand of the forests (Yavuz *et al.* 2012). In Slovenia, nesting on electricity poles appeared in 1965, the proportion of this type is 40% in 1979 and 80% since 1999 (Denac 2010). In Portugal, the proportion of nesting on electricity poles increased from 1% to 25% between 1984 and 2014, out of this 60% is the proportion of high voltage poles, which can hold multiple nests (Moreira *et al.* 2017). In Latvia, the proportion of nesting on electricity poles increased from 1% to 60% between 1974 and 2004, mostly without support (Janaus & Stipniece 2013). In Belarus, Storks nested exclusively on trees and building in 1967, however, nesting on electricity poles increased to 25% to 2004, but water towers have the same proportion, which is unusual compared to those of other countries (Samusenko 2013).

The breeding population of Hungary was estimated to 15000–16000 pairs, based on the first census in 1941, which was calculated considering a larger historical country size (Homonnay 1964). This estimate can be relatively correct as the areas excluded after the peace treaties of WW-II included mainly mountain habitats, unsuitable for Storks. However, according to the partial censuses, only half of this estimated number was likely to be realistic between 1948 and 1951 (Keve 1957). The population decreased further during the 1970s (4900 pairs), since which period it can be considered stable with 4800–5600 pairs (Magyar *et al.* 1998, Hadarics & Zalai 2008). According to the Common Bird Monitoring scheme, the population trend is uncertain between 1999 and 2012 (Szép *et al.* 2012). A likely reason of mortality for half of the known cases can be related to electrocution or collision with power lines or electricity poles, with 80% of the victims being juveniles (Lovászi & Rékási 2009).

Electricity pole as new nest site indicates both economical and conservation problems: the incidental shortcuts caused by the nest hinders electricity service, and birds – specially fledglings – are threatened by electrocution (Jakab 1991, Jakubiec 1991, Infante & Peris 2003, Lovászi & Rékási 2009). At local levels, collision with power lines and poles can contribute significantly to mortality rates (Goriup & Schulz 1991, Garrido & Fernandez-Cruz 2003, Galarza & García 2012), and electromagnetic field can decrease breeding success (Vaitkuviené & Dagys 2014). Prevention or at least mitigation of these threats is an important task. Possible solutions: lifting up nests with nest supports, establishing nest supports on electricity poles (Goriup & Schulz 1991, Mužinić & Cvitan 2001) or setting up independent poles specifically for Storks in potencial habitats (Santopaolo *et al.* 2013).

Conservation measures aimed at nest sites can bring spectacular results, for example, the Calabrian reintroduction succeeded using artificial platforms (Santopaolo 2013). The White Stork population in Europe is stable again, even increasing in a number of regions (BirdLife 2016). The protection of the species can only be efficient by regarding both the nest site and the habitat needs. There could be areas where habitats would be optimal but inhabitation is impossible due the lack of nest sites, or the other way around.

In this paper, we aimed to answer the following questions:

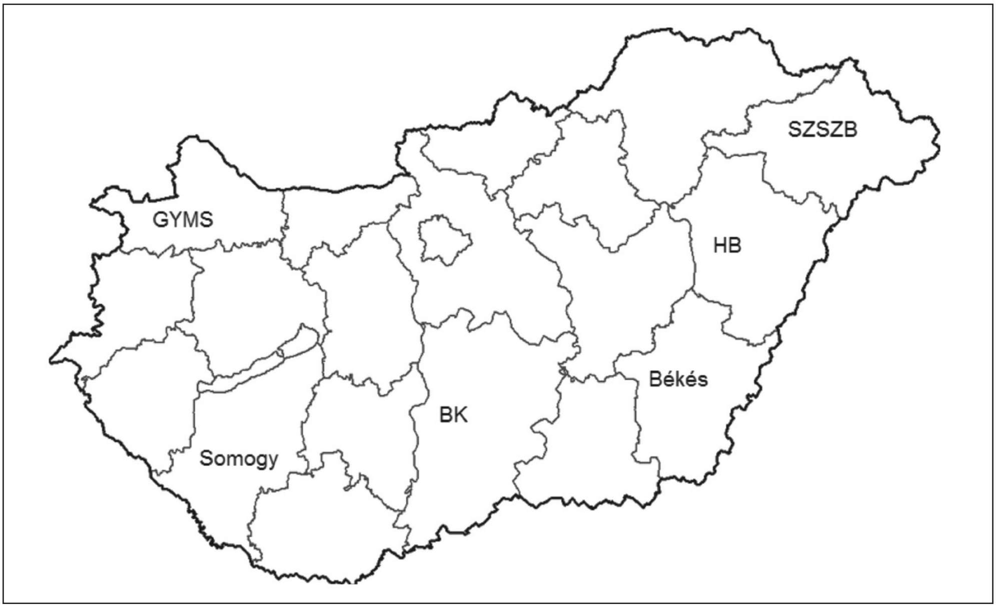
1. How the proportion of nest sites changed in six Hungarian counties during the last fifty years?
2. What are the primary drivers of shifting to electricity poles?
3. How successful were the conservation actions of the past decades?

Materials and Methods

The data were retrieved from two resources. First, between 1958–1989, paper forms of White Stork censuses conducted in every five years, published in the archives of Móra Ferenc Múzeum, Szeged. This information includes two types of protocols: postal forms (po) sent out by post offices, filled out by post workers; and more detailed questionnaires (qu) sent out to forestries, hunting companies, schools, filled out by foresters, hunters, teachers, students etc. Second, between 1994–2013, volunteers of BirdLife Hungary provided the data, and this database is now fully available in electronic format, provided by the Hungarian Monitoring Centre. There was only one observation by every method, so the number of White Stork pairs is probably underestimated and there could be also differences in productivity, but these estimates do not differ significantly from real values, as this study states (Aguirre & Vergara 2009). Nest site types are considered as reliable data, because most of the time nest site can be easily identified and can be surveyed at any time of the breeding season (Boguczki & Ożgo 1999).

For this study, we chose six out of the 19 Hungarian counties (namely Győr-Moson-Sopron, Somogy, Bács-Kiskun, Békés, Hajdú-Bihar és Szabolcs-Szatmár-Bereg County). We considered the following criteria: 1. data are available from every year 2. there should be enough breeding pairs for the analysis 3. they should represent different geographical and socio-economical regions of Hungary. Water permeability of soil types affects the amount of water covered areas which is in relation to the distribution of White Storks, therefore we present the soil types of the counties along with the main water bodies, the typical agricultural use and the human population density (Mezősi 2011, https://www.ksh.hu/).

- Győr-Moson-Sopron (GYMS): soil types: fluviosols, gleysols, phaeozems, chernozems (near rivers), luvisols (Transdanubian Mountains). Main waters: Danube, Rába, Rábca. Agricultural usage: 4.8% grassland, 53.5% arable land, 19.2% forest. Density: 107/km^2.
- Somogy: soil types: fluviosols, gleysols, phaeozems (near rivers and lakes), luvisols, arenosols, cambiosols. Main waters: Dráva, lake Balaton. Agricultural usage: 5.2% grassland, 42.2% arable land, 29.5% forest. Density: 52/km^2.
- Bács-Kiskun (BK): soil types: regosols, solonchaks, fluviosols (along Danube), chernozems (Bácska region). Main waters: Danube, alkaline, saline lakes. Agricultural usage: 12.3% grassland, 41.3% arable land, 20.9% forest. Density: 61/km^2.
- Békés: soil types: chernozems, rendzinas, phaeozems, vertisoils. Main waters: Körös, Berettyó. Agricultural usage: 5.5% grassland, 67.7% arable land, 4.6% forest. Density: 63/km^2.
- Hajdú-Bihar (HB): soil types: chernozems, solonetzes (Közép-Tisza region). Main waters: Tisza, Berettyó, alkaline-saline lakes. Agricultural usage: 17.7% grassland, 53.1% arable land, 11.1% forest. Density: 86/km^2.
- Szabolcs-Szatmár-Bereg (SZSZB): soil types: regosols, arenosols; phaeozems, fluviosols (along rivers). Main waters: Tisza. Agricultural usage: 10.8% grassland, 44.4% arable land, 21.1% forest. Density: 94/km^2 *(Map 1.)*.



Map 1. Location of the examined counties
1. térkép A vizsgált megyék elhelyezkedése

We categorised nest sites as follows:

- tree (tr): any species of woody plant, either dead or alive
- building (bu): any type of building, including those of economical usage (barns, pens etc.)
- roof (ro): the covering structure of a building of any material
- chimney (ch): the structure of a building used for ventillation
- electricity pole (ep): pole connected to the power line network
  without support (ep_ns): electricity pole without nest support
  with support (ep_s): electricity pole with nest support
- other (ot): independent poles, haystacks, water towers, ruins etc.

Data were filtered and processed with the R statistical computing software (R Core Team 2015). We summarized the number of nests (both occupied and unoccupied) in every year from the postal forms and the online database to see the overall population changes. We chose the postal forms for the 1958–1989 period because it gives a better estimation, especially for the early years. We applied linear regression to the changes of proportion of nest sites by counties in each data series (namely: the postal forms, the questionnaires and the online data). To investigate overall changes, we used linear mixed model (LMM) implemented in the lme4 R package (Bates *et al.* 2015). One model contained previous data, where the census type was added as a fixed predictor and the county identity provided the random variable, whereas another model contained the new data, including county identity as random effect term.

Since the new database contains the empty nest supports, the role of equipped nest supports, and hereby the success of nature conservation actions can be measured. We compared the proportion of empty nest supports to electricity poles and the proportion of unoccupied nests to electricity poles (where 100% was all of the possible nest sites, so all nests + empty nest supports). We applied linear regression for estimating the proportions by counties. For electricity poles with nest supports, we investigated seperately the proportion of empty nest supports and the unoccupied nests.

Results

Overall population changes based on numbers of nests

During the span of 10 years of the first three census, the number of Stork nests decreased in every county. The values remained more or less at these values between 1968 and 1984. Between 1994–2013, fluctuations due to insufficient data in the first years affected most counties, but if we take the highest numbers as a basis from this period, we can assume that population increased in every county after 1989 *(Table 1)*.

Changes of nest sites

Here we show the main characteristics of nest site changes; strengths and direction of trends is indicated more in depth in the tables *(Table 2, 3, 4)*.

Between 1958–89

The most profound change was in all counties, in both data sources, the significant increase on nests on electricity poles.

In the beginning, most common nest sites were trees and buildings in Somogy county. Decrease was more drastic and earlier at trees (in both data sources). Questionnaires show that roofs decreased more affected within the building category. Chimneys remained important even in 1989.

Similar to the previous, tree and building nests dominated in Bács-Kiskun in the early years. Despite the decrease, contribution of trees was still high in 1989 (postal forms). Within the building category, roofs decreased more (questionnaires).

Questionnaires show that greatest proportion of nests originally were on chimneys in Békés. In contrast to other counties, of contribution of roofs and trees remained always low.

In Hajdú-Bihar county, the other category emerged as the most important type, which was driven mainly by the contribution of haystacks (based on the notes of postal forms). The proportion of building nests was also high, especially on chimneys.

The majority of nests was found on buildings in Szabolcs-Szatmár-Bereg counties. The contribution of roofs was a bit higher than in other counties. In case of tree nests, fluctuation was strong in postal forms.

Based on the linear mixed model, the trends of the two data sources differed significantly in the case of other category: the postal forms showed a greater decrease. The difference between the six counties was the lowest at the electricity poles: 4.5% of variance was explained by the county as random variable. This contribution of variance was 47.6% at the trees, 45.9% at the buildings and 17.4% at the other category *(Table 5)*.

Between 1994–2013

The most striking change was the increase of the proportion of nests on electricity poles without supports in all counties and was significant in 5 out of 6 cases. In parallel, the proportion of nests on electricity poles with support decreased in 5 out of 6 cases. Altogether, this nest site still remained dominant in every county *(Table 6, 7)*.

In Győr-Moson-Sopron, the contribution of chimney and other category was 10–15%. Significant decrease was observed in case of the trees.

The overall proportion of nests on electricity poles significantly decreased in Somogy. The proportion of nests on chimneys and other sites amounted to 5–10%. No nest on roof was reported.

The only significant change in Bács-Kiskun was detected in the decrease of nests on roofs. The proportion of chimney nests was around 10–20%. The contribution of other category was 5–10%. No nest on trees was reported.

The overall proportion of nests on electricity poles significantly increased in Békés. There was a significant decrease in case of chimneys, although their contribution is still high (20–25%). There was a significant increase in case of roofs.

The contribution of chimney nests was around 5–10% in Hajdú-Bihar. There was a significant increase in case of tree nests.

The overall proportion of nests on electricity poles significantly decreased in Szabolcs-Szatmár-Bereg. The proportion of other category was higher due to the independent poles (20–10%), but also significantly decreased.

Based on the linear mixed model, the proportion of nests on electricity poles with support decreased significantly overall and 18.9% of the variance is explained by the differences between counties. There was a significant increase in case of electricity poles without support, 9–14.9% of variance provided by county identity as random factor. There was a significant decrease in case of the roofs (variance contribution of countries: 51.8%). A positive trend was observed in case of the chimney and tree category (variance contribution of counties respectively: 41.6% and 17.6%). A negative trend was observed at the other category (variance contribution of counties: 26.7%) *(Table 8)*.

The proportion of empty nest supports on electricity poles significantly increased in Bács-Kiskun, Hajdú-Bihar, Somogy és Szabolcs-Szatmár-Bereg. The proportion of unoccupied nests on electricity poles with support significantly increased in Somogy *(Table 9)*.

Discussion

The White Stork population in Europe drastically decreased between 1970 and 1990, which is hypothesised to be the result of decreasing of suitable habitats and nest sites, increasing mortality resultes by power lines, drought in the wintering areas, chemical crop control and the interactions among these effects (Goriup & Schulz 1991, Jakubiec 1991, Kanyamibwa *et al.* 1993, Schulz 1994). The population size reached its lowest number in 1984 with 135000 pairs and started to increase in the following decades (Thomsen & Hötker 2006). The population in Europe is now estimated to 224000–247000 pairs (BirdLife International 2016). The reasons of increase – between conservation actions – is attributed to the expansion of area to the north (Ots 2009), the occupation of habitats at higher altitudes (Tryjanowski *et al.* 2005b), the reoccupation to original breeding areas (Santopaolo 2013) and locally the advantageous changes in agriculture (Forgách 1997, Vaitkuviene & Dagys 2015). During the past decades, Storks fed also in rubbish dumps, which allows their permanent colonization in suboptimal habitats (Kruszyk & Ciach 2010), or even allowing wintering in the region (Tortosa *et al.* 2002, Gilbert *et al.* 2016).

The original proportion of the nest sites depended on traditional agricultural technology of the given county. While specialty of Somogy was represented by the woodland pastures, in Bács-Kiskun it was exemplified by loosely connected network of farms. In Győr-Moson-Sopron, Hajdú-Bihar és Szabolcs-Szatmár-Bereg, storks mainly nested on agricultural buildings inside villages. In Hajdú-Bihar county, the high proportion of nest on haystacks shows the significant use of meadows for mowing: 22–26% of nest was built on haystacks in 1941 (Homonnay 1964), but even in 1963, this category dominated over all the others. In Békés, extended arable lands was typical, which Storks avoid, since these habitats are suboptimal for them (Denac 2006a), that is why the amount of nest was relatively low. These nests were mainly built on chimneys, inside villages.

The changes connected with building practices have been reported worldwide (Goriup & Schulz 1991) and are also well-documented in written resources of Hungarian White Stork conservation (Jakab 1991). The proportion of nests on roofs decreased in a White Stork population in Poland, because the agricultural buildings with thatched roofs preferred by Storks disappeared with the modernisation of agriculture (Daniluk *et al.* 2006, Kosicki 2006). These types of buildings were often classified into the „other" categories in the postal forms, so the proportion of nests on roofs could be underestimated. Thatched roofs are more suitable for Storks than harder roof types from where the nest may easily fall down. However, human preferences are directed towards ceramic tiles and slate roofs, as these require less maintenance and are also more fireproof.

The proportion of nests on chimneys also decreased in almost every county. Based on the notes, the main reason of this is the modified shape of chimneys: the newer types are more slender and opened on the top in contrast with the sturdier ones, with holes on the sides. Sometimes the top is cone-shaped, especially aiming to deter storks.

According to the 1941 census, a certain proportion of the population – in all counties – nested outside the villages, near to small farms, almost exclusively on trees (Homonnay 1964). The possible reason is that the vicinity of these farms was especially rich in optimal habitats, to which storks tried to nest as close as possible (Ożgo & Boguczki 1999). We assume they preferred trees because suitable old trees were more abundant and also – based on the additional notes – because people did not tolerate the Storks on the buildings. This stable pattern was not present in our analysis because of the settlement pattern and agricultural changes. Where the changes occurred later – Bács-Kiskun in our case – the proportion of nests remained high.

In contrast to previous nest sites, it is improbable that the availability of trees drastically decreased for nesting. We did not find records of mass tree logging, although it is true that in primarily open areas, disappearance of even small number of trees can have a substantial impact on Storks. Grasslands without trees, even if considered as optimal habitats, are not occupied by Storks if travel costs from nearest possible nest site are larger than the energy gain of the habitat (Jakab 1989, Olsson & Arvid 2014).

The examined counties showed great differences in the availability and usage of traditional nest sites, in contrast, the shift to nesting on electricity poles happened almost synchronously everywhere. Thus, it is improbable that the disappearance of other nest site was the primary reason of this change. Since the population was already decreasing in the analysed period, it was not caused by the changes in nest sites. The structure of population has changed.

In Hungary, electricity was introduced to the last village in 1963 (http://mtva.hu/hu/sajto-es-fotoarchivum/5654-50-eve-fejezodoett-be-magyarorszagon-a-falvak-villamositasa), but electricity poles were used by Storks only occupied in larger amounts from 1968. At that time, the distribution of electricity poles was already equal everywhere, so the swift indeed happened independently from rural electrification. In certain regions of Poland, Storks also started to nest on electricity poles much later after they became abundant (Tryjanowski *et al.* 2009, Janiszewski *et al.* 2015). But in Wielkopolska region, differences in nest site choice remained between the earlier and later electrified western and eastern parts

(Boguczki & Ożgo 1999). Regional differences were also observed in the population of Olt river basin: the proportion of nests on electricity poles is still the highest in the N-NW part where electrification started and the first nest on this nest site was reported in the 1960s (Kósa *et al.* 2002).

The time of electrification explains the differences in patterns of nest site usage, but not the cause of why did electricity poles became attractive for Storks. A possible assumption is that Storks that nest on electricity poles have a higher productivity. In a study in Poland, no differences were found between nest site types neither in the number of fledged young nor in the proportion of occupied nests. However, in the case of electricity poles, productivity was affected by nest support: mean number of chicks was lower as the mean of all nest sites after the year the support was equipped, but significantly higher in the second year. Disturbance of the nest is unfavourable for the chicks for short terms, but in the long run, chicks are safer in nest with supports (Tryjanowski 2009). Based on a study in northern Hungary, productivity was significantly lower in nests on unsupported electricity poles. This could stem primarily from the fact that young and unexperienced individuals nest on these poles (Boldogh 2009). However, this could indicate preference indirectly, because earlier individuals occupy other nest sites sooner. In a former study on the same area, earliest, most experienced individuals occupy nests on chimneys first (Boldogh 1998), so higher productivity on this type is more affected by the age of Storks, not directly the nest site type.

Another assumption for the advantage of electricity poles is lower predation rates as well as human disturbance. The productivity of Storks on trees presumably decreased because of predators in Poland (Tryjanowski 2009). The role of the conflicts between Storks and humans in nest site selection was not examined as far as we know, possibly due to difficulties in sampling data.

Realising the increasing role of electricity poles, Hungarian Birdlife started to put on nest supports in cooperation with the electricity companies in the 1970s. From 1980, 3000 nest supports were equipped either under existing nests or to empty electricity poles or independent poles (Lovászi 2004). Further 650 nest supports were placed in the 1990s, 2000 between 2001–2002 and at least 1000 after that (Horváth *et al.* 2010).

In the 1990s, when the population was increasing, Storks started to occupy the empty nest supports, available in great abundance. At the turn of the millenium, most new nest were built on electricity poles with nest support. Out of the traditional nest sites, only the proportion of nest on chimneys remained significant, although to a different degree between counties.

As the density of population increased, it proved to be a general trend that out of nests on electricity poles, the proportion of nests with supports decreased and the ones without support increased, although empty nest supports were still available in high numbers. The proportion of empty nest supports (on electricity poles) increased in every county. This can be explained the same was as experienced in a study in Middle Poland, where it was found that nesting on electricity poles expanded fastest in the best habitats.

It becomes harder for the newcoming individuals to fit in the high density population, because they have to choose a nest site that is close to the feeding areas but not too close to the other pairs. The number of chicks is positively correlated with the distance of neighbors in optimal habitats (Nowakowski & Wasilewka 2006) and negatively correlated with the number of neighbors in suboptimal habitats, which is caused by strong intraspecific competition (Denac 2006b). The spatial situation of the nest has priority: the Storks began to use the electricity poles in large amounts because they easily found suitable ones due to the big coverage (Janiszewski *et al.* 2015). In an analogous way, an electricity poles with good situation but without nest support is a better choice than one in a bad place with nest support. The expanding White Stork population in western France started to nest mainly on trees, despite the mass presence of artificial nest platforms (Gadenne *et al.* 2014). The same was experienced in western Poland: first breeders built their nest more often to trees and unusual places, near to feeding areas (Tobolka *et al.* 2013).

The possible substitute for electricity pole is the independent pole erected specifically for Storks. The distraction of Storks from electricity poles with setting of independent poles was successful in Slovakia, where 25.1% and 37% was the respective proportion of these types in 1995, whereas contribution of electricity poles was 38% at the 1984 census (Fulín 1999). In Karkov region, Ukraine, the proportion of electicity pole nests was relatively high (18%) even in 1974 and increasing, possibly due the lack of alternative nest sites in the steppe, but now half of the population breeds on poles made specifically for them (Atemasova *et al.* 2016). However, they are not necessarily suitable for substitution of existing nests: in a German population, after nests from electricity poles were removed, independent poles were offered next to them directly, yet Storks rejected the new poles, so nest supports solved the problem (Köhler 1999). These pole types began to set up in larger numbers from 1989 in Hungary: in the 1994–2013 database, independent poles constitute almost exclusively the „other" nest site category, so it is easy to follow the trend. After the initial upturn, the proportion of nests on independent poles decreased like at the electricity poles. This is especially apparent in Szabolcs-Szatmár-Bereg, where there is a big amount of these poles. We can assume the same as with the electricity poles: after the nest sites with the best location were occupied, the remaining ones did not become more attractive compared to another possible nest sites. In Calabria, Italy, recolonization of White Stork was successfully facilitated with independent poles, the population grew threefold from 2007 to 2012. But the study underlined that it is important to keep distance between the poles, because competition arises within neighbor pairs too close (<600 m) to each other (Santopaolo 2013). This distance is not standard, however, since the quality of habitat affects the size of the territory (Ożgo & Boguczki 1999) and so the density of pairs. Storks still breed colonially in areas with high carrying capacity, for example in Spain (Vergara & Aguirre 2006), in Poland (Tryjanowski *et al.* 2005a) or in Nagyiván next to Hortobágy National Park, Hungary (golya.mme.hu).

Therefore, placement of nest supports and/or indepentent poles can truly be efficient only with the consideration of the habitat needs: it worth setting these tools up where reliable models confirm that the expected number of fledglings is high enough to sustain or even increase the population (Olsson & Arvid 2014). Beside that it is also important to protect and/or maintain the old, big nests, because those are occupied more often (Tryjanowski 2005b) and productivity is higher at those nests (Vergara 2010). White Stork is a good indicator of biodiversity, so by protection of this species, we also help the case of biodiversity of habitats (Latus *et al.* 2000) and farmland birds (Kosicki 2007, Tobolka *et al*. 2012).

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References

Aguirre, J. I. & Vergara, P. 2009. Census methods for White stork *(Ciconia ciconia)*: bias in sampling effort related to the frequency and date of nest visits. – Journal of Ornithology 150(1): 147–153. DOI: 10.1007/s10336-008-0329-3

Atemasova, T. A., Atemasov, A. A. & Brusentsova, N. A. 2016. White Stork at the Northern-East of Ukraine: trends in population dynamic at the edge of range. – In: Jerzak, L., Shephard, J., Aguirre, J. I., Shamoun-Baranes, J. & Tryjanowski, P. (eds.) The White Stork: studies in biology, ecology and conservation. – Oficina Wydawnicza Uniwersytetu Zielonogórskiego, Zielona Góra, pp. 63–71.

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

BirdLife International 2004. Birds in Europe: population estimates, trends and conservation status. – Cambridge, UK: Birdlife International, Birdlife Conservation Series, No.12. p. 47.

BirdLife International 2016. Species factsheet: *Ciconia ciconia* (2015) European Red List Assessment. – http://datazone.birdlife.org/userfiles/file/Species/erlob/supplementarypdfs/22697691_ciconia_ciconia.pdf

Boguczki, Z. & Ożgo, M. 1999. Changes in the nest site selection of the White Stork *Ciconia ciconia* in Wielkopolska (Western Poland) over the period 1974–1994. – In: Schulz, H. (ed.) Weissstorch im Aufwind? – White Storks on the up? – Proceedings of the International Symposium on the White Stork, Hamburg 1996. NABU, Bonn, pp. 437−442.

Boldogh, S. A. 2009. Védett gerincesek konzervációbiológiája – monitoring és fajmegőrzési programok tervezése és kivitelezése [Conservation biology of protected vertebrates – planning and implementation of conservation and monitoring programmes]. – Debreceni Egyetem Természettudományi Doktori Tanács, Juhász-Nagy Pál Doktori Iskola, pp. 51−65.

Boldogh, S. 1998. A fehér gólya *(Ciconia ciconia)* hatékony védelmét megalapozó vizsgálatok tapasztalatai Borsod-Abaúj-Zemplén megyében [Studies for the effective protection of the White Stork *(Ciconia ciconia)* in Borsod-Abaúj-Zemplén County, NE Hungary]. – Ornis Hungarica 8(Suppl.1): 133–136.

Cramp, S. & Simmons, K. E. L. 1977. White Stork. – In: Cramp S., Simmons K. E. L. (eds.) Handbook of the Birds of the Western Palearctic, Vol. 1. – Oxford University Press, Oxford, pp. 328–335.

Daniluk, J., Korbal-Daniluk, A. & Mitrus, C. 2006. Changes in population size, breeding success and nest location of a local White Stork *Ciconia ciconia* population in Eastern Poland. – In: Tryjanowski, P., Sparks, T. H. & Jerzak, L. (eds.) The White Stork in Poland: studies in biology, ecology and conservation. – Bogucki Wydawnictwo Naukowe, Poznań, pp. 15–21.

Denac, D. 2006a Resourse-dependent weather effect in the reproduction of the White Stork *Ciconia ciconia*. − Ardea 94(2): 233−240.

Denac, D. 2006b Intraspecific exploitation competition as cause for density dependent breeding success in the White Stork. – Waterbirds 29: 391–394.

Denac, D. 2010. Population dynamics of the White Stork *Ciconia ciconia* in Slovenia between 1999 and 2010. – Acrocephalus 31(145/146): 101–114. DOI: 10.2478/v10100-010-0007-4

Forgách, B. 1997. A fehér gólya (*Ciconia c. ciconia* L.) állományának helyzete Békés megyében [The situation of the White Stork population in Békés County]. – A Puszta 14: 133−138. (in Hungarian)

Fulín, M. 1999. The White Stork in Slovakia in 1994 and 1995. – In: Schulz, H. (ed.) Weissstorch im Aufwind? – White Storks on the up? – Proceedings of the International Symposium on the White Stork, Hamburg 1996. NABU, Bonn, pp. 437−442.

Gadenne, H., Cornulier, T., Eraud, C., Barbraud, J. C. & Barbraud, C. 2014. Evidence for density-dependent habitat occupancy at varying scales in an expanding bird population. – Population Ecology 56(3): 493–506. DOI: 10.1007/s10144-014-0435-4

Galarza, A. & García, I. 2012. Restocking White Stork *Ciconia ciconia* (L., 1758) population in Biscay: reintroduction in the Urdaibai Biosphere Reserve. – Munibe Ciencias Naturales 60: 191–200.

Garrido, J. R. & Fernandez-Cruz, M. 2003. Effects of power lines on a White Stork *Ciconia ciconia* population in central Spain. – Ardeola 50: 191–200.

Goriup, P. D. & Schulz, H. 1991. Conservation management of the White Stork. − In: Salathé, T. (ed.) Conserving Migratory Birds. − ICBP Techn. Publ. 12, Cambridge, pp. 97−127.

Gilbert, N. I., Correia, R. A., Silva, J. P., Pacheco, C., Catry, I., Atkinson, P. W., Gill, J. A. & Franco, A. M. A. 2016. Are White Storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident White Storks *(Ciconia ciconia)* from a partially migratory population. − Movement Ecology 4:7. DOI: 10.1186/s40462-016-0070-0

Hadarics, T. & Zalai, T. 2008. Nomenclator Avium Hungariae – An annonated list of the birds of Hungary. – MME Birdlife Hungary, Budapest, p. 78. (in Hungarian and English)

Homonnay, N. 1964. Magyarország és környező területei gólyaállományának mennyiségi felvételezése az 1941. évben [Quantitative census of the White Stork population of Hungary and neighboring areas in 1941]. − Aquila 69/70: 83−102. (in Hungarian and German)

Horváth, M., Demeter, I., Bagyura, J., Kovács, A., Lovászi, P., Nagy, K., Szügyi, K. & Tóth, P. 2010. Madarak és légvezetékek [Birds and overhead power lines]. – Magyar Madártani és Természetvédelmi Egyesület, Budapest, p. 25. (in Hungarian)

Infante, O. & Peris, S. 2003. Bird nesting on electric power supports in northwestern Spain. − Ecological Engineering 20: 321−326. DOI: 10.1016/S0925-8574(03)00013-2

Jakab, B. 1989. A talajtípusok szerepe a fehér gólya *(Ciconia ciconia)* elterjedésében Magyarországon [The role of soil types in the distribution of White Stork in Hungary]. – A Móra Ferenc Múzeum Évkönyve 1989–90(1): 519−531. (in Hungarian and German)

Jakab, B. 1991. A hazai madárbarát villamosművek szerepe a fehér gólya állományának alakulásában [The role of the bird friendly electric power industry in forming the White Stork population in Hungary]. – In: Király, Á. & Gazda, I. (eds.) Gólyavédelem a villamoshálózatokon [White Stork protection on electricity networks]. − A Magyar Tudománytörténeti Intézet Tudományos Közleményei 79., Magyar Elektrotechnikai Múzeum, Budapest, pp. 9–14. (in Hungarian)

Jakubiec, Z. 1991. Causes of breeding losses and adult mortality in White Stork *Ciconia ciconia* (L.) in Poland. − Studia Nature 37: 107–124.

Janaus, M. & Stipniece, A. 2013. The White Stork in Latvia from 1934 to 2005. – In: NABU. White Stork populations across the world – Results of the 6th International White Stork Census 2004/05., Berlin (Imprint)

Janiszewski, T., Minias, P. & Wojciechowski, Z. 2015. Selective forces responsible for transition to nesting on electricity poles in the White Stork *Ciconia ciconia*. – Ardea 103: 39–50. DOI: 10.5253/arde.v103i1.a4

Kanyamibwa, S., Bairlein, F. & Schierer, A. 1993. Comparison of survival rates between populations of the White Stork *Ciconia ciconia* in Central Europe. − Ornis Scandinavica 24: 297−302. DOI: 10.2307/3676791

Keve, A. 1957. White-Stork-Census in Hungary in the years 1948 and 1949. − Aquila 63−64: 211−225.

Kósa, F., Demeter, L., Papp, T., Philippi, F., Lutsch, H-J. & György, K. 2002. Distribution, population size and dynamics of the White Stork (*Ciconia ciconia* L.) in the upper and middle Olt river basin. – Tiscia Monograph Series 6: 205−233.

Kosicki, J. Z. & Kuźniak, S. 2006. Long-term population size and productivity dinamics of a local White Stork *Ciconia ciconia* population in Wielkopolska. – In: Tryjanowski, P., Sparks, T. H. & Jerzak, L. (eds.) The White Stork in Poland: studies in biology, ecology and conservation. – Bogucki Wydawnictwo Naukowe, Poznań, pp. 23−33.

Kosicki, J. Z., Sparks, T. H. & Tryjanowski, P. 2007. House Sparrows benefit from the conversation of White Storks. – Naturwissenschaften 94: 412−415. DOI: 10.1007/s00114-006-0207-x

Köhler, W. 1999. Bestandsentwicklung des Weißstorches in der Niederlausitz/Deutschland und Verluste an Freileitungen in Ostdeutschland [Population development of the White Stork in Niederlausitz/Germany and deaths caused by overhead lines in eastern Germany]. – In: Schulz, H. (ed.) Weissstorch im Aufwind? – White Storks on the up? – Proceedings of the International Symposium on the White Stork, Hamburg 1996. NABU, Bonn, pp. 437−442. (in German)

Kruszyk, R., Ciach, M. 2010. White Storks, *Ciconia ciconia*, forage on rubbish dumps in Poland – a novel behaviour in population. – European Journal of Wildlife Research 56: 83–87. DOI: 10.1007/s10344-009-0313-0

Latus, C., Kujawa, K., Glemnitz, M. & Nauk, P. A. 2000. The influence of landscape structure on White Stork's *Ciconia ciconia* nest distribution. – Acta Ornithologica 35: 97–102.

Lovászi, P. & Rékási, J. 2009. A fehér gólya [White Stork]. – 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. 186−192.

Lovászi, P. 2004. A fehér gólya *(Ciconia ciconia)* helyzete Magyarországon az 1941–2002 között [Status of the White Stork *(Ciconia ciconia)* in Hungary between 1941 and 2002]. – Aquila 111: 11–18. (in Hungarian with English Summary)

Magyar, G., Hadarics, T., Waliczky, Z., Schmidt, A., Nagy, T. & Bankovics, A. 1998. Nomenclator Avium Hungariae. Magyarország madarainak névjegyzéke [An Annotated List of the Birds of Hungary]. – KTM Természetvédelmi Hivatal Madártani Intézete – Magyar Madártani és Természetvédelmi Egyesület – Winter Fair, Budapest-Szeged, p. 32. (in Hungarian and English)

Mezősi, G. 2011. Magyarország természetföldrajza [Geography of Hungary]. – Akadémiai Kiadó, Budapest (in Hungarian)

Moreira, F., Encarnação, V., Rosa, G., Gilbert, N., Infante, S., Costa, J., D'Amico, M., Martins, R. C. & Catry, I. 2017. Wired: impacts of increasing power line use by a growing bird population. – Environmental Research Letters 12: 024019. DOI: 10.1088/1748-9326/aa5c74

Mužinić, J. & Cvitan, I. 2001. Choice of nest platform material for the White Stork *(Ciconia ciconia)*. – Israel Journal of Zoology 47: 167–171.

Nowakowski, J. J. & Wasilewska, B. 2006. The relationship between spatial distribution, intrapopulation competition and the reproduction parameters of White Stork *Ciconia ciconia* in the southern basin of the Biebrza River during the years 1994–1999. – In: Tryjanowski, P., Sparks, T. H. & Jerzak, L. (eds.) The White Stork in Poland: studies in biology, ecology and conservation. – Bogucki Wydawnictwo Naukowe, Poznań, pp. 99–113.

Olsson, O. & Arvid, B. 2014. A model for habitat selection and species distribution derived from central place foraging theory. – Oecologia 175(2): 537–548. DOI: 10.1007/s00442-014-2931-9

Omnuş, O., Bolat, Ü., Usta, T., Siki, M. & Altun, C. 2016. Filling the largest gap of the White Stork *(Ciconia ciconia)* population in the Western Palearctic region: the results of the first complete countrywide White Stork census in Turkey. – In: Jerzak, L., Shephard, J., Aguirre, J. I., Shamoun-Baranes, J. & Tryjanowski, P. (eds.) The White Stork: studies in biology, ecology and conservation. – Oficina Wydawnicza Universytetu Zielonogórskiego, Zielona Góra, pp. 63–71.

Ots, M. 2009. The White Stork *(Ciconia ciconia)* in Estonia till year 2008. – Hirundo 22: 32–42.

Ożgo, M. & Boguczki, Z. 1999. Home range and intersexual differences in foraging habitat use of a White Stork *(Ciconia ciconia)* breeding pair. – In: Schulz, H. (ed.) Weissstorch im Aufwind? – White Storks on the up? – Proceedings of the International Symposium on the White Stork, Hamburg 1996. NABU, Bonn, pp. 437−442.

Pelle, Z. 1999. Status and biology of the White Stork in Yugoslavia. – In: Schulz, H. (ed.) White Storks on the up? – Proceedings of the International Symposium on the White Stork, Hamburg 1996. NABU, Bonn, pp. 219−221.

Petrov, T., Iankov, P. & Georgiev, D. 1999. Population status of the White Stork *(Ciconia ciconia)* in Bulgaria in the years 1994/95. – In: Schulz, H. (ed.) Weissstorch im Aufwind? – White Storks on the up? – Proceedings of the International Symposium on the White Stork, Hamburg 1996. NABU, Bonn, pp. 241−247.

R Core Team 2015. R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/

Samusenko, I. 2013. The breeding population of the White Stork in Belarus in 2004–2005. – In: NABU 2013. White Stork populations across the world. – Results of the 6th International White Stork Census 2004/05., Berlin

Schulz, H. 1994. The White Stork *Ciconia ciconia* – In: Tucker, G. M. & Heath, M. F. (eds.) Birds in Europe and their conservation status. − BirdLife Conservation Series 3. BirdLife International, Cambridge, U.K., pp. 100–101.

Santopaolo, R., Godino, G., Golia, S., Mancuso, A., Monterosso, G., Pucci, M., Santopaolo, F. & Gustin, M. 2013. Increase of White Stork *Ciconia ciconia* population attracted by artificial nesting platforms. – Conservation Evidence 10: 67−69.

Szép, T., Nagy, K., Nagy, Zs. & Halmos, G. 2012. Population trends of common breeding and wintering birds in Hungary, decline of long-distance migrant and farmland birds during 1999–2012. – Ornis Hungarica 20(2): 13–63. DOI: 10.2478/orho-2013-0007

Thomsen, K. & Hötker, H. 2006. The 6th International White Stork Census: 2004–2005. – In: Boere, G. C., Galbraith, C. A. & Sroud, D. A. (eds.) Waterbirds around the World. – The Stationery Office, Edinburgh, pp. 493−495.

Tobolka, M., Sparks, T. H. & Tryjanowski, P. 2012. Does the White Stork *Ciconia ciconia* reflect farmland bird diversity? – Ornis Fennica 89: 222–228.

Tobolka, M., Kúzniak, S., Zolnierowicz, K., Sparks, T. H. & Tryjanowski, P. 2013. New is not always better: low breeding success and different occupancy pattern in newly built nests of a long-lived species, the White Stork *Ciconia ciconia*. – Bird Study 60: 399–403. DOI: 10.1080/00063657.2013.818934

Tortosa, F. S., Caballero, J. M. & Reyes-Lopez, J. 2002. Effect of rubbish dumps on breeding success in the White Stork in southern Spain. – Waterbirds 25: 39–43. DOI: 10.1675/1524-4695(2002)025[0039:EORDOB]2.0.CO;2

Tryjanowski, P., Jerzak, L. & Radkiewicz, J. 2005a Effect of water level and livestock on the productivity and numbers of breeding White Storks. – Waterbirds 28: 378–382. DOI: 10.1675/1524-4695(2005)028[0378:EOWLAL]2.0.CO;2

Tryjanowski, P., Sparks, T. H. & Profus, P. 2005b Uphill shifts in the distribution of the White Stork *Ciconia ciconia* in southern Poland: the importance of nest quality. – Diversity and Distributions 11: 219−223. DOI: 10.1111/j.1366-9516.2005.00140.x

Tryjanowski, P., Kosicki, J. Z., Kuźniak, S. & Sparks, T. H. 2009. Long-term changes and breeding success in relation to nesting structures used by the White Stork *Ciconia ciconia*. – Annales Zoologici Fennici 46: 34−38. DOI: 10.5735/086.046.0104

Tucakov, M. 2006. Population development, nest site selection and conservation measures for White Stork *Ciconia ciconia* along the lower Tamiš River (Vojvodina, N Serbia). − Acrocephalus 27: 13–20.

Vergara, P. & Aguirre, I. J. 2006. Age and breeding success related to nest position in a White Stork *Ciconia ciconia* colony. − Acta Oecologica 30: 414–418. DOI: 10.1016/j.actao.2006.05.008

Vergara, P., Gordo, O. & Aguirre, J. I. 2010. Nest size, nest building behaviour and breeding success in a species with nest reuse: The White Stork *Ciconia ciconia.* – Annales Zoologici Fennici 47(3): 184–194. DOI: 10.5735/086.047.0303

Vaitkuvienė, D. & Dagys, M. 2014. Possible effects of electromagnetic field on White Storks *Ciconia ciconia* breeding on low-voltage electricity line poles. − Zoology and Ecology 24(4): 289−296. DOI: 10.1080/21658005.2014.962783

Vaitkuvienė, D. & Dagys, M. 2015. Two-fold increase in White Stork *(Ciconia ciconia)* population in Lithuania: a consequence of changing agriculture? – Turkish Journal of Zoology 39: 144–152. DOI: 10.3906/zoo-1402-44

Yavuz, K. E., Yavuz, N., Tavares, J. & Barış, Y. S. 2012. Nesting habits and breeding success of the White Stork, *Ciconia ciconia*, in the Kızılırmak delta, Turkey. – Zoology in the Middle East 57: 19–26. DOI: 10.1080/09397140.2012.10648959

Table 1. Number of nest by counties in every year
1. táblázat A fészkek száma megyénként és évenként

	1958	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**	**1994**	**1999**	**2000**	**2001**	**2002**
GYMS	277	202	148	139	130	146	107	109	141	4	157	1
Somogy	586	515	306	263	225	235	177	84	106	9	7	7
BK	530	409	271	262	179	256	150	16	38	6	66	3
Békés	319	202	218	182	196	199	154	0	0	0	2	253
HB	1010	795	466	481	495	402	350	0	261	0	2	243
SZSZB	1026	723	461	424	447	421	349	301	353	218	263	405

	2003	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**
GYMS	21	256	181	177	33	22	183	183	181	182	171
Somogy	154	307	283	298	302	121	139	106	103	119	75
BK	57	241	92	46	127	51	131	92	202	194	149
Békés	32	119	81	278	370	375	387	403	403	423	417
HB	195	225	251	610	471	134	722	581	434	286	140
SZSZB	485	625	535	571	535	578	588	529	385	535	610

Table 2. Proportions of nest sites by counties in the 1958–1989 period, based on postal forms
2. táblázat A fészekalapok arányai megyénként az 1958–1989-es periódusban, a postai adatlapok alapján

GYMS	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ep	0.00	0.01	0.02	0.08	0.28	0.45	0.60
tr	0.13	0.11	0.05	0.11	0.07	0.04	0.00
bu	0.79	0.83	0.87	0.76	0.62	0.49	0.36
ot	0.08	0.06	0.05	0.04	0.04	0.02	0.04
Somogy	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ep	0.00	0.00	0.03	0.09	0.23	0.53	0.64
tr	0.48	0.45	0.44	0.30	0.21	0.11	0.02
bu	0.49	0.54	0.50	0.56	0.48	0.35	0.33
ot	0.03	0.00	0.02	0.05	0.08	0.00	0.01
BK	1958	1963	1968	1974	1979	1984	1989
ep	0.00	0.00	0.01	0.09	0.28	0.48	0.60
tr	0.50	0.52	0.47	0.43	0.33	0.19	0.14
bu	0.45	0.46	0.50	0.42	0.33	0.31	0.25
ot	0.04	0.02	0.02	0.06	0.05	0.02	0.02
Békés	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ep	0.00	0.00	0.01	0.07	0.36	0.52	0.49
tr	0.05	0.10	0.07	0.06	0.07	0.02	0.01
bu	0.90	0.88	0.86	0.84	0.56	0.45	0.48
ot	0.05	0.02	0.07	0.03	0.01	0.00	0.02

HB	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ep	0.00	0.00	0.02	0.10	0.30	0.56	0.69
tr	0.12	0.14	0.18	0.19	0.16	0.11	0.04
bu	0.58	0.65	0.64	0.56	0.44	0.30	0.25
ot	0.30	0.21	0.16	0.15	0.09	0.03	0.01
SZSZB	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ep	0.00	0.00	0.00	0.08	0.25	0.48	0.64
tr	0.09	0.12	0.14	0.24	0.19	0.12	0.07
bu	0.84	0.76	0.79	0.57	0.47	0.33	0.26
ot	0.07	0.11	0.06	0.11	0.09	0.06	0.03

Table 3. Proportion of nest sites by counties in the 1958–1989 period, based on questionnaires
3. táblázat A fészekalapok arányai megyénként az 1958–1989-es periódusban, a kérdőívek alapján

GYMS	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ep	0.00	0.01	0.05	0.12	0.27	0.49	0.73
ot	0.03	0.01	0.02	0.03	0.01	0.00	0.04
ro	0.29	0.21	0.32	0.18	0.07	0.02	0.00
ch	0.59	0.63	0.52	0.62	0.61	0.44	0.23
tr	0.09	0.15	0.09	0.04	0.04	0.04	0.00
Somogy	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ep	0.00	0.00	0.05	0.21	0.28	0.58	0.68
ot	0.06	0.06	0.03	0.02	0.00	0.03	0.01
ro	0.11	0.22	0.13	0.09	0.01	0.04	0.03
ch	0.23	0.32	0.61	0.45	0.57	0.29	0.21
tr	0.60	0.40	0.18	0.24	0.14	0.06	0.07
BK	1958	1963	1968	1974	1979	1984	1989
ep	0.00	0.00	0.05	0.12	0.35	0.44	0.52
ot	0.00	0.02	0.05	0.07	0.05	0.00	0.02
ro	0.00	0.00	0.09	0.09	0.01	0.01	0.11
ch	0.00	0.14	0.27	0.36	0.25	0.32	0.32
tr	1.00	0.84	0.55	0.35	0.34	0.22	0.03
Békés	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ep	0.00	0.00	0.00	0.07	0.29	0.55	0.57
ot	0.00	0.03	0.03	0.07	0.03	0.01	0.05
ro	0.00	0.00	0.03	0.01	0.01	0.02	0.00
ch	1.00	0.90	0.93	0.82	0.64	0.37	0.34
tr	0.00	0.06	0.03	0.03	0.03	0.05	0.03
HB	1958	1963	1968	1974	1979	1984	1989
ep	0.00	0.00	0.04	0.38	0.50	0.71	0.91

Békés	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ot	0.00	0.00	0.05	0.11	0.02	0.03	0.01
ro	0.17	0.00	0.55	0.11	0.09	0.03	0.00
ch	0.75	0.00	0.19	0.28	0.27	0.16	0.06
tr	0.08	1.00	0.17	0.11	0.13	0.06	0.02
SZSZB	**1958**	**1963**	**1968**	**1974**	**1979**	**1984**	**1989**
ep	0.00	0.00	0.01	0.05	0.44	0.60	0.70
ot	0.00	0.01	0.01	0.01	0.04	0.02	0.16
ro	0.28	0.55	0.68	0.24	0.22	0.14	0.06
ch	0.51	0.32	0.12	0.53	0.17	0.14	0.06
tr	0.21	0.12	0.19	0.16	0.13	0.10	0.03

Table 4. Linear regression of nest sites by counties in the 1958–1989 period. The first abbrevation indicates the nest site, the second the data source in the upper left corners

4. táblázat A fészekalapok lineáris regressziói megyénként az 1958–1989-es periódusban. Az első rövidítés a fészekalapot, a második a felmérés típusát jelzi minden bal felső sarokban

GYMS									
ep (qu)	estimate	std. error	t value	p value	ep (po)	estimate	std. error	t value	p value
(intercept)	-44.45	8.463	-5.252	0.003	(intercept)	-39.433	6.696	-5.889	0.002
year	0.023	0.004	5.28	0.003	year	0.02	0.003	5.919	0.002
tr (qu)	estimate	std. error	t value	p value	tr (po)	estimate	std. error	t value	p value
(intercept)	7.091	1.996	3.553	0.016	(intercept)	6.769	2.069	3.272	0.022
year	-0.004	0.001	-3.522	0.017	year	-0.003	0.001	-3.237	0.023
ro (qu)	estimate	std. error	t value	p value	bu (po)	estimate	std. error	t value	p value
(intercept)	19.274	3.679	5.239	0.003	(intercept)	30.683	6.612	4.64	0.006
year	-0.01	0.002	-5.199	0.003	year	-0.015	0.003	-4.538	0.006
ch (qu)	estimate	std. error	t value	p value	bu (qu)	estimate	std. error	t value	p value
(intercept)	17.711	7.228	2.45	0.058	(intercept)	36.985	7.148	5.174	0.004
year	-0.009	0.004	-2.382	0.063	year	-0.018	0.004	-5.085	0.004
ot (qu)	estimate	std. error	t value	p value	ot (po)	estimate	std. error	t value	p value
(intercept)	-0.124	1.08	-0.115	0.913	(intercept)	2.981	0.747	3.992	0.01
year	0	0.001	0.133	0.9	year	-0.001	0	-3.931	0.011

Somogy									
ep (qu)	estimate	std. error	t value	p value	ep (po)	estimate	std. error	t value	p value
(intercept)	-43.384	6.158	-7.045	0.001	(intercept)	-42.891	8.095	-5.298	0.003
year	0.022	0.003	7.084	0.001	year	0.022	0.004	5.326	0.003
tr (qu)	estimate	std. error	t value	p value	tr (po)	estimate	std. error	t value	p value
(intercept)	28.104	5.95	4.723	0.005	(intercept)	31.224	2.918	10.7	1.23E-04
year	-0.014	0.003	-4.686	0.005	year	-0.016	0.001	-10.6	1.29E-04
ro (qu)	estimate	std. error	t value	p value	bu (po)	estimate	std. error	t value	p value
(intercept)	9.117	3.355	2.718	0.042	(intercept)	12.521	4.617	2.712	0.042
year	-0.005	0.002	-2.693	0.043	year	-0.006	0.002	-2.611	0.048
ch (qu)	estimate	std. error	t value	p value	bu (qu)	estimate	std. error	t value	p value
(intercept)	0.835	11.027	0.076	0.943	(intercept)	9.952	10.872	0.915	0.402
year	0	0.006	-0.044	0.967	year	-0.005	0.006	-0.876	0.421
ot (qu)	estimate	std. error	t value	p value	ot (po)	estimate	std. error	t value	p value
(intercept)	2.827	1.047	2.701	0.043	(intercept)	0.147	2.2	0.067	0.949
year	-0.001	0.001	-2.677	0.044	year	0	0.001	-0.054	0.959

BK									
ep (qu)	estimate	std. error	t value	p value	ep (po)	estimate	std. error	t value	p value
(intercept)	-33.344	4.436	-7.517	0.001	(intercept)	-40.575	6.877	-5.9	0.002
year	0.017	0.002	7.56	0.001	year	0.021	0.003	5.931	0.002
tr (qu)	estimate	std. error	t value	p value	tr (po)	estimate	std. error	t value	p value
(intercept)	60.072	5.441	11.04	1.06E-04	(intercept)	25.914	3.772	6.869	0.001
year	-0.03	0.003	-10.96	1.10E-04	year	-0.013	0.002	-6.772	0.001
ro (qu)	estimate	std. error	t value	p value	bu (po)	estimate	std. error	t value	p value
(intercept)	-3.317	3.528	-0.94	0.39	(intercept)	14.846	3.109	4.775	0.005
year	0.002	0.002	0.953	0.385	year	-0.007	0.002	-4.65	0.006
ch (qu)	estimate	std. error	t value	p value	bu (qu)	estimate	std. error	t value	p value
(intercept)	-14.988	6.22	-2.41	0.061	(intercept)	-18.305	9.027	-2.028	0.098
year	0.008	0.003	2.446	0.058	year	0.009	0.005	2.057	0.095
ot (qu)	estimate	std. error	t value	p value	ot (po)	estimate	std. error	t value	p value
(intercept)	-0.362	1.96	-0.185	0.861	(intercept)	0.815	1.374	0.593	0.579
year	0	0.001	0.199	0.85	year	0	0.001	-0.568	0.594

Békés									
ep (qu)	estimate	std. error	t value	p value	ep (po)	estimate	std. error	t value	p value
(intercept)	-39.41	7.463	-5.28	0.003	(intercept)	-38.636	7.441	-5.192	0.003
year	0.02	0.004	5.307	0.003	year	0.02	0.004	5.22	0.003
tr (qu)	estimate	std. error	t value	p value	tr (po)	estimate	std. error	t value	p value
(intercept)	-0.644	1.527	-0.422	0.691	(intercept)	3.847	1.721	2.235	0.076
year	0	0.001	0.442	0.677	year	-0.002	0.001	-2.204	0.079
ro (qu)	estimate	std. error	t value	p value	bu (po)	estimate	std. error	t value	p value
(intercept)	-0.498	0.731	-0.681	0.526	(intercept)	33.224	6.257	5.31	0.003
year	0	0	0.695	0.518	year	-0.016	0.003	-5.196	0.003
ch (qu)	estimate	std. error	t value	p value	bu (qu)	estimate	std. error	t value	p value
(intercept)	47.095	5.98	7.875	0.001	(intercept)	46.598	6.322	7.371	0.001
year	-0.024	0.003	-7.759	0.001	year	-0.023	0.003	-7.259	0.001
ot (qu)	estimate	std. error	t value	p value	ot (po)	estimate	std. error	t value	p value
(intercept)	-1.403	1.666	-0.842	0.438	(intercept)	2.565	1.489	1.722	0.146
year	0.001	0.001	0.86	0.429	year	-0.001	0.001	-1.704	0.149

HB									
ep (qu)	estimate	std. error	t value	p value	ep (po)	estimate	std. error	t value	p value
(intercept)	-59.628	6.427	-9.278	2.45E-04	(intercept)	-46.585	8.099	-5.752	0.002
year	0.03	0.003	9.332	2.38E-04	year	0.024	0.004	5.781	0.002
tr (qu)	estimate	std. error	t value	p value	tr (po)	estimate	std. error	t value	p value
(intercept)	28.91	23.822	1.214	0.279	(intercept)	4.186	3.434	1.219	0.277
year	-0.015	0.012	-1.204	0.282	year	-0.002	0.002	-1.179	0.291
ro (qu)	estimate	std. error	t value	p value	bu (po)	estimate	std. error	t value	p value
(intercept)	12.439	13.526	0.92	0.4	(intercept)	25.841	5.439	4.751	0.005
year	-0.006	0.007	-0.91	0.405	year	-0.013	0.003	-4.661	0.006
ch (qu)	estimate	std. error	t value	p value	bu (qu)	estimate	std. error	t value	p value
(intercept)	22.642	16.464	1.375	0.227	(intercept)	35.081	21.522	1.63	0.164
year	-0.011	0.008	-1.361	0.232	year	-0.018	0.011	-1.613	0.168
ot (qu)	estimate	std. error	t value	p value	ot (po)	estimate	std. error	t value	p value
(intercept)	-0.933	3.097	-0.301	0.775	(intercept)	17.559	1.757	9.994	1.71E-04
year	0	0.002	0.311	0.768	year	-0.009	0.001	-9.916	1.78E-04

SZSZB									
ep (qu)	estimate	std. error	t value	p value	ep (po)	estimate	std. error	t value	p value
(intercept)	-48.538	9.287	-5.226	0.003	(intercept)	-41.858	7.804	-5.364	0.003
year	0.025	0.005	5.253	0.003	year	0.021	0.004	5.391	0.003
tr (qu)	estimate	std. error	t value	p value	tr (po)	estimate	std. error	t value	p value
(intercept)	7.78	2.518	3.09	0.027	(intercept)	0.42	4.567	0.092	0.93
year	-0.004	0.001	-3.041	0.029	year	0	0.002	-0.061	0.953
ro (qu)	estimate	std. error	t value	p value	bu (po)	estimate	std. error	t value	p value
(intercept)	24.5	13.074	1.874	0.12	(intercept)	40.044	3.951	10.135	1.60E-04
year	-0.012	0.007	-1.852	0.123	year	-0.02	0.002	-9.989	1.72E-04
ch (qu)	estimate	std. error	t value	p value	bu (qu)	estimate	std. error	t value	p value
(intercept)	18.423	10.187	1.809	0.13	(intercept)	42.923	10.148	4.23	0.008
year	-0.009	0.005	-1.785	0.134	year	-0.021	0.005	-4.177	0.009
ot (qu)	estimate	std. error	t value	p value	ot (po)	estimate	std. error	t value	p value
(intercept)	-6.792	2.854	-2.38	0.063	(intercept)	2.394	2.037	1.175	0.293
year	0.003	0.001	2.393	0.062	year	-0.001	0.001	-1.137	0.307

Table 5. LMM of nest sites for the 1958–1989 period. First part indicates the nest site, second part the type of variable in the upper left corners. The model compares the postal form to the questionnaires

5. táblázat A fészekalapok lineáris vegyes modellje az 1958–1989-es periódusra. Az első szó a fészekalapot, a második a változó típusát jelzi minden bal felső sarokban. A modell a postai adatlapot hasonlítja a kérdőívekhez

bu, random:		variance	std. dev.	ep, random:		variance	std. dev.
county	(intercept)	0.01957	0.1399	county	(intercept)	0.000475	0.0218
residual		0.02307	0.1519	residual		0.010079	0.1004
bu, fixed:	estimate	std. error	t value	ep, fixed:	estimate	std. error	t value
(intercept)	25.8368	3.136143	8.238	(intercept)	-43.2131	2.0725	-20.851
year	-0.01284	0.001589	-8.083	year	0.02202	0.00105	20.969
source (po)	0.058383	0.033146	1.761	source (po)	-0.02919	0.02191	-1.332
tr, random:		variance	std. dev.	eg, random:		variance	std. dev.
county	(intercept)	0.0175	0.1323	county	(intercept)	0.000387	0.01967
residual		0.01926	0.1388	residual		0.001837	0.04286
tr, fixed:	estimate	std. error	t value	eg, fixed:	estimate	std. error	t value
(intercept)	16.97768	2.865058	5.926	(intercept)	1.62465	0.88471	1.836
year	-0.00851	0.001451	-5.862	year	-0.00081	0.000448	-1.804
source (po)	-0.01018	0.030281	-0.336	source (po)	0.029663	0.009352	3.172

Table 6. Proportion of nest sites by counties in the 1994–2013 period
6. táblázat A fészekalapok aránya megyénként az 1994–2013-as periódusban

GYMS	1994	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
ep_s	0.92	0.87	0.25	0.80	1.00	0.86	0.68	0.81	0.81	0.30	0.32	0.75	0.77	0.67	0.65	0.63
ep_ns	0.04	0.05	0.00	0.06	0.00	0.00	0.08	0.10	0.10	0.03	0.05	0.10	0.11	0.11	0.14	0.15
ot	0.01	0.03	0.50	0.03	0.00	0.05	0.06	0.03	0.02	0.24	0.14	0.08	0.04	0.08	0.07	0.06
ro	0.01	0.00	0.00	0.02	0.00	0.05	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00
ch	0.02	0.04	0.25	0.08	0.00	0.05	0.16	0.06	0.06	0.42	0.50	0.06	0.07	0.13	0.13	0.16
tr	0.01	0.01	0.00	0.01	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00
Somogy	1994	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
ep_s	0.85	0.76	0.89	0.86	0.86	0.71	0.73	0.75	0.73	0.74	0.72	0.75	0.61	0.63	0.64	0.65
ep_ns	0.04	0.09	0.00	0.00	0.00	0.11	0.10	0.11	0.11	0.11	0.08	0.12	0.20	0.18	0.16	0.23
ot	0.04	0.04	0.11	0.14	0.14	0.08	0.06	0.06	0.06	0.06	0.09	0.06	0.08	0.07	0.07	0.01
ro	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ch	0.08	0.09	0.00	0.00	0.00	0.09	0.11	0.08	0.09	0.10	0.10	0.06	0.09	0.11	0.13	0.11
tr	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.00
BK	1994	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
ep_s	0.63	0.61	0.50	0.64	1.00	0.82	0.66	0.77	0.67	0.77	0.69	0.64	0.62	0.68	0.72	0.64
ep_ns	0.13	0.13	0.00	0.05	0.00	0.12	0.10	0.07	0.02	0.06	0.04	0.16	0.15	0.12	0.09	0.09
ot	0.06	0.11	0.33	0.08	0.00	0.02	0.07	0.05	0.09	0.06	0.06	0.11	0.09	0.07	0.06	0.07
ro	0.06	0.00	0.00	0.05	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
ch	0.13	0.16	0.17	0.20	0.00	0.02	0.17	0.11	0.22	0.11	0.22	0.08	0.14	0.12	0.12	0.19
tr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Békés	1994	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
ep_s	n.a.	n.a.	n.a.	0.50	0.65	0.50	0.63	0.60	0.57	0.59	0.59	0.57	0.55	0.53	0.53	0.53
ep_ns	n.a.	n.a.	n.a.	0.00	0.09	0.09	0.08	0.07	0.14	0.15	0.16	0.18	0.21	0.22	0.22	0.22
ot	n.a.	n.a.	n.a.	0.00	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
ro	n.a.	n.a.	n.a.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ch	n.a.	n.a.	n.a.	0.50	0.21	0.38	0.26	0.30	0.26	0.22	0.21	0.21	0.20	0.20	0.21	0.21
tr	n.a.	n.a.	n.a.	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HB	1994	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
ep_s	n.a.	0.81	n.a.	0.50	0.84	0.85	0.79	0.81	0.77	0.78	0.77	0.75	0.75	0.74	0.70	0.62
ep_ns	n.a.	0.08	n.a.	0.00	0.11	0.06	0.09	0.08	0.12	0.11	0.10	0.15	0.17	0.16	0.19	0.15
ot	n.a.	0.03	n.a.	0.00	0.02	0.03	0.02	0.07	0.04	0.04	0.03	0.03	0.03	0.03	0.04	0.10
ro	n.a.	0.01	n.a.	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
ch	n.a.	0.06	n.a.	0.50	0.03	0.05	0.09	0.03	0.07	0.07	0.10	0.06	0.06	0.06	0.06	0.10
tr	n.a.	0.00	n.a.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
SZSZB	1994	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
ep_s	0.68	0.72	0.80	0.76	0.73	0.71	0.72	0.74	0.74	0.73	0.73	0.73	0.71	0.64	0.72	0.72
ep_ns	0.04	0.06	0.03	0.05	0.07	0.07	0.08	0.07	0.07	0.10	0.10	0.10	0.13	0.17	0.15	0.17
ot	0.24	0.17	0.11	0.16	0.17	0.18	0.15	0.15	0.15	0.15	0.14	0.14	0.13	0.16	0.10	0.09
ro	0.01	0.01	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
ch	0.02	0.04	0.04	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
tr	0.01	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00

Table 7. Linear regression of nest sites by counties in the 1994–2013 period. The abbrevation indicates the nest site in the upper left corners

7. táblázat A fészekalapok lineáris regressziói megyénként az 1994–2013-as periódusban. A rövidítés a fészekalapot jelzi minden bal felső sarokban

GYMS					Békés				
ep	estimate	std. error	t value	p value	ep	estimate	std. error	t value	p value
(intercept)	12.055	23.511	0.513	0.616	(intercept)	-27.214	8.605	-3.163	0.009
year	-0.006	0.012	-0.48	0.638	year	0.014	0.004	3.245	0.008
ep_s	estimate	std. error	t value	p value	ep_s	estimate	std. error	t value	p value
(intercept)	25.291	21.79	1.161	0.265	(intercept)	6.802	6.998	0.972	0.352
year	-0.012	0.011	-1.129	0.278	year	-0.003	0.003	-0.891	0.392
ep_ns	estimate	std. error	t value	p value	ep_ns	estimate	std. error	t value	p value
(intercept)	-13.236	3.459	-3.827	0.002	(intercept)	-34.016	3.434	-9.907	8.12E-07
year	0.007	0.002	3.847	0.002	year	0.017	0.002	9.948	7.79E-07
ro	estimate	std. error	t value	p value	ro	estimate	std. error	t value	p value
(intercept)	1.153	1.226	0.941	0.363	(intercept)	-0.684	0.146	-4.692	0.001
year	-0.001	0.001	-0.936	0.365	year	0	0	4.704	0.001
ch	estimate	std. error	t value	p value	ch	estimate	std. error	t value	p value
(intercept)	-15.258	13.921	-1.096	0.292	(intercept)	31.495	9.817	3.208	0.008
year	0.008	0.007	1.106	0.287	year	-0.016	0.005	-3.182	0.009
tr	estimate	std. error	t value	p value	tr	estimate	std. error	t value	p value
(intercept)	0.632	0.293	2014.02.16	0.049	(intercept)	0.089	0.487	0.183	0.858
year	0	0	-2.15	0.05	year	0	0	-0.178	0.862
ot	estimate	std. error	t value	p value	ot	estimate	std. error	t value	p value
(intercept)	2.418	12.595	0.192	0.851	(intercept)	-2.686	1.157	-2.321	0.041
year	-0.001	0.006	-0.185	0.856	year	0.001	0.001	2.346	0.039
Somogy					HB				
ep	estimate	std. error	t value	p value	ep	estimate	std. error	t value	p value
(intercept)	6.401	2.523	2.537	0.024	(intercept)	-8.79	14.672	-0.599	0.56
year	-0.003	0.001	-2.202	0.045	year	0.005	0.007	0.658	0.523
ep_s	estimate	std. error	t value	p value	ep_s	estimate	std. error	t value	p value
(intercept)	27.541	4.871	5.654	5.95E-05	(intercept)	32.357	4.362	7.417	2.27E-05
year	-0.013	0.002	-5.502	7.80E-05	year	-0.016	0.002	-7.242	2.79E-05
ep_ns	estimate	std. error	t value	p value	ep_ns	estimate	std. error	t value	p value
(intercept)	-21.141	4.162	-5.08	1.68E-04	(intercept)	-18.344	3.896	-4.709	0.001
year	0.011	0.002	5.105	1.60E-04	year	0.009	0.002	4.741	0.001
ro	estimate	std. error	t value	p value	ro	estimate	std. error	t value	p value
(intercept)	0	0	NA	NA	(intercept)	-0.286	0.641	-0.447	0.665
year	0	0	NA	NA	year	0	3.20E-04	0.453	0.661
ch	estimate	std. error	t value	p value	ch	estimate	std. error	t value	p value
(intercept)	-7.547	3.642	-2.072	0.057	(intercept)	-5.164	3.566	-1.448	0.178
year	0.004	0.002	2.094	0.055	year	0.003	0.002	1.466	0.173
tr	estimate	std. error	t value	p value	tr	estimate	std. error	t value	p value
(intercept)	-0.756	0.355	-2.128	0.052	(intercept)	-2.041	0.841	-2.427	0.036
year	0	1.77E-04	2.14	0.051	year	0.001	4.19E-04	2.43	0.035
ot	estimate	std. error	t value	p value	ot	estimate	std. error	t value	p value
(intercept)	2.902	3.549	0.818	0.427	(intercept)	-5.522	3.706	-1.49	0.167
year	-0.001	0.002	-0.797	0.439	year	0.003	0.002	1.501	0.164

BK					SZSZB				
ep	estimate	std. error	t value	p value	ep	estimate	std. error	t value	p value
(intercept)	-5.68	11.229	-0.506	0.621	(intercept)	6.401	2.523	2.537	0.024
year	0.003	0.006	0.575	0.575	year	-0.003	0.001	-2.202	0.045
ep_s	estimate	std. error	t value	p value	ep_s	estimate	std. error	t value	p value
(intercept)	-2.008	11.434	-0.176	0.863	(intercept)	3.434	3.251	1.056	0.309
year	0.001	0.006	0.236	0.817	year	-0.001	0.002	-0.834	0.419
ep_ns	estimate	std. error	t value	p value	ep_ns	estimate	std. error	t value	p value
(intercept)	-3.671	5.195	-0.707	0.491	(intercept)	-15.267	1.949	-7.833	1.75E-06
year	0.002	0.003	0.723	0.482	year	0.008	0.001	7.88	1.63E-06
ro	estimate	std. error	t value	p value	ro	estimate	std. error	t value	p value
(intercept)	4.3	1.492	2.883	0.012	(intercept)	1.476	0.376	3.932	0.002
year	-0.002	0.001	-2.876	0.012	year	-0.001	1.87E-04	-3.918	0.002
ch	estimate	std. error	t value	p value	ch	estimate	std. error	t value	p value
(intercept)	-2.404	6.362	-0.378	0.711	(intercept)	1.541	0.582	2.647	0.019
year	0.001	0.003	0.399	0.696	year	-0.001	2.90E-04	-2.603	0.021
tr	estimate	std. error	t value	p value	tr	estimate	std. error	t value	p value
(intercept)	0	0	NA	NA	(intercept)	0.422	0.241	1.748	0.102
year	0	0	NA	NA	year	0	1.20E-04	-1.726	0.106
ot	estimate	std. error	t value	p value	ot	estimate	std. error	t value	p value
(intercept)	4.784	7.264	0.659	0.521	(intercept)	9.394	2.364	3.974	0.001
year	-0.002	0.004	-0.647	0.528	year	-0.005	0.001	-3.911	0.002

Table 8. LMM of nest sites for the 1994–2013 period. First part indicates the nest site, the second the type of variable in the upper left corners

8. táblázat A fészekalapok lineáris vegyes modellje az 1994–2013-es periódusra. Az első szó a fészekalapot, a második a változó típusát jelzi minden bal felső sarokban

ep, random		variance	std. dev.	ch, random		variance	std. dev.
megye	(intercept)	0.002	0.047	megye	(intercept)	0.006	0.075
residual		0.015	0.122	residual		0.008	0.089
ep, fixed		std. error	t value	ch, fixed	estimate	std. error	t value
(intercept)	-2.879	5.361	-0.537	(intercept)	-0.293	3.904	-0.075
year	0.002	0.003	0.685	year	2.06E-04	0.002	0.106
ep_s, random		variance	std. dev.	tr, random		variance	std. dev.
megye	(intercept)	0.003	0.056	megye	(intercept)	2.62E-06	0.002
residual		0.013	0.116	residual		1.23E-05	0.004
ep_s, fixed	estimate	std. error	t value	tr, fixed	estimate	std. error	t value
(intercept)	13.034	5.081	2.565	(intercept)	-0.073	0.154	-0.474
year	-0.006	0.003	-2.429	year	3.77E-05	7.65E-05	0.493
ep_ns, random		variance	std. dev.	ot, random		variance	std. dev.
megye	(intercept)	2.90E-04	0.017	megye	(intercept)	0.002	0.039
residual		0.002	0.041	residual		0.004	0.064
ep_ns, fixed	estimate	std. error	t value	ot, fixed	estimate	std. error	t value
(intercept)	-16.1	1.78	-9.036	(intercept)	3.298	2.825	1.168
year	0.008	0.001	9.093	year	-0.002	0.001	-1.14
ro, random		variance	std. dev.				
megye	(intercept)	4.47E-06	0,002				
residual		8.54E-05	0.009				
ro, fixed	estimate	std. error	t value				
(intercept)	1.331	0.404	3.298				
year	-0.001	2.01E-04	-3.287				

Table 9. Linear regressions of the unoccupied nests on electricity poles with support (left column) and the empty electricity poles with support (right column) by counties

9. táblázat Lineáris regresszió a lakatlan fészkekre fészektartós villanyoszlopon (bal oszlop) és az üres fészektartókra villanyoszlopon (jobb oszlop)

ep_t, unoccupied					ep_t, empty				
GYMS	estimate	std.error	t value	p value	GYMS	estimate	std.error	t value	p value
(intercept)	12.743	23.652	0.539	0.599	(intercept)	-5.012	7.136	-0.702	0.494
year	-0.006	0.012	-0.532	0.603	year	0.003	0.004	0.709	0.49
Somogy	estimate	std.error	t value	p value	Somogy	estimate	std.error	t value	p value
(intercept)	-23.561	8.829	-2.669	0.018	(intercept)	-42.858	8.704	-4.924	2.24E-04
year	0.012	0.004	2.689	0.018	year	0.021	0.004	4.938	2.18E-04
BK	estimate	std.error	t value	p value	BK	estimate	std.error	t value	p value
(intercept)	-10.625	5.191	-2.047	0.06	(intercept)	-14.806	3.804	-3.892	0.002
year	0.005	0.003	2.063	0.058	year	0.007	0.002	3.909	0.002
Békés	estimate	std.error	t value	p value	Békés	estimate	std.error	t value	p value
(intercept)	-5.923	7.007	-0.845	0.415	(intercept)	0.234	3.146	0.074	0.942
year	0.003	0.003	0.86	0.407	year	0	0.002	-0.069	0.946
HB	estimate	std.error	t value	p value	HB	estimate	std.error	t value	p value
(intercept)	15.972	14.53	1.099	0.293	(intercept)	-44.326	7.456	-5.945	6.76E-05
year	-0.008	0.007	-1.088	0.298	year	0.022	0.004	5.967	6.54E-05
SZSZB	estimate	std.error	t value	p value	SZSZB	estimate	std.error	t value	p value
(intercept)	-0.528	4.419	-0.119	0.907	(intercept)	-31.262	4.187	-7.466	3.03E-06
year	3.19E-04	0.002	0.145	0.887	year	0.016	0.002	7.514	2.82E-06

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Habitat selection of the Great Bustard *(Otis tarda)* in Körös-Maros National Park

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Abstract We investigated relationships among bustard presence data as response as well as properties of habitat patches such as shape, size, type of land use and landscape connectivity in 2015, employing bustard occurrence data in Körös-Maros National Park (KMNP hereafter). Additionally, we aimed to present a geometrical approach of habitat choice in animals, focusing on geometric properties rather than vegetation structure. Here we applied landscape metrics approach, providing landscape classification by analysing spatial patterns in potentially important landscape objects, disregarding linear constructions. Our findings show insignificant differences between shape metrics of selected and non-selected habitat patches, in line with previous studies concluding that bustards choose habitats based on habitat type classes rather than on geometric properties. Further, our results indicate that the original habitats of the study species, adapted to extensive, open steppes, became strongly fragmented, resulting in the absence of large contiguous areas. Within the study area, landscape connectivity values represent optimal habitat conditions, probably as a result of highly patchy structure of the landscape and relatively small nearest neighbour distances of habitat patches. Thus, our findings also indicate that Great Bustards adapted to modified landscape structures. Our landscape analytical approach provides a methodological framework which can be applied on habitat selection tactics in a number of species of key conservation importance.

Keywords: Great Bustard, landscape metrics, habitat patch, land cover, CORINE

Összefoglalás A túzok (*Otis t. tarda* L.) élőhelyválasztása és az élőhelyfoltok alakja, mérete, művelési ágankénti összetétele és táji szerkezete közötti összefüggéseket vizsgáltuk 2015-ös előfordulási adatok alapján a Körös-Maros Nemzeti Park területén. A vizsgálat célja egy olyan módszer bemutatása, mely a fajok élőhelyeinek nem növényzeti jellegű összetételére koncentrál, hanem annak geometriai sajátosságai közötti összefüggéseit vizsgálja. A vizsgálatokat a tájmetria eszköztárával végeztük, amely a tájat alkotó elemek területi mintázatának elemzésével ökológiai alapú tájleírást tesz lehetővé. A tájban vizuálisan elkülöníthető egységek számszerű vizsgálatával foglalkozik, amely minden esetben egy adott felszínborítási kategória összefüggő területrészleteit tartalmazza, zavaró vonalas létesítmények nélkül, létrehozva így a legrészletesebb folttérképet. Az eredmények azt mutatják, hogy a vizsgálati területen nincs szignifikáns különbség az élőhelyül választott területegységek alaki tényezőjében. A térségben a túzok területválasztása nem az alaki mutató függvénye. A vizsgálat eredményei alátámasztják, hogy az eredetileg nagy, nyílt sztyeppei területeket kedvelő faj élőhelyei feldarabolódtak, a nagy összefüggő felszínborítási formák megszűntek. A megfigyelések 90%-a 10 és 300 hektár közötti élőhelyfoltokra esik, annak ellenére, hogy 300 hektárnál nagyobb, összefüggő tájfoltok is rendelkezésre állnak. A vizsgálati területen az összefüggőségi értéke kiváló létfeltételeket számszerűsít, melyet a táj rendkívül mozaikos jellege és a tájfoltok egymáshoz viszonyított kis távolsága okozhat. Ezek alapján kijelenthető, hogy a vizsgált populáció nem egy maradványterületen, hanem a faj számára kiváló létfeltételeket biztosító kultúrtájban él. A túzok tehát viszonylag jól alkalmazkodott a megváltozott természeti körülményekhez, amely fennmaradásának alapját jelentheti. A kutatás kiterjesztésével más élőhelyekre, több évre visszamenő adatsorok vizsgálatával lehetőség adódik különböző adottságú életterek egymással való összehasonlítására, mellyel további értékes, a faj nemzetközi megmentését célzó intézkedések meghozatalára nyílhat lehetőség.

Kulcsszavak: túzok, tájmetria, élőhelyfoltok, felszínborítás, CORINE

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Introduction

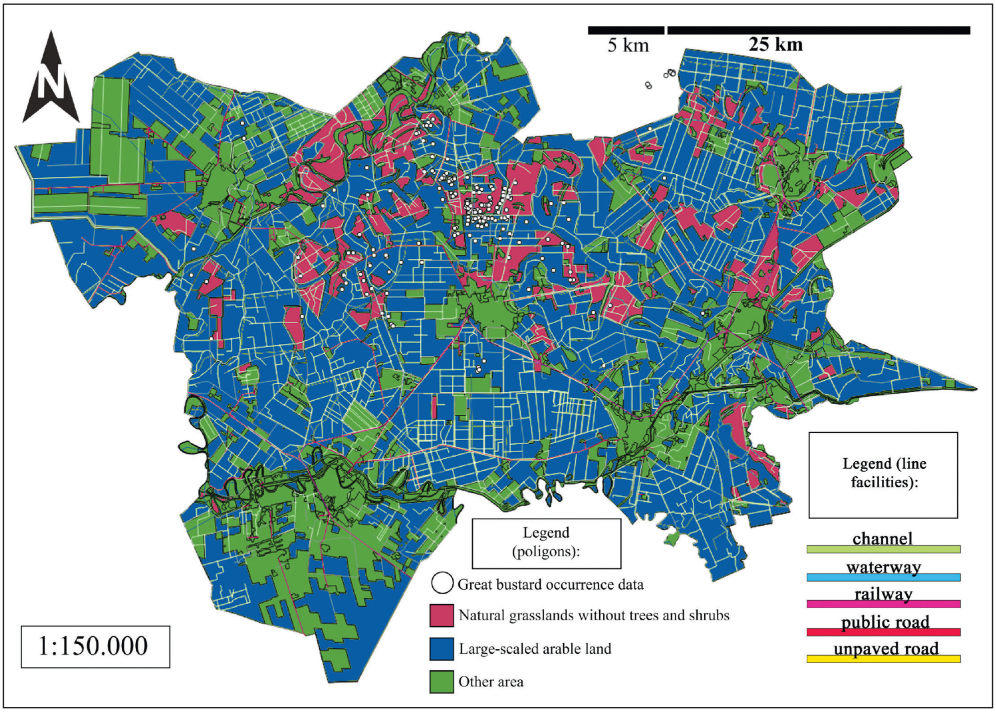
Human landscape modification activities are known to cover several milennia, showing high variance in different historical periods. These processes also substantially modified the landscape composition of the current area of Hungary. One of the most influential projects was represented by water regulation programmes aiming at converting natural habitats into agricultural areas, supposed to significantly influence habitat availability for the Great Bustard *(Otis tarda)*, recognised as an emblematic bird of Hungarian conservation.

The Great Bustard *(Otis tarda)* is a bird of key conservation concern distributed in the Eurasian steppe zone, and classified as an endangered flagship and umbrella species of steppe habitats (IUCN 2016). Significant part of the Central-European population of the Great Bustard is found in Hungary (Sterbetz 1979, Alonso & Palacín 2010, Alonso 2014), where the primary role of Great Bustard conservation is represented by Körös-Maros National Park, where 40% of the Hungarian population aggregates. Similarly to other regions within its distribution, bustards prefer agricultural areas providing food and potential nest sites in larger quantities than in seminatural habitats: from the 1960s onwards, formerly extensive agricultural areas turned into industrialised farmlands with increased use of pesticides, fertilisers and soil chemicals (Fatér & Nagy 1992, Faragó *et al.* 2014). Amplified by the country-wide ploughing and forestation of grasslands, this process led to significant changes in landscape structures which presumably forced bustards to occupy intensively cultivated areas, considered as suboptimal habitats. This led to the formation of smaller, closed and isolated populations, many of which have disappeared during the past few decades. This pattern was also amplified by the effects of high voltage electricity lines (Lóránt & Vadász 2014). During the late 1970s, agricultural intensification accelerated, including regions in East-Hungary harbouring the largest bustard populations. Additionally, the Hungarian population was further affected by harsh winters during the mid-1980s. Thus, agricultural areas functioned probably as ecological traps, whilst bustards were attracted to microclimatic conditions and improved food availability of these habitats during reproduction. However, the timing of first and second alfalfa harvests, hay-cutting, and autumn wheat harvest coincide with primary and supplementary broods of the Great Bustard. Further, the prescriptions of bustard-friendly agricultural programmes do not fully comply with the ecological characteristics of bustard breeding (Németh *et al.* 2009).

Here we apply landscape geometrical approach to identify key area and shape properties of habitats important in driving habitat selection tactics of the Great Bustard. We aim to find landscape properties to inform conservation management focusing on bustard-friendly agricultural schemes.

Materials and Methods

Our study was conducted in Dévaványa-Ecseg area of KMNP between January and October in 2015. Our dataset includes EOV coordinates (D72/EOV EPSG:23700) of observed bustards as well as date and time of the observation, recorded by the staff of KMNP Directorate, using handheld GPS. As the birds were not individually identifiable, the same location might refer to multiple observations. All locations were assigned to digitized polygons of habitat patches. As a base map, we used the 1:50,000 scaled habitat map available by the Institute of Geodesy, Cartography and Remote Sensing (http://www.nyme.hu/22677.html?&L=4), which identifies 80 land use types. In addition to bustard location points and the CLC50 shape files, we included shape files of dykes, roads, unpaved roads, landscape protection areas, nature reserves and railways as potential environmental predictors in further analyses. In total, the 967 polygons were cropped into 2816 polygons by artificial linear structures *(Map 1)*. In 2015, 224 observation points were recorded, 10 out of which were located outside of the boundary of the selected settlements. Thus, we obtained 77 polygons identified by 214 observation points *(Map 1)* and using their attribute tables, we calculated the following spatial metric of each polygon: (1) area, (2) perimeter, (3) ratio of perimeter and area (SI = shape index hereafter), (4) includes or excludes bustard observation point, (5) habitat type. Only for polygons with bustard observations, we included season. Next, we calculated landscape connectivity index, which aims at assessing the relationship between



Map 1. Detailed area coverage of the study area with bustard occurrence data
1. térkép A vizsgálati terület részletes felszínborítása a túzok előfordulási adatokkal

landscape structure and ecological needs of a particular species. To do so, we employed the patch cohesion index (PCI hereafter) *(Figure 1)* (Opdam *et al.* 2003, Szabó 2009, Pătru-Stupariu *et al.* 2017). By definition, PCI is not significantly different from zero in areas where ecological processes important for the study species are limited, whereas undisturbed landscape ecology provides PCI = 100 values. In other words, this metric approaches 0 as the proportion of the landscape comprised of the focal class decreases and becomes increasingly subdivided and less physically connected (Pătru-Stupariu *et al.* 2017). Spatial statistics were computed using ArcGis 9.2 (ESRI, Redlands, CA, 2006).

$$COHESION=\left[1-\frac{\sum_{j=1}^{n}p_{ij}}{\sum_{j=1}^{n}p_{ij}\sqrt{a_{ij}}}\right]\left[1-\frac{1}{\sqrt{A}}\right]^{-1}\times 100$$

Figure 1. Determination of Cohesion Index (Szabó 2009), where pij: circumference of ij spot, aij: area of ij spot, A: total area

1. ábra A kohéziós index meghatározása (Szabó 2009), ahol pij: ij folt kerülete, aij: ij folt területe, A: összterület

Results

Shape indices

Large-scale arable fields covered 63.5% of the total of the study area. Considering polygons including bustard observation points, bustards were detected in 52 large-scale arable fields out of the 77 polygons (67.5%). Bustard presence is strongly related to the total area of large-scale arable fields (χ^{2}-approximation of Kruskal-Wallis-test, df=1, $\chi^2 = 35.46$, $p < 0.0001$). Out of this, 19 polygons are classified as natural grasslands without trees and bushes (24.7%), contrasting the 10% cover of this habitat type within the total study area. Bustards selected these two habitat types in 92.2% of the observations.

The shape index of polygons including bustard points amounted to SI = 0.006, whereas for those without bustards SI = 0.004. Considering seasonality, SIwinter = 0.006, SIspring = 0.005, SIsummer = 0.006, SIautumn = 0.004. We found a significant relationship between polygon selection (yes or no) and shape index: shape index of polygons selected by bustards were significantly lower, showing a preference for more compact polygons with relatively small boundaries (χ^{2}-approximation of Kruskal-Wallis, $\chi^2 = 71.523$, $p < 0.0001$).

Habitat selection

In total, polygons covered 46 hectares in average (N = 2816), owing to the high density of abandoned dykes. Out of this set, polygons including bustard observations had an average area of 157.1 hectares (N = 77), 10.4% of which had areas exceeding 300 hectares (N = 8). Further, areas of 1.35% of the total polygon set was less than 300 hectares and the areas of 41 polygons exceeded this limit.

Considering land use types, bustards tend to prefer large-scale arable fields (N = 77, representing 67.5%) over natural grasslands without trees and bushes (χ^{2}-test, $\chi^2 = 0.676$, df

= 1, p = 0.418). Interestingly, majority of polygons including arable fields were located in the close proximity of grassland areas, which warrants further analyses considering this spatial relationship.

Landscape connectivity

Considering all N = 77 polygons, we calculated PCI = 99.94, suggesting optimal landscape connectivity conditions, indicating a highly patchy habitat structure and low mean neighbour distance of suitable habitat polygons.

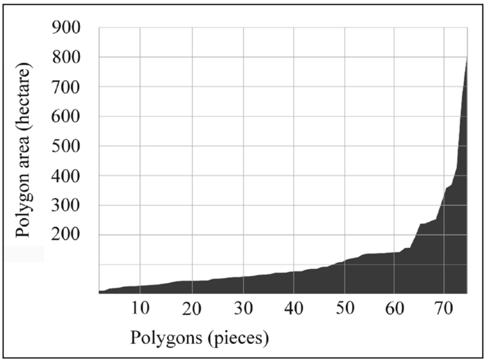


Figure 2. The distribution of the average area of the polygons observed with the Great Bustards

2. ábra A túzokkal megfigyelt poligonok átlagterület eloszlása

Discussion

A number of studies reported that the Great Bustard has successfully adapted to cultural landscapes created by human-induced changes in land use (Alonso & Palacín 2010, Alonso 2014, Janó & Végvári 2016). However, bustards experience dramatic population declines at longer temporal scales, as a result of habitat loss due to intensification and industrialisation of agricultural technologies. In contrast, the ratio of the cover of agricultural areas and grasslands selected by bustards is close to 1:1 (Fatér & Nagy 1992).

Based on the results of the first and second Hungarian Great Bustards surveys carried out in 1985 and 1986, the ratio of bustards breeding in autumn wheat, legumes and grasslands were found to be approximately equal (Faragó 1990). However, based on the habitat type of saved broods, 49.44% of eggs were found in alfalfa, which is probably related to the intensity of agricultural management.

Our findings thus imply that bustards show no preference for contiguous areas exceeding 300 hectares, not considering artificial linear objects (paved and dirt roads, railway lines and dykes). Although large, contiguous habitat patches of the study species – formerly typical bird of extensive open steppes – became highly fragmented, it would find suitable habitat patches larger than 300 hectares.

As the Great Bustard is highly mobile and classified as partial migrant in Central Europe irregularly migrating to the Mediterranean region in harsh winters, it would be able to find larger contiguous habitat patches. This suggests that majority of the Hungarian population does not need habitats of this size.

The Great Bustard has adapted to the relatively high cover of arable lands within the study region, by preferring agricultural areas over grasslands even if grassland is available in its vicinity. Such habitat structures are available within the framework of agri-environmental schemes. This allows agricultural activities supported by the state which involves priorities for the ecological needs of bustards, by providing subsidies for farmers with decreased incomes as a result of bustard-friendly agricultural management. This framework thus supports bustard-specific agricultural management in key bustard regions, which might be extended to other key bustard regions, including Kiskunság region and North-West Hungary, where this system is not yet implemented, preferably during the next legal extension of agri-environmentaly schemes focusing on bustard conservation.

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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. & Palacín, C. 2010. The world status and population trends of the Great Bustard *(Otis tarda)*: 2010 update – Chinese Birds (2):141–147. DOI 10.5122/cbirds.2010.0007

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

Faragó, S. 1990. A túzok Magyarországon [The Great Bustard in Hungary]. – Venatus, Sopron (in Hungarian)

Fatér, I. & Nagy, Sz. 1992. A természet szolgálatában alapítvány. Javaslat túzokkíméleti területek kialakítására a környezetileg érzékeny területek rendszerében [A proposal for the creation of wildlife areas in the environmentally sensitive areas]. Unpublushed case study by MME-WWF (in Hungarian)

Janó, G. & Végvári, Z. 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

Lóránt, M. & Vadász, Cs. 2014. The effect of above-ground medium voltage power lines on displaying site selection of the Great Bustard *(Otis tarda)* in Central Hungary. – Ornis Hungarica 22(2): 42–49. DOI: 10.2478/orhu-2014-0017

Németh, Á., Lóránt, M. & Vadász, Cs. 2009. Mennyire tekinthető hasznosnak az Agrár-Környezetgazdálkodási Program túzokvédelmi célprogramjaiban szereplő előírások? [How effective are the management regulations of the Great Bustard Protection Agro-Environmental Program?]. – Természetvédelmi Közlemények 15: 226–234. (in Hungarian with English Summary)

Opdam, P., Verboom, J. & Pouwels, R. 2003. Landscape cohesion: an index for the conservation potential of landscapes for biodiversity. – Landscape Ecology 18(2): 113–126.

Pătru-Stupariu, I., Stupariu, M. S., Stoicescu, I., Peringer, A., Buttler, A. & Fürst, C. 2017. Integrating geo-biodiversity features in the analysis of landscape patterns. – Ecological Indicators 80: 363–375.

Sterbetz, I. 1979. Magyarország túzokállománya 1977-ben [The stock of the Great Bustard in Hungary 1977]. – Állattani Közlemények 65: 127–136. (in Hungarian with German Summary)

Szabó, Sz. 2009. Tájmetriai mérőszámok alkalmazási lehetőségeinek vizsgálata a tájanalízisben [Examining application possibilities for landscape metrics in the landscape analysis]. – Habilitation thesis, Department of Landscape Protection and Environmental Geography, University of Debrecen (in Hungarian)

Ornis Hungarica 2018. 26(1): 95–101.
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Intra- and interspecific nest parasitism of Common Moorhen (review of cases and new data)

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Abstract Based on data available so far, it seems that Common Moorhens *(Gallinula chloropus)* rarely, but regularly lay one or more eggs in the nests of Common Little Bittern *(Ixobrychus minutus)*. Three such incidents from Hungary are hereby added to the cases known to date. However, Common Moorhens do not only lay eggs in other species' nests, but also in the nests of conspecifics, while other species may also parasitise the nest of Common Moorhens. The present study summarises these aspects.

Keywords: intraspecific and interspecific nest parasitism, Common Moorhen, Common Little Bittern

Összefoglalás A vízityúk *(Gallinula chloropus)* az eddig rendelkezésre álló adatok alapján úgy tűnik, hogy ritkán, de rendszeresen rakja egy vagy több tojását törpegém *(Ixobrychus minutus)* fészkébe. Az eddigi esetszámot további három magyarországival sikerült kiegészíteni. A vízityúk azonban nem csak más fajok, hanem fajtársai fészkeibe is rakhat tojásokat, illetve más fajok az ő fészkeit parazitálhatják. Ezeket az eseteket foglalja össze a tanulmány.

Kulcsszavak: fajon belüli és fajok közötti fészekparazitizmus, vízityúk, törpegém

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Introduction

Giving birth to young or incubating eggs and eventually caring for the offspring till their independence are general forms of reproductive behaviour in mammals and birds. However, in other classes, mainly partial parental care is known. For birds, caring for their offspring may take weeks or months, and especially among mammals even longer periods of parental care are typical. This is a rather energy-consuming process with many hazardous components. It is common in the bird order Cuculiformes that certain species use other species to raise their offspring. Within the order, all 53 species in the subfamily Cuculinae follow this strategy (del Hoyo *et al.* 1997). However, this classic brood-parasitism is also typical for several other species, e.g. for the Black-headed Duck *(Heteronetta atricapilla)*, but some examples where nestlings are raised by other species can also be found among weavers (Ploceidae). The number of truly brood-parasitic species is approximately 80 (Payne 1977).

In addition, numerous species are known to lay occasionally some or all of their eggs in the nests of other species (interspecific nest parasitism). Some females attempt to increase their breeding success with this strategy, but there can also be a number of other reasons for placing some or all of their eggs in other species' nests.

It was only in the 1970s, when researchers turned their attention to another interesting phenomenon, i.e. nest parasitism between conspecifics (intraspecific nest parasitism). Yom-Tov (1980) mentioned 53 species in which this fact has been proved. After this impressive publication, activities to better explore nest parasitism have increased, and hence the published lists of taxa in 1989 contained more than twice as many species (MacWrither 1989, Rohwer & Freeman 1989).

The probability of intraspecific nest parasitism is higher if suitable nesting sites are insufficient, and if the breeding season is long. These factors increase the probability that nidifugous species lay their eggs in host nests (Yom-Tov 2001). A reason for this can be that nidifugous species have larger clutches than those of nidicolous species of the same size (Ar & Yom-Tov 1978). These birds usually begin incubation after laying the last or the second last egg, and their incomplete clutches are unattended in the period preceding incubation. Furthermore, caring for an increased number of offspring, i.e. for their own and for the offspring of the nest parasites, does not require much additional effort on behalf of the hosts in the case of nidifugous species (Sorensen 1992).

It is widely known that if the nests of certain species are condensed in a small area, e.g. in large bird colonies, or in sites with a high nest density, or where available nesting sites are insufficient, the rate of intraspecific nest parasitism can be significantly higher (Yom-Tov 1980).

Due to the increasing research in the field of breeding biology, the number of species known to employ intraspecific nest parasitism continuously grows. The updated list by Yom-Tov (2001) contains 234 species in 18 orders, in which multiple evidence has been found for intraspecific nest parasitism. The most numerous among them are the species belonging to the orders Anseriformes (74), Galliformes (32) and Chradriiformes (19). However, there are several species, in which the occurrence of intraspecific nest parasitism has been revealed since then, such as the Eurasian Thick-knee *(Burchinus oedicnemus)* or the Mediterranean Gull *(Larus melanocephalus),* and the Whiskered Tern *(Chlidonias hybridus)* (Haraszthy 2018 in print).

Significantly less information is available on interspecific nest parasitism. It may even happen that a parasitic species that has nidifugous chicks lays eggs in the nests of species whose nestlings are nidicolous. Many questions are unresolved in interspecific nest parasitism. It is still not known whether individual females parasitise always the same host species or if they vary them. Nor is it known what proportion of females within each parasitic species apply this strategy or how successful they are. Hötker (2000) concluded that in Pied Avocets *(Recurvirostra avosetta)* significantly more chicks hatch from the usual four-egg clutches than from parasitised clutches with an increased number of eggs.

Another interesting point about interspecific nest parasitism is that a species can be a parasite and a host at the same time. The Common Moorhen *(Gallinula chloropus)* is a good example. Moreover, it may lay its eggs in the nests of nidifugous as well as nidicolous species, while so far only nidifugous species are known to lay their eggs in the nests of this species.

The Common Moorhen is a widespread species, inhabiting three continents. The species is native in large parts of North, West and Southern Africa. It is also widespread all over Europe, except for most of Scandinavia. The breeding range extends east in Asia nearly to the

Baikal region, and the species is resident in South and Southeast Asia to the western parts of the Indonesian archipelago (Taylor 1996).

The Common Moorhen is a considerably adaptable species, breeding in a variety of habitats. Originally, it inhabited both smaller and larger standing waters that had large reedbeds and at least patches of open water, but later it also occupied slowly flowing canals with reed belts. Today, Common Moorhens can be found at city ponds as well as in smaller or larger wetlands created by the most diverse industrial activities (Cempulik 1993). Nests were originally built on reed or reedmace, sometimes in small bushes in such vegetation, but almost always directly above water. Among those Common Moorhens breeding in cities, it is not uncommon to build the nest several metres high on trees (Engler 1983).

Originally, the Common Moorhen was a territorial species, but its adaptation to smaller wetlands resulted in partially abandoning this behaviour. Colonial breeding of several pairs is increasingly more common, and polyandry and polygyny also occur more and more often in this formerly primarily monogamous species, while there are also several records of interspecific brood parasitism (e.g. Gibbons 1986, Post & Seals 2000, Forman 2003).

So far, relatively little attention has been paid to the breeding biology of the Common Moorhen. What is known best that intraspecific nest parasitism can be significant in populations with higher densities. However, egg pattern does not allow distinction of eggs from stranger females. Proving that two or more females lay eggs in an observed nest is only possible if several new eggs are laid in the nest on a single day, or if new eggs are laid in a nest several days after the clutch is complete. Proving the identity of eggs from stranger females is thus only possible in constantly monitored nests.

Common Moorhen eggs in the nests of different species

In several cases, Common Moorhens laid their eggs in the nests of the closely related Common Coot *(Fulica atra)* that shared the same habitat. However, the first observations of such incidents occurred in bird parks where the two species bred in large numbers in each others' immediate vicinity. In these English bird parks goose, duck and swan species are kept in captivity, in pairs or smaller groups. Each pair or group has a small pond surrounded by some lawn. The smaller ponds also have patches of reed or reedmace, offering ideal nesting sites to the wild Common Moorhens. Density is particularly high in such places, since the wildfowl fodder available in abundance is also favoured by Common Moorhens (Gibson 1986, Forman 2003).

Cases are also known when Common Moorhens laid an egg in a Grey Partridge *(Perdix perdix)* and in a Little Grebe *(Tachybaptus ruficollis)* nest (Engler 1983). In Great Britain, a Black-headed Gull *(Larus ridibundus)* successfully hatched two Common Moorhen eggs laid next to its own egg. The nestlings later joined a pair of Common Moorhens that were leading their own chicks (Jones 1988). Meniaia *et al.* (2014) found a Common Moorhen egg in a Ferruginous Duck *(Aythya nyroca)* nest during their research at Lake Tonga in Algeria. This nest also contained a White-headed Duck *(Oxyura leucocephala)* egg. The same researchers found 7 Common Moorhen eggs in an abandoned Purple Swamphen *(Porphyrio porhyrio)* nest, too.

The author found three Common Moorhen eggs next to eight duck eggs in a Mallard *(Anas platyrhynchos)* nest at Dinnyés on 23 May 2004. In the above cases, with the exception of the Black-headed Gull, the Common Moorhen eggs were laid into the nests of nidifugous species. The egg laid in the Grey Partridge nest is of particular interest, as that species has a different habitat from that of the Common Moorhen.

In addition to the above observations made in Europe and North Africa, only one occasion, an egg of the closely related Common Gallinule *(Gallinula galeata)* was found in the nest of the North American Boat-tailed Grackle *(Quiscalus major)* that nests colonially in reedbeds, which is particularly interesting as this species is extremely far from the genus *Gallinula* in taxonomy, ecology, and especially in breeding behaviour (Post & Seals 1989).

Common Moorhen eggs in nests of *Ixobrychus* bitterns

By 2010, only seven cases have been revealed when Common Moorhens laid their eggs in the nest of an *Ixobrychus* bittern species. Common Little Bittern *(Ixobrychus minutus),* which is also native in Hungary, was parasitised in only three of these cases (David *et al.* 2005, Pardo-Cervera *et al.* 2010, Samraoui *et al.* 2012), while in four instances the eggs were laid in Yellow Bittern *(Ixobrychus sinensis)* nests (Ueda 1993, Ueda & Narui 2004). This is also interesting because Common Moorhens laid their conspicuously marked eggs in the nests of species that share the same habitat but have snow white clutches. The nestlings of *Ixobrychus* bitterns are nidicolous, fed by their parents in the nest.

In addition to the three cases published so far where Common Moorhens parasitised the nests of Common Little Bitterns, similar cases are known from Hungary that have not been published until recently or not at all, while one of them was published only in Hungarian and in a place where it could not become widely known.

Description of the Hungarian cases

1. – On 3 June 1962, Jenő Radetzky found a three-egg clutch of Common Little Bittern in Soponya, with a Common Moorhen egg in the nest (Solti 2012).
2. – On 10 June 1979, Rékási (1980) found Common Little Bittern nests under three Purple Heron nests in a colony of the latter species at Madaras, and one of them contained three typically patterned Common Moorhen eggs alongside three white Common Little Bittern eggs. Ten days later, this clutch had been robbed by a European Water Vole *(Arvicola amphibius)*, while the other two nests that only contained eggs of Common Little Bittern were unharmed. The question arises whether the parasitised nest had been deserted by the Common Little Bittern which thus opened the way to nest robbery?
3. – On 29 May 2005, the author found a nest in the reed belt of the Hortobágyi-Halastó (Hortobágyi Fishponds) with five Common Little Bittern eggs and a Common Moorhen egg next to them. The nest was built on reed stems in the vicinity of a mixed heron colony with nests of Glossy Ibis *(Plegadis falcinellus)*, Black-crowned Night-heron *(Nycticorax*

nycticorax), Great White Egret *(Ardea alba)*, Little Egret *(Egretta garzetta),* Squacco Heron *(Ardeola ralloides),* and Pygmy Cormorant *(Microcarbo pygmeus)*.

From the above records it can be concluded that the first two event took place much earlier than the other cases published so far (David *et al.* 2005, Pardo-Cervera *et al.* 2010, Samraoui *et al.* 2012), and one of them is the first known case when more than one (3) Common Moorhen eggs were found in a Common Little Bittern nest.

The three records from Hungary indicate that in all likelihood Common Moorhens significantly more often lay one or more eggs in the nests of Common Little Bitterns or possibly of other species than so far supposed.

Numerous examples are known for intraspecific nest parasitism in Common Moorhens, as well as in other species. Even when nests are thoroughly monitored, it is not easy to reveal this phenomenon due to the great similarity of eggs. Based on the growing number of proven cases, numerous authors assume that intraspecific nest parasitism is significantly more frequent than previously supposed (Macwhirter 1989, Lyon 1993). It is widely accepted that a nest can be considered to be parasitised if two eggs are laid in it on the same day, or if a new egg or eggs are laid in the nest at least two days after the clutch became complete (Lyon 1993). In the last decades, research has shown that in the various Coot and Moorhen species intraspecific nest parasitism occurs frequently. In the American Coot *(Fulica americana)*, Lyon (1993) found at least one egg from stranger females in 41% out of 417 nests. In Namibia, Jamiesoni *et al.* (2000) found stranger eggs in 43% of the nests of Red-knobbed Coot *(Fulica cristata)*, and in 21–36% of the nests of Lesser Moorhen *(Gallinula angulata)*. Meniaia *et al.* (2014) found eggs from stranger females in 10 nests (7.6%) among those discovered at Lake Tonga in Algeria.

On 9 June 1974, the author found 15 eggs and three hatchlings in a Common Moorhen nest built under a Purple Heron nest in the Kunkápolnási Marsh (Csukás Marsh), Hortobágy, Hungary. On 8 May 1977, László Vilmos Szabó found a 21-egg clutch of Common Moorhen in a nest built on european ash *(Fraxinus excelsior)* sprouts in the flooded Vajdalaposi Forest Hortobágy (based on his diary and photo).

Common Little Bitterns breed in reedbeds and nests are thus found during targeted research, therefore, parasitism on them by Common Moorhen is only underpinned by occasional records. However, based on the cases observed abroad and in Hungary, it can be assumed that Common Moorhens lay eggs in Common Little Bittern nests more often than previously supposed.

Parasitised nests of Common Moorhen

Common Moorhens do not only parasitise the nests of other species, but can also become victims of brood parasitism. Fredrickson (1971) found two Ruddy Duck *(Oxyura jamaicensis)* eggs in the nest of the closely related Common Gallinule in Iowa, USA. In Algeria, Meniaia *et al.* (2014) studied 60 and 71 Common Moorhen nests in 2011 and in 2012 respectively, and found an egg each from Ferruginous Duck, White-headed Duck and Purple Swamphen.

Recommendations

The above data indicates that the breeding behaviour of the Common Moorhen is rather complex. There are several open questions to be answered to get closer to understanding this complex and interesting breeding system. Questions to clarify include what happens to the Common Moorhen eggs laid in the nests of other species? Will they reach maturity, and if so, does its likelihood depend on the parasitised species, or is it a matter of chance? Beyond these life history traits, there are some important evolutionary biology questions as well. Are the females more inclined to parasitism more successful than those that only lay eggs in their own nests? Whether females inclined to parasitism lay more eggs or not. Is the presence of parasitism in a female's life contextual or permanent?

There are some questions that can be answered by methods tested in other host-parasitic systems (e.g. Moskát *et al.* 2003, Hauber *et al.* 2006, Honza & Moskát 2008). The white eggs of the Common Little Bittern and the spotted eggs of the Common Moorhen are so different from each other that deception of the host species can be ruled out. How do Common Little Bitterns react to Common Moorhen eggs? Do they desert the parasitised nest, remove the stranger egg, or perhaps ignore it?

To sum up, it is to be clarified whether these cases occur from time to time by mere accident, or we are witnessing a change in the species' breeding strategy that has evolutionary advantages?

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References

Ar, A. & Yom-Tov, Y. 1978. The evolution of parental care in birds. – Evolution 32: 655–669. DOI: 10.1111/j.1558-5646.1978.tb04610.x

Cempulik, P. 1993. Breeding ecology of the Moorhen *Gallinula chloropus* in Upper Silesia (Poland). – Acta Ornithologica 28: 75–89.

David, A., Vass, C. & Coroiu, I. 2005. A new casse of interspecific brood parasitism in the Common Moorhen *Gallinula chloropus*. – Avocetta 29: 33–39.

del Hoyo, J., Elliot, A. & Sargatal, J. (eds.) 1977. Hanbook of the Birds of the World, Vol. 4. Sandgrouse to Cuckoos. – Lynx Editions, Barcelona

Engler, H. 1983. Die Teichralle [Common Gallinule]. – Die Neue Brehm-Bücherei 536., A. Ziemsen Verlag, Wittenberg, Lutherstadt (in German)

Forman, D. 2003. Moorhen interspecific brood parasitism. – British Birds 96: 429–431.

Fredrickson, L. H. 1971. Common Gallinule breeding biology and development. – The Auk 88: 914–919. DOI: 10.2307/4083849

Gibbons, D. V. 1986. Brood parasitism and cooperative nesting in the Moorhen, *Gallinula chloropus*. – Behavioral Ecology and Sociobiology 19: 221–232.

Haraszthy, L. 2018. Fészkek és tojások [Nest and eggs]. – Pro Vértes Nonprofit Zrt., Csákvár (in Hungarian)

Hauber, M. E., Moskát, Cs. & Bán M. 2006. Experimental shift in hosts' acceptance threshold of inaccurate-mimic brood parasite eggs. – Biology Letters 2(2): 239–241. DOI: 10.1098/rsbl.2005.0438

Honza, M. & Moskát, Cs. 2008. Egg rejection behaviour in the Great Reed Warbler *(Acrocephalus arundinaceus)*: the effect of egg type. – Journal of Ethology 26: 389–395. DOI: 10.1007/s10164-008-0093-0

Hötker, H. 2000. Conspecific nest parasitism in the Pied Avocet *Recurvirostra avosetta*. – Ibis 142: 280–288. DOI: 10.1111/j.1474-919X.2000.tb04867.x

Jamieson, I. G., McRaer, S. B., Simmons, R. E. & Trewby, M. 2000. High rates of conspecific brood parasitism and egg rejection in Coots and Moorhens in ephemeral wetlands in Namibia. – The Auk 117(1): 250–255. DOI: 10.1642/0004-8038(2000)117[0250:HROCBP]2.0.CO;2

Jones, G. 1988. Moorhen and Black-headed Gull apparently laying in same nest. – British Birds 81: 642–643.

Lyon, B. E. 1993. Conspecific brood parasitism as a flexible reproductive tactic in American Coots. – Animal Behaviour 46: 991–928. DOI: 10.1006/anbe.1993.1273

MacWhirter, R. B. 1989. On the rarity of intraspecific brood parasitism. – Condor 91: 485–492. DOI: 10.2307/1368333

Meniaia, Z., Samraoui, F., Alfarhan, A. H. & Samraoui, B. 2014. Nest-site selection, breeding success and brood parasitism in the Common Moorhen *Gallinula chloropus* in Algeria. – Zoology and Ecology 24(4): 305–313. DOI: 10.1080/21658005.2014.959281

Moskát, Cs., Karcza, Zs. & Csörgő, T. 2003. Egg rejection in European Blackbirds *(Turdus merula):* the effect of mimicry. – Ornis Fennica 80: 86–91.

Pardo-Cervera, F., Sørensen, I. H., Jensen-Ruiz, X. & Sanchez-Alonso, C. 2010. Breeding biology of the Little Bittern *Ixobrychus minutus* in the Ebro delta (NE Spain). – Ardeola 57(2): 407–416. DOI: 10.1080/00063657.2012.733335

Payne, R. B. 1977. The ecology of brood parasitism in birds. – Annual Review of Ecology and Systematics 8: 1–28. DOI: 10.1146/annurev.es.08.110177.000245

Post, W. & Seals, C. A. 1989. Common Moorhen parasitizes a Boat-tailed Grackle nest. – The Wilson Bulletin 101: 508–509.

Post, W. & Seals, C. A. 2000. Breeding biology of the Common Moorhen in an impounded cattail marsh. – Journal of Field Ornithology 71: 437–442. DOI: 10.1648/0273-8570-71.3.437

Rékási, J. 1980. Madártani megfigyelések a madarasi nádasban fészkelő gém fajokon [Ornithological observations on the heron species breeding in the reedbed at Madaras]. – Állattani Közlemények 67: 125. (in Hungarian with English Summary)

Rohwer, F. C. & Freeman, S. 1989. The distribution of inraspecific nest parasitism in birds. – Canadian Journal of Zoology 67: 239–253. DOI: 10.1139/z89-035

Samraoui, F., Nedjah, R. Boucheker, A., Alfarhan, A. H. & Samraoui, B. 2012. Breeding ecology of the Little Bittern *Ixobrychus minutus* in Northeast Algeria. – Bird Study 59: 496–503. DOI: 10.1080/00063657.2012.733335

Solti, B. 2012. Radetzky Jenő tojásgyűjteményének katalógusa [The catalogue of the Jenő Radetzky oological collection]. – Folia Historico Naturalia Musei Matraensis 36: 123–138. (in Hungarian)

Sorenson, M. D. 1992. Comment: Why is conspecific nest parasitism more frequent in waterfowl than in other birds? – Canadian Journal of Zoology 70: 1856–1858. DOI: 10.1139/z92-253

Taylor, B. T. 1996. Common Moorhen. – In: del Hoyo, J., Elliott, A. & Sargatal, J. (eds.) Handbook of the Birds of the World, Vol. 3. Hoatzin and Auks. – Lynx Edition, Barcelona, pp. 200–201.

Ueda, K. 1993. A case of inter-specific brood parasitism in the Moorhen *Gallinula chloropus*. – Strix 12: 224–226.

Ueda, K. & Narui, Y. 2004. A new breeding tactic of the Common Moorhen: interspecific

brood parasitism of Bittern nests. – Ornithological Science 3: 163–166. DOI: 10.2326/osj.3.163

Yom-Tov, Y. 1980. Intraspecific nest parasitism in Birds. – Biological Reviews 55: 93–108. DOI: 10.1111/j.1469-185X.1980.tb00689.x

Yom-Tov, Y. 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. – Ibis 143: 133–143. DOI: 10.1111/j.1474-919X.2001.tb04177.x

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Evolution and presence of diurnal predatory birds in the Carpathian Basin

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Kessler, J. (E.) 2018. Evolution and presence of diurnal predatory birds (Ord. Accipitriformes, and Falconiformes) in the Carpathian Basin. – Ornis Hungarica 26(1): 102–123. DOI: 10.1515/orhu-2018-0008

Abstract The author describes the presence of the oldest extinct diurnal birds of prey species in the world and fossilized representatives of different families, as well as the presence of recent species in the Carpathian Basin among fossilized remains. In case of ospreys, one of the oldest known materials is classified as a new extinct species named *Pandion pannonicus*. The text is supplemented by a plate and a size chart.

Keywords: birds of prey, evolution, Carpathian Basin, Osprey, eagles, buzzards, vultures, falcons, *Pandion pannonicus* sp.n.

Összefoglalás A szerző bemutatja a nappali ragadozók kihalt fajait és a különböző családok fosszilis képviselőit, valamint a recens fajok Kárpát-medencei jelenlétét a fosszilis maradványokban. A halászsasok között itt kerül először leírásra egy új faj is *(Pandion pannonicus)*, amely egyben az egyik legrégebbi is az eddig ismert anyagokból. A szöveget egy ábra és egy mérettáblázat egészíti ki.

Kulcsszavak: ragadozó madarak, evolúció, Kárpát-medence, halászsas, sas, ölyv, keselyű, sólyom, *Pandion pannonicus* sp.n.

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Introduction

Accipitridae is the most populous family in terms of species (eagles, goshawks, kites, harriers and vultures belong in the group). Their oldest representatives are known from the Eocene of England (*Palaeocircus cuvieri* Milne-Edwards, 1871) and Germany (*Messelastur granulator* Peters, 1994), while the other extinct genera and species are known from the Oligocene (*Aquila hypogaea* Milne-Edwards, 1892; *Milvus deperditus* Milne-Edwards, 1871, France, *Buteo grangeri* Wetmore and Case, 1934, USA) and the Miocene (*Halliaetus piscator* Milne-Edwards, 1871; *Aquila depredator* Milne-Edwards, 1871; *A. pennatoides* Gaillard, 1939; *A. prisca* Milne-Edwards, 1863; *Milvus incertus* Gaillard, 1939, France). From the Eocene and Oligocene of France *Plesiocathartes europaeus* Gaillard, 1908; *P. kelleri* Mayr, 2002; *Paleohierax gervaisii* (Milne-Edwards, 1863); from the Miocene of Spain *Plesiocathartes gaillardi* Crusafont and Villalta, 1955 and *Neophrontops ricardionsis* Rich, 1980 species from the Miocene of the USA are regarded to be the earliest reports of Old World vultures. Recent species are known since the Quaternary.

Ospreys (Pandionidae) are only presented with one cosmopolitan extant species. A typical feature is the special shape of their distal phalanges, which are unlike any other. Their earliest forms are reported from the Oligocene of Egypt and Hungary (Máriahalom) (*Pandion* sp. and *Pandion pannonicus* n.sp.). Two fossil species were identified from the Miocene of the USA (*Pandion homalopterus* Warter, 1976; *P. lovensis* Becker, 1985). The recent species is known since the Quaternary.

The only recent species of the Sagittaridae lives in the Savannahs of Africa. They have especially long legs and prey on smaller vertebrates, mainly snakes. They nest on the crowns of trees. Their fossilized finds are thought to be the species *Pelargopappus magnus* (Milne-Edwards, 1868) and *Amphiserpentarius schlosseri* (Gaillard, 1908) from the Oligocene and Miocene of France. Recent species are known since the Quaternary.

New World vultures (Cathartidae) live in America. Their earliest extinct species have been reported from the Oligocene of the USA (*Phasmagyps patritus* Wetmore, 1927), the Oligocene of Brasil (*Brasilogyps faustoi* Alvarenga, 1985) and the Miocene of the USA (*Hadrogyps aigiloeus* Emslie, 1988), apart from numerous other extinct species from the Neogene and Pleistocene. Recent species are known since the Quaternary.

Members of the Falconidae are the swiftest diurnal predators, with typical narrow wings and a toothlike formation on the upper edge of their beaks. They are also capable of "smashing" flight. Their fossilized finds are rare, the earliest one is known from the late Miocene of Ukraine (*Falco medius* Umans'ka, 1981), the Miocene of the USA (*Falco ramenta* Wetmore, 1936), and the Miocene of Argentina (*Badiostes patagonicus* Ameghino, 1895 and *Thegornis musculosus* Ameghino, 1895).

Members of the extinct Teratornithidae family were birds of prey of enormous sizes. Their wingspan may have reached 7–7.5 meters, with a weight of about 70 kilograms. Their earlies known species is the *Argentavis magnificans* (Campbell and Tonni, 1980) from the Miocene of Argentina, which may have been the largest as well. Species of the eponymous *Teratornis* genus (*T. merriami* Miller and Loye, 1909; *T. incredibilis* (Howard, 1952); *T. woodburnensis* (Campbell and Allison, 2002)) are known from the Pleistocene of the USA (Brodkorb 1964, Olson 1985, Bochenski 1997, Mlíkovský 2002).

Systematics

Finds of the fossil and subfossil diurnal predators of the Carpathian Basin are the following:

Abbreviations: MN 13 (6.8–5.3 MY) – Upper Miocene; **MN 15** (4.5–3.2MY) – Middle Pliocene; **MN 16-17** (3.2–1.8MY) MY) – Upper Pliocene; **Q1-Q2**(1.8–0.5 MY) – Lower Pleistocene; **Q3** (Q3/I-Q3/II, 500.000–120.000 Y) – Middle Pleistocene; **Q4/I** (120.000 – 12.000Y) – Upper Pleistocene; **Q4/II** (12.000 Y – recent age) **–** † – extinct/fossil species or subspecies.

Ord. Accipitriformes (Vieillot, 1816)
Fam. Accipitridae (Vieillot, 1816)

Vultures are typical scavengers of open areas (rocky cliffs and plains). Apart from the relatively small Egyptian Vulture *(Neophron percnopterus)*, they are quite large, hence they do not really have any natural enemies. Their skeletal remains thus come from deaths of natural causes. They typically remained in crevices of rocks and caves they used for nesting and as feeding/resting places.

–*Aegypius* Savigny, 1809

–*Aegypius monachus* (Linnaeus, 1766)

Known from the Carpathian Basin **Q3/I:** Hundsheim (Austria) (Mlikovskỳ 1998, 2002); **Q4/I:** Cserépfalu – Subalyuk Cave (Hungary) (Jánossy 1962a, 1977); Nándori Cave (Nandru, Romania) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003); **Q4/II:** Teufelslucken (Austria) (Soergel 1966); Balatonlelle hemp fields (Gál 2005); Visegrád Castle (Hungary) (Bökönyi & Jánossy 1965, Jánossy 1977). Finds from Europe outside the Carpathian Basin: **Q1-2:** Spain; **Q3:** France; **Q4**: Bulgaria, Croatia, France, Georgia, Germany, Greece, Italy, Russia, Spain (Tyrberg 1998).

– *Gyps* Savigny, 1809

– *Gyps* † *melitensis* Lydekker, 1890

Known from the middle Pleistocene of Austria (Hundsheim (Jánossy 1974) and Repolusthöhle (Jánossy 1989) (**Q3/II**) and Hungary (Vértesszőlős 2 (**Q3/I**)). The extinct species was identified according to its dimensions.

Apart from the typical site (Zebbug Cave, Malta) it is also known from the site of Ta Kandija in Malta, Corsica, Crete, Mosbach (Germany), late Pleistocene sites of France (Soulabé and Harrpons), as well as from Monaco (Tyrberg 1998).

– *Gyps fulvus* (Hablizl, 1873)

Known from the Carpathian Basin **Q3/I:** Hundsheim (Austria) (Mlikovskỳ 1998, 2002); **Q4/I:** Krapina (Croatia) (Lambrecht 1915, V. Malez 1973, 1984); Varbó – Lambrecht Kálmán Cave (Hungary) (Jánossy 1977, 1986); Oláhszászka – Néravölgyi Cave (Sasca Româna – Valea Nerei) (Jurcsák & Kessler 1988); Torda Gorge – Binder Cave (Turda, Romania) (Jurcsák & Kessler 1988), **Q4/II:** Dunaújváros – Intrecisa (Jánossy 1985); Pilismarót-Malompatak (Hungary) (Jánossy 1985); Kőrösgyéres (Girișul de Criș) (Jurcsák & Kessler 1986); Peterd – Torda Gorge-Magyar Cave (Petrești – Turda Romania) (Kessler & Gál 1998, Gál 2004); Vársonkolyos – Kismagyar Cave (Suncuiuș – Peștera Napișteleu, Romania) (Jurcsák 1974, Kessler 1977, Gál 2002a). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan; **Q4:** Croatia, France, Georgia, Greece, Italy, Romania, Spain (Tyrberg 1998);

– *Gypaetus* Storr, 1784

– *Gyapaetus barbatus* Linnaeus, 1758

Known from the Carpathian Basin **Q4/I:** Cserépfalu – Subalyuk Cave (Jánossy 1960, 1962a, 1977, 1986); Hámor – Szeleta Cave (Lambrecht 1915, 1933); Ölyveskőér (Hungary) (Jánossy 1960); Ohábaponor – Bordu Mare Cave (Ohaba Ponor, Romania) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003); **Q4/II:** Kazánszoros – Töröklik Cave (Cazanele Mari – Cuina Turcului, Romania) (Kessler 1974c, Fischer & Stephan 1977); Padina as *Gypaetus/Aegypius/Gyps sp* (Serbia) (Classon 1980, Gál 2004). Finds from Europe outside the Carpathian Basin: **Q3:** France; **Q4:** Belgium, France, Georgia, Greece, Italy, Spain (Tyrberg 1998);

– † *Gypaetus asiaticus* (Burchak-Abramovich, 1971)

An extinct species reported from the Middle Pleistocene of Georgia (Tyrberg, 1998).

– *Neophron percnopterus* (Linnaeus, 1758)

Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan; **Q4:** Bulgaria, Croatia, France, Greece, Spain (Tyrberg 1998);

– *Circus* (Lacépéde, 1799)

– *Circus macrourus* (Gmelin, 1771)

Known from the Carpathian Basin **Q4/I:** Pilisszántó I. Shelter Cave (Hungary) (Lambrecht 1915, 1933, Jánossy 1977, 1986); Nándori Cave (Nandru, Romania) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan, France; **Q4:** Czech Republic, France, Italy, Russia (Tyrberg 1998);

– *Circus cyaneus* (Linnaeus, 1758)

Known from the Carpathian Basin **Q2:** Osztramos 2 (Jánossy 1972, 1977, 1986); **Q4/I:** Bajót – Jankovich Cave (Lambrecht 1933, Jánossy 1977, 1986); Budapest – Remetehegy Shelter Cave (Kormos 1914; Lambrecht 1933, Jánossy 1977, 1986); Hámor – Puskaporos (Lambrecht 1912a, 1916, 1933, Jánossy 1977, 1986); Pilisszántó I – Shelter Cave (Hungary) (Lambrecht 1915, 1933, Jánossy 1977, 1986); Detrekőszentmiklós – Pálffy Cave (Dzeráva Skála – Plavecky Mikulas, Slovakia) (Lambrecht 1913, 1933). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan, France; **Q4:** Austria, Croatia, Czech Republic, France, Italy, Russia, Spain, Ukraine (Tyrberg 1998);

– *Circus aeruginosus* (Linnaeus, 1758)

Known from the Carpathian Basin **Q3/II:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, 1991, M. Malez & Rukavina 1979); **Q4/II:** Röszke – Ludvár (Jánossy 1985, Gál 2004, 2007b); Tác-Gorsium (Hungary) (Bökönyi 1984, Jánossy 1985). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan; **Q4:** Bulgaria, Croatia, Czech Republic, Georgia, Germany, Italy, Netherlands, Russia (Tyrberg 1998);

– *Circus pygargus* (Linnaeus, 1758)

Finds from Europe outside the Carpathian Basin: **Q3:** France; **Q4:** Czech Republic, Italy, Ukraine (Tyrberg 1998);

– *Circus* sp.

Known from the Carpathian Basin **Q1:** Osztramos 2 (Hungary) (Jánossy 1972, 1986); Betfia 2 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Jánossy 1977, 1986, Kessler 1975, Gál 2002a); **Q4/II:** Ecsegfalva 23. (Hungary) (Pike-Tay *et al.* 2004, Gál 2007b); Révi Caves (Peșteri din Vadu Crișului) (Kessler 1977b, 1982); Révtízfalusi Cave (Peștera din Zece Hotare, Romania) (Kessler 1985). Finds from Europe outside the Carpathian Basin: **Q4:** France, Spain (Tyrberg 1998);

– *Circaetus* (Viellot, 1816)

– *Circaetus gallicus* (Gmelin, 1788)

Known from the Carpathian Basin **Q4/II:** Röszke – Ludvár (Hungary) (Jánossy 1985, Gál 2004, 2007b). Finds from Europe outside the Carpathian Basin: **Q4:** France, Italy, Spain (Tyrberg 1998);

– *Accipiter* (Brisson, 1760)

– *Accipiter gentilis* (Linnaeus, 1758)

Known from the Carpathian Basin **Q3/I**: Betfia 7/4 (Romania) (Kessler 1975, Jánossy 1977, Gál 2002a; **Q3/II:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, 1991, M. Malez & Rukavina 1979); **Q4/I:** Budapest – Remetehegy Shelter Cave (Lambrecht 1933, Jánossy 1977, 1986); Varbó – Lambrecht Kálmán Cave (Hungary) (Jánossy 1977, 1986); **Q4/II:** Bajcsa (Gál 2002b); Dunaújváros – Intrecisa (Jánossy 1985); Ecsegfalva 23. (Pike-Tay *et al.*, 2004, Gál 2007a, 2007b); Mezőzombor cemetery (Jánossy 1985, Gál 2007b); Tác-Gorsium (Bökönyi 1984, Jánossy 1985); Tác – Fövény-puszta (Hungary) (Jánossy 1977); Berettyószéplak (Suplacu de Barcău) (Jurcsák & Kessler 1986, Gál, 2004); Körösbánlaki Cave (Peștera din Bălnaca) (Kessler 1982); Püspökfürdő Lake (Lacul din Băile 1 Mai) (Kessler 1974b, 1985); Révi Caves (Peșteri din Vadu Crișului) (Kessler 1977, 1982); Szegyestel – Drăcoaia Cave, Caves in the Szegyestel valley (Peștera Drăcoaia, Peșteri din Valea Sighiștelului, Romania) (Kessler 1982). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan; **Q4:** Croatia, Czech Republic, France, Italy, Turkey (Tyrberg 1998);

– *Accipiter gentilis* † *brachydactylus* (Mourer-Chauviré, 1975)

Extinct subspecies. Finds from Europe outside the Carpathian Basin: **Q3:** France (Tyrberg 1998);

– *Accipiter nisus* (Linnaeus, 1758)

Known from the Carpathian Basin **Q1:** Beremend 17 (Hungary) (Jánossy 1987, Kessler 2009); Betfia 9 (Gál 2002a); **Q3/I:** Hundsheim (Austria) (Mlikovskỳ 2009); **Q3/II:** Tarkő (Hungary) (Jánossy 1962b, 1976, 1977, 1986); **Q4/I**: Budapest – Remetehegy Shelter Cave (Hungary) (Kormos 1914, Lambrecht 1933, Jánossy 1977, 1986); **Q4/II**: Bajcsa (Gál 2002b); Jósvafő – Musztáng Cave (Kessler 2009); Legény Cave (Hungary) (Lambrecht 1933); Esküllő – Kis Cave (Aștileu – Peștera Mica) (Kessler 1985); Kazánszoros – Töröklik Cave (Cazanele Mari – Cuina Turcului, Romania) (Kessler 1974c, Fischer & Stephan 1977). Finds from Europe outside the Carpathian Basin: **Q3:** Czech Republic, France, Italy, Spain; **Q4:** Austria, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Grece, Italy, Spain, Ukraine, United Kingdom (Tyrberg 1998);

– *Accipiter* sp.

Finds from Europe outside the Carpathian Basin: **Q4:** Germany, Portugal, Russia, Spain (Tyrberg 1998);

– *Milvus* Lacépéde, 1799

– † *Milvus brachypterus* (Jánossy, 1977)

Described from the early Pleistocene of Nagyharsány Hill 1-4. (Bihar level, **Q1**) (Jánossy 1977). The skeletal remain indicates a type with shorter, but more stout wing structure than that of the recent kite species according to Jánossy. Its morphological characteristics also match its genus.

Known only from the typical sites, still described by Lambrecht (1916) as "*Archibuteo lagopus*".

– *Milvus migrans* (Boddaeert, 1783)

Q4/II: Vlassac (Serbia) (Jánossy 1977);

Finds from Europe outside the Carpathian Basin: **Q3:** France; **Q4:** Czech Republic, France, Italy (Tyrberg 1998);

– *Milvus milvus* (Linnaeus, 1758)

Finds from Europe outside the Carpathian Basin: **Q4:** France, Italy, Spain, United Kingdom (Tyrberg 1998);

– *Milvus* sp.

Q4/II: Starcevo (Serbia) (Classon 1980, Gál 2004);

Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan (Tyrberg 1998);

– *Pernis* (Cuvier, 1817)

– *Pernis apivorus* (Linnaeus, 1758)

Known from the Carpathian Basin **Q4/I:** Varbó – Lambrecht Kálmán Cave (Hungary) (Jánossy 1964, 1977); Nándori Cave (Curata Nandru, Romania) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003). Finds from Europe outside the Carpathian Basin: **Q3:** Czech Republic; **Q4:** Germany (Tyrberg 1998);

– *Buteo* (Lacepede, 1799)

– *Buteo buteo* (Linnaeus, 1758)

Known from the Carpathian Basin **Q1:** Betfia 2 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Jánossy 1977, Kessler 1975, Gál 2002a); **Q3:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, 1991); **Q4/I:** Cserépfalu – Subalyuk Cave (Jánossy 1960, 1962a, 1977, 1986); Diósgyőr – Tapolca Cave (Jánossy 1977, 1978, 1986); Varbó – Lambrecht Kálmán Cave (Hungary) (Jánossy 1964, 1977, 1986); **Q4/II:** Budapest – Gellért Hill (Jánossy 1977); Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007a, 2007b); Gyula Castle (Hungary) (Jánossy 1977, 1985); Révi Caves (Peșteri din Vadu Crișului, Romania) (Kessler 1982). Finds from Europe outside the Carpathian Basin: **Q1-2:** Ukraine; **Q3:** France, Georgia, Turkey; **Q4:** Croatia, France, Georgia, Germany, Greece, Italy, Luxemburg, Poland, Portugal, Spain, United Kingdom (Tyrberg 1998);

– *Buteo lagopus* (Pontoppidan, 1763)

Known from the Carpathian Basin **Q1:** Nagyharsány Hill (Hungary) (Lambrecht 1916); **Q2:** Nagyharsány Hill 1-4 (Hungary) (Jánossy 1977, 1986); **Q4/I:** Budapest – Remetehegy Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1977, 1986); Kesztölc – Bivak Cave (Hungary) (Jánossy 1977, 1986); Nándori Cave (Curata Nandru, Romania) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003); Detrekőszentmiklós – Pálffy Cave (Dzeráva Skála-Plavecky Mikulas, Slovakia) (Lambrecht 1913, 1933, Mottl 1938, 1941); **Q4/II:** Caves of Vársonkolyos (Peșteri din Şuncuiuș, Romania) (Kessler 1982). Finds from Europe outside the Carpathian Basin: **Q4:** Czech Republic, France, Germany, Italy, Moldova, Ukrajne, United Kingdom (Tyrberg 1998);

– *Buteo rufinus* (Cretzschmar, 1827)

Known from the Carpathian Basin **Q4/I:** Pilisszántó I. – Shelter Cave (Hungary) (Lambrecht 1915, 1933, Jánossy 1986). Finds from Europe outside the Carpathian Basin: Q3: Azerbaijan, France; **Q4:** France, Luxemburg, Spain (Tyrberg 1998);

– *Buteo* sp. foss. indet.

Known from the Carpathian Basin **MN 13:** Polgárdi 4 (Hungary) (Jánossy 1995, Kessler 2009);

– *Buteo* sp. indet.

Known from the Carpathian Basin **Q3/I:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, 1991). Finds from Europe outside the Carpathian Basin: **Q1-2:** Spain; **Q3:**

Russia; **Q4:** Croatia, France, Germany, Poland, Russia (Tyrberg 1998);

– ***Aquila (*****Brisson, 1760)**

– ***Aquila chrysaetus*** **(Linnaeus, 1758)**

Known from the Carpathian Basin **MN 16:** Villány 3 (Hungary) (Jánossy 1977, 1983, 1986); **Q4/I:** Krapina (Lambrecht 1915, V. Malez 1973, 1984, 1988); Veternica (Croatia) (V. Malez 1973, 1988); Cserépfalu – Subalyuk Cave (Jánossy 1960, 1962a, 1977, 1986); Pilisszántó (Lambrecht 1915, 1933, Jánossy 1977, 1986); Mérk (Hungary) (Lambrecht 1912); Körösmart (Râpa, Romania) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002a); **Q4/II:** Dunaújváros – Intrecisa (Jánossy 1985); Csákvár – Esterházy Cave (Kretzoi 1954); Mezőfény (Gál 2004); Tápiószele – Tüzköves (Jánossy 1977); Tiszalúc-Sarkad (Jánossy 1985, Gál 2007b); Visegrád Castle (Hungary) (Gál 2005); Kazánszoros-Töröklik (Cazanele Mari – Cuina Turcului, Romania) (Kessler 1974c, Fischer & Stephan 1977). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan, Czech Republic, France, Georgia, Italy; **Q4:** Austria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Italy, Moldova, Spain, Ukraine, United Kingdom (Tyrberg 1998);

– ***Aquila heliaca*** **(Savigny, 1809)**

Known from the Carpathian Basin **Q2:** Somssich Hill 2 (Hungary) (Jánossy 1983, 1986); **Q3/I:** Hundsheim (Austria) (Jánossy 1974, 1977); Betfia 7/4 (Romania) (Kessler 1975, Jánossy 1977, Gál 2002a); **Q4/I:** Varbó – Lambrecht Kálmán Cave (Hungary) (Jánossy 1964, 1977); **Q4/II:** Teufelslucken (Austria) (Soergel 1966); Vlassac (Serbia) (Jánossy 1977). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan; **Q4:** Austria, Georgia, Italy, Switzerland (Tyrberg 1998);

– ***Aquila clanga*** **(Pallas, 1811)**

Known from the Carpathian Basin **Q1:** Betfia 9 (Romania) (Kessler 1985, Gál 2002a); **Q4/I:** Nándori Cave (Curata Nandru, Romania) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan, France; **Q4:** France, Germany, Italy (Tyrberg 1998);

– ***Aquila clanga/pomarina***

Known from the Carpathian Basin **Q4/II:** Ludas-Budzsák (Hungary) (Bökönyi 1984, Gál 2004);

– ***Aquila pomarina*** **(C.L.Brehm, 1831)**

Known from the Carpathian Basin **Q4/II:** Tiszaszőlős – Gomaháza-Puszta (Hungary) (Gál 2007b). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan; **Q4:** Bulgaria, Romania (Tyrberg 1998);

– ***Aquila rapax*** **(Cabanis, 1854)**

Known from the Carpathian Basin **Q4/II:** Bajcsa – Castle (Hungary) (Gál 2002b). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan, Czech Republic; **Q4:** Germany, Moldova (Tyrberg 1998);

– ***Aquila adalberti*** **(Brehm, 1861)**

Finds from Europe outside the Carpathian Basin: **Q4:** Spain (Tyrberg 1998);

– † ***Aquila chrysaetos bonifacti*** **(Mourer-Chauviré, 1975)**

Finds from Europe outside the Carpathian Basin: **Q3:** France (Tyrberg 1998);

– † ***Aquila chrysaetos simurg*** **(Weeseie, 1987)**

Extinct subspecies. Finds from Europe outside the Carpathian Basin: **Q4:** Greece (Tyrberg 1998);

– *Aquila* sp.

Known from the Carpathian Basin **Q3/I:** Hundsheim (Austria) (Mlikovskỳ 2009); **Q4/II:** Starcevo (Serbia) (Classon 1980, Gál 2004). Finds from Europe outside the Carpathian Basin: **Q1-2:** Bulgaria; **Q3:** Italy, Ukraine; **Q4:** Austria, Belgium, Czech Republic, France, Georgia, Germany, Italy, Russia, Spain, United Kingdom (Tyrberg 1998);

– *Haliaeetus* (Savigny, 1809)

– † *Haliaeetus* aff. *angustipes* (Jánossy, 1983)

A metacarpus (III.) was described based on a fragment from the Lower Pleistocene of Betfia 5 (Jánossy 1983, Gál 2002a).

The only defining characteristic is the slimness of the fossilized tarsometatarsus compared to the recent specimens, which can be shown on the fossil found on the typical site in the Czech Republic. Based on finds from the early Pleistocene Betfia and Bugiuleşt (Romania, the southern slope of the Carpathian Basin), Erika Gál (Gál 2002a) described the same characteristic, which we experienced firsthand. Gracility also meant an adaptation to the environment, which can also be seen for example on the typically narrow tarsometatarsus of harriers. The two types of predators may have lived in similar environments and may have nested in reed beds and underbushes during the Pliocene and the lower Pleistocene. The recent white-tailed eagles, however, live in floodplain forests and nests on trees. This may explain the size difference of the skeletal remains of their legs. Erika Gál describes it from the early Pleistocene finds of Bugiuleşti (Romania) (Gál 2002a), while Mlikovskỳ (1998, 2002) describes it as belonging to the recent species.

– *Haliaeetus albicilla* (Linnaeus, 1758)

Known from the Carpathian Basin **Q4/I:** Krapina (Croatia) (Lambrecht 1915, V. Malez 1973, 1984, 1988); Esküllő – Igric Cave (Aștileu-Peștera Igrița) (Kormos 1914, 1916); Nándori Cave (Curata Nandru) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003); Ohábaponor (Peștera Ohaba Ponor, Romania) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003); **Q4/II:** Balatonlele hemp fields **(**Gál 2005**)**; Berettyószentmárton **(**Jánossy 1977, 1985, Gál 2007a, 2007b); Dunaújváros-Intrecisa (Jánossy 1985); Gyula – Castle (Jánossy 1977, 1985); Kisköre-Szingegát (Jánossy 1985, Gál 2004, 2007a, 2007b); Ludas – Budzsák (Bökönyi 1984, Gál 2004); Röszke – Ludvár, Szegvár – Tüzköves, Szerencs – Taktaföldvár, Szolnok – Szanda (Jánossy 1985, Gál 2004, 2007a, 2007b); Tác – Gorsium (Bökönyi 1984, Jánossy 1985); Tiszalök – Rázom (Jánossy 1977); Tiszalúc – Sarkad (Hungary) (Jánossy 1985, Gál 2007a, 2007b); Peterd – Torda Gorge-Magyar Cave (Petrești – Turda, Peștera Ungurească, Romania) (Kessler & Gál 1998, Gál 2004); Padina (Classon 1980, Gál 2004); Vlassac (Serbia) (Jánossy 1977). Finds from Europe outside the Carpathian Basin: **Q1.2:** Netherlands; **Q3:** Azerbaijan, Czech Republic, France, Germany, Greece, Italy; **Q4:** Austria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Italy, Poland, Russia, Spain, United Kingdom (Tyrberg 1998);

– ?*Haliaeetus* sp. foss. indet.

Known from the Carpathian Basin **MN 1-4:** Erősd (Lambrecht 1929).

(Note: the Lambrecht paper quoted in the literature numerous times does not contain the description from Erősd. There is no such material either in the collection of NHMUS (Natural History Museum of Hungary) or GGIH (Geological and Geophysical Institute of Hungary))

– *Hieraetus* (Kaup, 1844)

– *Hieraetus pennatus* (Gmelin, 1788)

Known from the Carpathian Basin **Q4/II:** Ecsegfalva (Hungary) (Pike-Tay *et al.* 2004, Gál 2007a, 2007b). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan; **Q4:** Spain, Russia, United Kingdom (Tyrberg 1998);

– *Hieraetus fasciatus* (Viellot, 1822)

Finds from Europe outside the Carpathian Basin: **Q3:** France; **Q4:** Italy, Malta, Spain (Tyrberg 1998);

– † *Buthierax pouliani* (Kretzoi, 1977)

Finds from Europe outside the Carpathian Basin: **Q3:** Greece (Tyrberg 1998).

Fam. Pandionidae Savigny, 1809

– ***Pandion* Savigny, 1809**

– † *Pandion pannonicus* sp. n.

Holotype – material: distal phalanx (phalanx 3., digiti II.)

Site and age: Máriahalom (Hungary), Upper Oligocene (MP 25). „The village of Máriahalom is located in the northeastern boarder of the Mány-Zsámbék basin, 47 km north-west from Budapest. The sand pit is situated on the south-western side of the road between the townships of Úny and Máriahalom." (Rabi & Botfalvi 2008). The fossil remains – collected among other by Zoltán Evanics – contains fish, reptiles, birds and mamals. The fossil material of birds is very fragmented, containing elements from the aquatic environment. This material is in the collection of the Department of Paleontology at Eötvös Loránd University, Budapest, Hungary.

Diagnosis: Smaller than fossil and recent known osprey species, but it should be a much earlier species described according to a typical osprey skeletal part. The *tuberculum extensorium* (a) is oblique with a blunt end; the *cotyla articularis* (b) has an assymmetrical curve; the neck of the *tuberculum flexorium* (c) is short, the lower part is convex in the middle; the *corpus phalangis* (d) is wide and curved; (the *apex phalangis* is damaged) *(Figure 1.1)*.

Etymology: After the name of Pannonia province.

Dimensions: Total measurable length is A = 20.50 mm (it might have been 22–24 mm), length of the joint surface (from the tub. extens. to the end of the tub. flex.) B = 9.76 mm, the middle width of the *tuberculum flexorium* is (C) = 3.51 mm; the biggest width of the *tuberculum flexorium* is (D) = 5.23 mm, the biggest width of the claw shaft is (E) = 4.94 mm. *(Figure 1.2)*.

Comparative material: *Pandion haliaetus* recent ph.3.dig.II. distal phalanges (NHMUS n = 4, male and female: C.58.11.1; 69.9.17; 791000; 830.621 = A: 23.92–27.13 mm; B: 9.64–12.12 mm; D=5.17–5.83 mm) and ph.2.dig.I.; ph.4.dig.III.; ph.5.dig.IV.distal phalanges *(Figure 1.5)*.

Abrevations: NHMUS – Natural History Museum of Hungary, Budapest.

Method: For the discussed skeletal part, the anatomical terminology (after: Lambrecht 1933, Baumel *et al.* 1979, Solti 1996, Kessler 2013a) and method of measurement (Solti

1996, Kessler 2013) of the bone in question is given, illustrated by the appropriate bone of the fossil specimens and recent species.

Description: The typical osprey claw, the *tuberculum flexiorum major* (all of its skeletal parts differ from other diurnal predators!), can easily be identified due to its elongated form. The shape of the end of the projection decides which finger the claw may have belonged to (on the first finger it is asymmetrical, on the second it is flattened and protuberant in the middle, on the third it is semi-circularly protruberand, on the fourth it is cone shaped, see *Plate, Figure 4–7.* The issue is caused by the difference of the bottom part of the fossil's *tuberculum flexorium* compared to both the four claws of the recent species, as well as in the case of known fossilized claws which partially come from different fingers and earlier layers.

Discussion: The two known fossil species are either larger than the recent species, or match it in size. The first fossilized species was described by S. L. Warter (1976) from the middle Miocene (14.5–13 million years) layers of Sharkstooth Hill, California (USA), with the name *Pandion homalopteron* Warter, 1976 (Warter 1976), based on the humerus and ulna. The size is similar to that of the recent species, or slightly bigger.

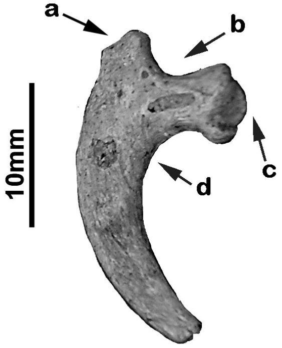
The second known fossil species was also reported from North America by Becker (1985) from the upper Miocene river sediments of Love Bone Bed, Florida (9 million years) (Alachua Formation). The find consists of a distal femur, a complete and a distal tibiotarsus, a complete and a somewhat partial tarsometatarsus and 3 claws, and is named *Pandion lovensis* Becker, 1985 (Becker 1985). Sadly, only one of the claws (Ph 2. dig. I.) is presented as picture (https://www.floridamuseum.ufl.edu/florida-vertebrate-fossils/species/pandion-lovensis/) *(Figure 1.8),* with no description available. We did not receive the requested information of the other two, thus they cannot serve as basis for comparison. The dimensions of the other three skeletal parts, however, confirm that the sizes match those of the recent *Pandion haliaetus*.

The third find is known from the early Pliocene (Yorktown Formation) of Lee Crek Mine (North Carolina, USA) (Olson & Rassmusen 2001). They also reported a claw (p. 298) of which they only gave the B and D dimensions (B = 12.6 mm; D=5 mm) and identified it as *Pandion* sp. The *tuberculum flexorium* differs from that of the find from Máriahalom, and according to its characteristics, it is a phalanx 5. digiti IV *(Figure 1.9)*. Also from Florida, but the middle Pliocene (Bone Valley Formation) comes another *Pandion* claw, which is mentioned without details (Brodkorb 1972).

The earlist find (Olson 1985, Rasmussen *et al.* 1987) comes from the lower Oligocene of Fayum, Egypt (Jebel Quatrami Formation); from there the distal epiphisys of a humerus (width F = 16.9 mm, in case of the recent species 22–24.8 mm) and a damaged carpometatarsus was described (its length was A = 83 mm, in case of the recent species 80-87.5 mm), reported as Pandionidae, gen et species indet.

The dimensions of the two fossil species match those of the recent subspecies found in America and Europe (including sexual dimorphism), but the tarsometatarsus of the fossilized species from Florida is longer and its trochlea more robust than those of recent representatives (see *Table 1* with measurements). This, of course indicates that the phalanges connected to them must also be larger, so as the claws. The material from Máriahalom, however, is somewhat smaller than the appropriate recent claws. Since the morphological

1



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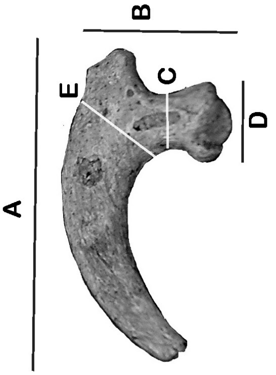

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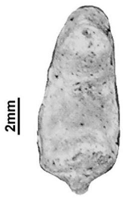

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Figure 1.
1. *Pandion pannonicus* n. sp. Phalanx 3, Digiti II. a – *tuberculum extensorium;* b – *cotyla articularis*; c – *tuberculum flexorium*; d – *corpus phalangis*
2. Method of measurement: A – total length; B – length of the joint surface; C – middle width of the *tuberculum flexorium*; D – biggest width of the *tuberculum flexorium*; E – biggest width of the claw shaft
3. *Pandion pannonicus* n. sp. proximal view of the claw
4. *Pandion haliaetus* rec. Phalanx 2, Digiti I.
5. *Pandion haliaetus* rec. Phalanx 3, Digiti II.
6. *Pandion haliaetus* rec. Phalanx 4, Digiti III.
7. *Pandion haliaetus* rec. Phalanx 5, Digiti IV.
8. *Pandion lovensis* Becker, 1985 foss. Phalanx 2, Digiti I.
9. Pandionidae sp. foss. from Lee Crek Mine, Phalanx 5, Digiti IV.

1. ábra
1. *Pandion pannonicus* n. sp. Phalanx 3, Digiti II. a – *tuberculum extensorium;* b – *cotyla articularis*; c – *tuberculum flexorium*; d – *corpus phalangis*
2. A mérési modell: A – teljes hossz; B – ízesülési felület hossza; C – *tuberculum flexorium* közepének szélessége; D – *tuberculum flexorium* legnagyobb szélessége; E – karomcsont test legnagyobb szélessége
3. *Pandion pannonicus* n. sp. karomcsont proximális nézetből
4. *Pandion haliaetus* rec. Phalanx 2, Digiti I.
5. *Pandion haliaetus* rec. Phalanx 3, Digiti II.
6. *Pandion haliaetus* rec. Phalanx 4, Digiti III.
7. *Pandion haliaetus* rec. Phalanx 5, Digiti IV.
8. *Pandion lovensis* Becker, 1985 foss. Phalanx 2, Digiti I.
9. Pandionidae sp. foss. from Lee Crek Mine, Phalanx 5, Digiti IV.

characteristics are impossible to mistake for the skeletal part of any other bird of prey, due to its age, it is evident that it can not be identical to the recent species. Also, since it is one of the oldest such finds in the world, it can be responsibly described as a new taxon, despite not being able to tell exactly which finger the claw belonged to!

Spread: ospreys are exceptionally rare around the world among fossilized finds (as a cosmopolitan species). The recent species is known from the Upper Pliocene of Villány (Villány 3) and a few finds from the Quaternary, for example the Upper Pleistocene sediments of the Cioraei Cave in Romania (Kessler & Gál 2001, Kessler 2009). The latter was identified from a claw (phalanx 4. digiti III). It probably belongs to a male specimen.

Ospreys have typical lifestyles, feeding on fish. Thus, their presence indicates such an environment (large, open waters: rivers, lakes, seas). Currently, it is a rare species in the Carpathian Basin, as a migrant or summer vagrant. Its presence in the upper Oligocene also indicates a seashore environment.

– *Pandion haliaetus* (Linnaeus, 1758)

Known from the Carpathian Basin **MN 16-17:** Villány 3 (Hungary) (Kessler 2009). Finds from Europe outside the Carpathian Basin: **Q3:** Italy, United Kingdom; **Q4:** Georgia, Germany, Italy, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998); Romania (Gál & Kessler 2001).

Table 1. Osprey bones measurement
1. táblázat Halászsas csontok mérettáblázata

dimensions of bones in mm	***Pandion homalopteron***	***Pandion lovensis***	***Pandion pannonicus***	***Pandionidae Fayum***	**Pandionidae Lee Crek Mine**	**Pandion hali aetus Cioarei**	**Pandion haliaetus rec.**
Humerus							
A (total lenght)	151.00						135.00–154.00
C (width of proximal epiphysis	27.50						25.00–28.50
E (width of shaft)	12.00						11.00–12.00
F (width of distal epiphysis)	24.50			16.90			22.00–24.80
Ulna							
A (total lenght)	120.00						166.00
Carpometacarpus							
A (total lenght)				83.00			80.00–87.50
Femur							
E (thichness of diaphysis)		7.20					7.00–8.30
F (thickness of distal epiphysis)		15.20					14.00–17.40
G (width of dsital epiphysis)		12.80					12.70–14.20
Tibiotarsus							
A (total lenght)		124.80					115.00–130.80
C (thickness of proximal epiphysis)		17.00					15.90–18.50
D (width of proximal epiphysis)		13.10					12.30–14.20
Tarsometatarsus							
A (total lenght)		59.50					49.00–54.90
F (thickness of distal epiphysis)		16.40					14.00–15.90
Phalanx 2. Digiti I.							
A (total lenght)		cca. 27.0					24.04–27.77
B (thickness of proximal end)		cca. 12.0					10.81–11.85
C (middle width of tub.flexor.)		cca. 4.6					4.51–4.90
D (biggest width of tub. flexor.)		cca. 5.5					5.23–5.79
E (biggest width of the corpus)		cca. 6.0					4.76–6.67
Phalanx 3. Digiti II.							
A (total lenght)			cca. 22–24				23.92–27.13

dimensions of bones in mm	*Pandion homalopteron*	*Pandion lovensis*	*Pandion pannonicus*	*Pandionidae Fayum*	Pandionidae Lee Crek Mine	Pandion hali aetus Cioarei	Pandion haliaetus rec.
B (thickness of proximal end)			9.76				9.64–12.12
C (middle width of tub.flexor.)			3.51				3.58–5.15
D (biggest width of tub. flexor.)			5.23				5.17–5.83
E (biggest width of the corpus)			4.94				5.06–5.42
Phalanx 4. Digiti III.							
A (total lenght)						35.40	24.13–26.78
B (thickness of proximal end)						11.20	10.26–12.23
C (middle width of tub.flexor.)							3.65–5.15
D (biggest width of tub. flexor.)						5.10	4.76–5.79
E (biggest width of the corpus)							4.89–5.72
Phalanx 5. Digiti IV.							
A (total lenght)							23.57–26.16
B (thickness of proximal end)					12.60		9.99–11.12
C (middle width of tub.flexor.)							4.00–4.74
D (biggest width of tub. flexor.)					5.00		4.83–5.27
E (biggest width of the corpus)							5.12–5.60

Ord. Falconiformes (Leach, 1820)
Fam. Falconidae (Vigors, 1824)

Falcons and kestrels are diurnal predators of open areas. They are especially swift flyers, also indicated by their physique and wings. Their preys fit their sizes, which indicates their environments, as do their mating habits. Their sexual dimorphism is indicated by their difference in size; the females are significantly larger than the males. Specimens capable of flight but not yet sexually mature *(subadultus)* are richly represented even in large groups among fossilized material (for example in cave 4 of Calvary Hill in Tatabánya). Falcons – especially before maturing – are wanderers, while kestrels mostly migrate.

– *Falco* (Linnaeus, 1758)

– † *Falco* aff. *antiquus* (Mourer-Chauviré, 1975)

It was identified from the middle Pleistocene sediments of the Cserépfalu-Hórvölgy Cave (Hungary) (Jánossy 1977, 1986, Kessler 2009). Finds from Europe outside the Carpathian Basin: **Q3:** France (Tyrberg 1998). It belongs to bigger falcons and is a transition between the Saker Falcon and the Gyrfalcon. The fossilized species was described from the La Fage site in France **(Q3)** (Mourer-Chauviré 1975), but according to Mlikovskỳ (2002) there are no morphological differences when compared to the recent Saker Falcon *(Falco cherrug)*.

– † *Falco tinnunculus atavus* (Jánossy, 1972)

Known from the Carpathian Basin **MN 13:** Polgárdi 5 (Hungary) (Jánossy 1995, Kessler 2009); **MN 15:** Beremend 26 (Hungary) (Kessler 2009); Csarnóta 2 (Jánossy 1977, Kessler 2009); **MN 16:** Beremend 15 (Hungary) (Jánossy 1987, Kessler 2009); **Q1:** Németóvár (Deutsch-Altenburg, Austria) (Jánossy 1981); Beremend 16, 17 (Hungary) (Jánossy 1992); Betfia 2, 9, (Romania) (Jánossy 1977, Kessler 1975, Gál 2002a); **Q2:** Nagyharsány Hill 1-4, Somssich Hill 2 (Jánossy 1977, 1981, 1982, 1983, 1986); Villány 5 (Hungary) (Kessler 2009); Betfia 7, „Aven" (Kessler 1975, Jánossy 1977, Gál 2002a); Betfia 5, 7/2-3 (Romania) (Kessler 1975, Jánossy 1977, Gál 2002a); Méhész (4E) (Vcelare, Slovakia) (Jánossy 1977); **Q3/I:** Hundsheim (Austria) (Jánossy 1974, 1977); Tarkő 1-16 (Hungary) (Jánossy1977) Betfia 7/4 (Romania) (Kessler 1975, Jánossy 1977, Gál 2002a); Gombaszög (Gombasek, Slovakia) (Kessler 2009). Finds from Europe outside the Carpathian Basin: **Q1-2:** France; **Q3:** Czech Republic, France, Netherlands, Poland (Tyrberg 1998).

The diagnosis of fossil subspecies is based on the proportions of the dimensions, according to which it is more solid than the recent species. It has been reported from several lower and middle Pleistocene sites from all across Europe. Despite the fact that Mlikovskỳ (2002) classifies it as belonging to the recent species, in our opinion, the distinction of the fossil subspecies is justified due to the age of the finds and the size differences mentioned above.

– *Falco tinnunculus* (Linnaeus, 1758)

Known from the Carpathian Basin **Q3/II:** Cserépfalú – Hórvölgy Cave (Jánossy 1962a, 1977, 1986); Süttő 1-4 (Hungary) (Jánossy 1977, 1986); **Q4/I:** Merkestein (Austria) (Wettstein & Mühlhofer 1938); Budapest – Remete Cave (Jánossy 1977, 1986); Budapest – Remetehegy Cave (Kormos 1914, Lambrecht 1933, Jánossy 1977, 1986); Cserépfalu – Subalyuk Cave (Jánossy 1962a, 1977, 1986); Csobánka – Kiskevély Cave (Jánossy1977); Érd (Jánossy 1977, 1986); Felsőtárkány – Peskő Cave (Lambrecht 1912, 1933, Jánossy 1977, 1986); Hámor – Puskaporos Shelter Cave (Lambrecht 1912, 1916, 1933, Jánossy 1977, 1986); Hámor – Herman Ottó Cave (Lambrecht 1915, 1933); Pilisszántó I. – Shelter cave (Lambrecht 1915, 1933, Jánossy 1977, 1986); Répáshuta – Balla Cave (Lambrecht 1912, 1933); Szilvásvárad-Istállóskő Cave (Lambrecht 1912, 1933, Jánossy 1952, 1977, 1986); Tatabánya – Calvary Cave n. 4. (Gál 2004, 2005); Tatabánya – Szelim Cave (Jánossy 1977, 1986); Vaskapu Cave (Hungary) (Mottl 1941, Válóczi 1999); Hidegszamos – Csont Cave (Someșul Rece – Peștera cu Oase) (Lambrecht 1915); Körösmart (Râpa) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002a); Nándori Cave (Curata-Nandru, Romania) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003); Detrekőszentmiklós – Pálffy Cave (Dzeráva Skála-Plavecky Mikulas, Slovakia) (Lambrecht 1913, 1933); **Q4/II:** Teufelslucken (Soergel 1966); Tropfsteinhöhle (Austria) (Fladerer 1993). Felsőnyék – Várhegy (Gál 2007a); Felsőtárkány – Petényi Cave (Hungary) (Jánossy 1977, 1986); Herkulesfürdő – Rabló Cave (Băile Herculane – Peștera Hoţilor) (Kessler 1980-81, Gál 2002a); Remetelórév – Bólyikői Cave (Lorău-Peștera Piatra Boiului) (Kessler 1982); Révtizfalusi Cave (Peștera din Zece Hotare) (Kessler 1985); Szegyestel – Drăcoaia-Cave (Peștera Drăcoaia – Valea Sighiștelului) (Kessler 1982); Székelykeresztúr (Cristuru Săcuiesc, Romania) (Gál 2008); Finds from Europe outside the Carpathian Basin: **Q1-2:** Czech Republic, Greece; **Q3:** Azerbaijan, Czech Republic, France, Georgia, Italy, Spain, Ukraine; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Croatia, Czech Republic, France, Georgia, Germany, Greece, Ireland, Italy, Moldova, Montenegro, Poland, Portugal, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998);

– *Falco vespertinus* (Linnaeus, 1766)

Known from the Carpathian Basin **MN 16:** Betfia 13 (Romania) (Kessler 1975, Gál 2002a); **Q1:** Betfia 2, 7, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Jánossy 1977, Kessler 1975, Gál 2002a); **Q1-2:** Betfia „Aven" (Romania) (Kessler 1975, Jánossy 1977, Gál 2002a); **Q2:** Somssich Hill 2 (Hungary) (Jánossy 1983); **Q3/I:** Hundsheim (Austria) (Mlikovskỳ 2009); Betfia 7/4 (Hungary) (Kessler 1975, Jánossy 1977, Gál 2002a); **Q4/I:** Budapest – Remetehegy Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1977, 1986); Cserépfalu – Subalyuk Cave (Jánossy 1962a, 1977, 1986); Hámor – Puskaporos Shelter Cave (Lambrecht 1912a, 1916, 1933, Jánossy 1977, 1986); Pilisszántó I. Shelter Cave (Lambrecht 1915, 1933, Jánossy 1977, 1986); Szilvásvárad-Istállóskői Cave (Hungary) (Lambrecht 1912b, 1933, Jánossy 1952, 1955, 1977, 1986); Ohábaponor – Bordu Mare Cave (Ohaba Ponor – Peștera Bordu Mare, Romania) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003). Finds from Europe outside the Carpathian Basin: **Q3:** Czech Republic, France; **Q4:** Bulgaria, France, Georgia, Germany Italy, Moldova, Spain, Ukraine (Tyrberg 1998);

– *Falco subbuteo* (Linnaeus, 1758)

Known from the Carpathian Basin **Q1:** Betfia 9 (Romania) (Kessler 1975, Gál 2002a); **Q1-2:** Betfia „Aven" (Romania) (Kessler 1975, Jánossy 1977, Gál 2002a); **Q3/II:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, 1991, Malez & Rukavina 1979); **Q4/I:** Kesztölc-Bivak Cave (Jánossy 1977); Tatabánya – Szelim (Hungary) Cave (Jánossy 1977, 1986); Segyestel – Tibocoaia Cave (Valea Sighiștelului-Peștera Tibocoaia) (Kessler 1982, 1985, Gál 2002a); Detrekőszentmiklós – Pálffy Cave (Dzeráva Skála-Plavecky Mikulas, Slovakia) (Lambrecht 1913, 1933); **Q4/II:** Körösbánlaki Cave (Peștera din Bălnaca) (Kessler 1982); Peterd – Turda Gorge-Magyar Cave (Petrești – Turda, Peștera Ungureasca) (Kessler & Gál 1998, Gál 2004); Révi Caves (Peșteri din Vadu Crișului) (Kessler 1982); Szegyestel – Drăcoaia Cave (Valea Sighiștelului, Peștera Drăcoaia, Romania) (Kessler 1982). Finds from Europe outside the Carpathian Basin: **Q3:** Czech Republic, France, Georgia, Germany, Italy; **Q4:** Austria, Croatia, France, Georgia, Germany, Greece, Italy, Spain, Ukraine, United Kingdom (Tyrberg 1998);

– *Falco cherrug* (Gray, 1844)

Known from the Carpathian Basin **Q1:** Betfia 9 (Hungary) (Kessler 1985, Gál 2002a); **Q3/I;** Betfia 7/4 (Hungary) (Kessler 1975, Jánossy 1977, Gál 2002a); **Q4/I:** Pilisszántó I. – Shelter Cave (Hungary) (Lambrecht 1915, 1933, Jánossy 1977, 1986); **Q4/II:** Remetelórév – Bólyikő Cave (Lorău – Peștera Piatra Boiului) (Kessler 1982); Szegyestel – Drăcoaia Cave (Valea Sighiștelului – Peștera Drăcoaia, Romania) (Kessler 1982). Finds from Europe outside the Carpathian Basin: **Q3:** Czech Republic; **Q4:** Croatia, Slovenia, Ukraine (Tyrberg 1998);

– *Falco peregrinus* (Tunstall, 1771)

Known from the Carpathian Basin **Q4/I:** Bajót – Hóman Cave (Jánossy 1977, 1986); Bajót – Jankovich Cave (Lambrecht 1933, Jánossy 1977, 1986); Cserépfalu – Subalyuk

(Jánossy 1962a, 1977, 1986); Hámor – Puskaporos Shelter Cave (Lambrecht 1912a, 1916, 1933, Jánossy 1977, 1986); Kesztölc – Bivak Cave (Hungary) (Jánossy 1977, 1986). Finds from Europe outside the Carpathian Basin: **Q3:** Azerbaijan, Czech Republic, France; **Q4:** Austria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Italy, Moldova, Poland, Russia, Spain, United Kingdom (Tyrberg 1998);

– *Falco rusticolus* (Linnaeus, 1758)

Known from the Carpathian Basin **Q3/II:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, 1991, Malez & Rukavina 1979); **Q4/I:** Bajót – Hóman Cave (Jánossy 1977, 1986); Tatabánya – Szelim Cave (Hungary) (Jánossy 1977, 1986); Detrekőszentmiklós – Pálffy Cave (Dzeráva Skála – Plavecky Mikulas, Slovakia) (Lambrecht 1913, 1933). Finds from Europe outside the Carpathian Basin: Q3: Czech Republic; Q4: Czech Republic, France, Germany, Italy, Spain (Tyrberg 1998);

– *Falco columbarius* (Linnaeus, 1758)

Known from the Carpathian Basin **Q1:** Betfia 9 (Kessler 1985, Gál 2002a); **Q1-2:** Betfia 7, „Aven" (Kessler 1975, Jánossy 1977, Gál 2002a); **Q3/I:** Betfia 7/4 (Kessler 1975, Jánossy 1977, Gál 2002a); **Q3/II:** Süttő 1-4. (Jánossy 1977, 1986); **Q4/I:** Budapest-Remetehegy Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1977, 1986); Felsőtárkány – Peskő Cave (Lambrecht 1912b, 1933, Jánossy 1977, 1986); Hámor – Puskaporos Shelter Cave (Lambrecht 1912a, 1916, 1933, Jánossy 1977, 1986); Szilvásvárad – Istállóskői Cave (Lambrecht 1912b, 1933, Jánossy 1952, 1955, 1977, 1986); Tatabánya – Szelim Cave (Jánossy 1977, 1986, Varbó – Lambrecht Kálmán Cave (Hungary) (Jánossy 1977, 1986); Măgura – Valea Coacăzei (Măgura-Peştera din Valea Coacăzei, Romania) (Gál 2002a); Detrekőszentmiklós – Pálffy Cave (Dzeráva Skála – Plavecky Mikulas) (Lambrecht 1913, 1933); Óruzsin – Antal Cave (Oruzer, Slovakia) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933); **Q4/II:** Körösbánlaki Cave (Peștera din Bălnaca, Romania) (Kessler 1982). Finds from Europe outside the Carpathian Basin: **Q3:** Czech Republic, France, Germany, Italy, Ukraine; **Q4:** Croatia, Czech Republic, France, Georgia, Germany, Italy, Poland, Spain, Ukraine, United Kingdom (Tyrberg 1998);

– *Falco naumanni* (Fleischer, 1818)

Finds from Europe outside the Carpathian Basin: **Q3:** France, Spain; **Q4:** Austria, France, Georgia, Greece, Italy, Russia, Spain, Ukraine (Tyrberg 1998);

– *Falco eleonarea* (Géné, 1839)

Finds from Europe outside the Carpathian Basin: **Q3:** France, Italy; **Q4:** France, Greece, Italy, Spain; (Tyrberg 1998);

– *Falco* sp. foss. indet.

Known from the Carpathian Basin **MN 13:** Polgárdi 4 (Hungary) (*F.* cf. *cherrug* size) (Kessler 2009); **MN 15:** Beremend 26 (Hungary) (*F.* cf. *peregrinus* size) (Kessler 2009);

– *Falco* sp.

Known from the Carpathian Basin **Q1:** Betfia 9 (Romania) (Kessler 1985, Gál 2002a); **Q1-2:** Betfia 7 (Romania) (Kessler 1975, Jánossy 1977a, Gál 2002a); **Q2:** Kiskóh – Bear's Cave (Chișcău – Peștera Urșilor, Romania) (Kessler 1982, Jurcsák & Kessler 1988, Gál 2002a); **Q3/I;** Berfia 7/4 (Romania) (Kessler 1975, Jánossy 1977, Gál 2002a); **Q4/I:** Veternica (Croatia) (V. Malez 1973, 1988, Malez-Bačić 1975); Ohábaponor – Bordu Mare Cave

(Ohaba Ponor – Peștera Bordu Mare, Romania) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003); **Q4/II:** Legény Cave (Hungary) (Lambrecht 1933); Kisderzsida (Derșida Mică) (Bindea 2008); Körösbánlaki Cave (Peștera din Bălnaca, Romania) (Kessler 1982). Finds from Europe outside the Carpathian Basin: **Q4:** Belgium, Bosnia – Hrzegovina, Bulgaria, France, Germany, Italy, Moldova, Montenegro, Poland, Russia, Spain, United Kingdom (Tyrberg 1998).

Conclusions

The family of eagles, vultures, buzzards and kites (Accipetridae) is well-represented in fossilized and subfossilized remains in the Carpathian Basin, as well as in the whole of Europe. Practically, every recent species is represented. Four extinct species, as well as two subspecies, were identified from the Quaternary (*Gyps melitensis* Lydekker, 1890; *Gypaetus asiaticus* Burchak-Abramovich, 1971; *Aquila chrysaetos simurg* Weeseie, 1987; *Accipiter gentilis brachydactylus* Mourer-Chauviré, 1975; *Milvus brachypterus* Jánossy, 1977 and *Haliaeetus* aff. *angustipes* Jánossy, 1983).

The family of falcons (Falconidae) is present with numerous species and rich fossilized and subfossilized material in the Carpathian Basin. They have a few problematic extinct species (*Falco antiquus* Mourer-Chauviré, 1975) and subspecies (*Falco tinnunculus atavus* Jánossy, 1972).

Regarding fossilized species from the family of ospreys (Pandionidae), apart from the one found in Máriahalom, only two have been described previously: *Pandion homalopteron* (Warter 1976), *Pandion lovensis* (Becker 1985). Pandion bones were also found in the lower Oligocene material of the Fayum site in Egypt (Eocene-Oligocene boundary, Priabonian-Rupelian, approx. 30 million years) Thus, the find from Máriahalom is the fourth of its kind, as well as one of the earliest ones in the world.

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References

Becker, J. J. 1985. *Pandion lovensis*, a New Species of Osprey from the Late Miocene of Florida. – Proceedings of the Biological Society of Washington 98: 314–320.

Bindea, D. (ed.) 2008. Arheozoologia Transilvaniei in pre- si protoistorie [Transylvanian archaeozoology archaeozoology in Prae- and Protoistory]. – Trognost Cluj-Napoca (in Romanian)

Bocheński, Z. 1997. List of European fossil bird species. – Acta Zoologica Cracoviensia 40(2): 293–333.

Bökönyi, S. 1984. Animal husbandry and hunting in Tác-Gorsium [The Vertebrate fauna of the Roman Town in Pannonia]. – Akadémiai Kiadó, Budapest (in Hungarian)

Bökönyi, S. & Jánossy, D. 1965. Szubfosszilis vadmadár leletek Magyarországon – Subfossile Wildvogelfunde aus Ungarn [Subfossil wild bird remians from Hungary]. – Vertebrata Hungarica 7: 85–99. (in Hungarian and German)

Brodkorb, P. 1964. Catalogue of fossil Birds, Part 2 (Anseriformes through Galliformes). – Bulletin of the Florida State Museum, Biological Sciences 8(3): 195–335.

Brodkorb, P. 1972. New discoveries of pliocene birds in Florida. – In: Voous, K. H. (ed.) Proceedings of the XV. International Ornithological Congress, Abstract, p. 634. Leiden

Čapek, V. 1917. A püspökfürdői preglaciális madárfauna [The Preglaciale bird fauna from Püspökfürdő]. – Barlangkutatás 5: 66–74. (in Hungarian)

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)

Gál, E. 2002a Avifauna pleistocenă a României [Pleistocene bird faunas of Romania – (Unpublied C.Sc dissertation)]. – Universitatea din Bucureşti, Facultatea de Geologie București (in Romanian)

Gál, E. 2002b Madárleletek a bajcsai várból [Bird finds from the Bajcsa Castle]. – In: Kovács, Gy. (ed.) Weitschawar – Bajcsa-vár, 101–105 + 4 ábra, Zalaegerszegi Múzeumok Igazgatósága, Zalaegerszeg (in Hungarian)

Gál, E. 2003. Bird remains from two Romanian caves: Curata Cave (Nandru) and Bordu Mare Cave (Ohaba Ponor). – ICAZ 2002. Abstracts, p. 56.

Gál, E. 2004. 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. 2005. 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. 2007a The Neolitic avifauna of Hungary within the context of the Carpathian Basin. – Antaeus 27: 273–286.

Gál, E. 2007b Fowling in lowlands. Neolitic and Chalcholitic bird exploitation in South-East-Romania and the Great Hungarian Plain. – Archaeolinqua, Series Minor 24., Budapest

Gál, E. 2008. Faunal and taphonomic approach to a Late Pleistocene cavern bird bone assemblage in North-West Hungary. – Géobios 41: 79–90.

Hamar, M. & Csák, K. 1969. Contribuţii la cunoaşterea faunei de vertebrate pleistocene din Dealul Burzău (com. Rîpa, jud. Bihor) – jung Wurm [Contribution to the knownledge of Pleistocene vertebrate fauna from Burzau Hill (Village Rîpa, Bihor County) – Lower Würm]. – Studii şi cercetări biologice Seria, Zoologie 21(6): 425–432. (in Romanian)

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. 1960. Steinadler (*Aquila chrysaetos* L.) und Bartgeier (*Gypaetus barbatus* L.) aus dem Pleistozan Ungarns [Golden Eagle (*Aquila chrysaetos* L.) and Bearded Vulture (*Gypaetus barbatus* L.) from the Pleistocene of Hungary]. – Vertebrata Hungarica 2: 133–136. (in German)

Jánossy, D. 1962a Eine fossile Vogelfauna aus den Mosuterien-Schichten der Subalyuk-Höhle im Bükk-Gebirge [Fossil avifauna from the Mousterian layers of Subalyuk Cave in the Bükk Mountains]. – Aquila 67–68: 175–188. (in German)

Jánossy, D. 1962b Vorlaufige Mitteilung über die Mittelpleistozäne Vertebratenfauna der Tarkő-Felsnische (NO-Ungarn, Bükk-Gebirge) [Preliminary notification of the Middle Pleistocene vertebrate fauna of the

Tarkő Rock (NE Hungary, Bükk Mountains)]. – Annales Historico Naturales Musei Nationalis Hungarici 54: 155–176. (in German)

Jánossy, D. 1965. Fossiler Vogelfauna aus Mousterien Schichten der Curata-Hohle (Rumanien) [Fossil bird fauna from Mousterian layers of Curata Cave (Romania)]. – Vertebrata Hungarica 7(1–2): 106–116. (in German)

Jánossy, D. 1972. Middle Pliocene Microvertebrate fauna from the Osztramos Loc.1 (Northern Hungary). – Annales Historico Naturales Musei Nationalis Hungarici 64: 27–48.

Jánossy, D. 1974. 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. 1976. Die Felsnische Tarkő und die Vertebratenfauna ihrer Ausfüllung [The cavity of Tarkő and the vertebrate fauna of Their Filling]. – Karszt- és Barlangkutatás 8: 3–106. (in German)

Jánossy, D. 1977. Plio-pleistocene bird remains from the Carpathian Basin. III. Strigiformes, Falconiformes, Caprimulgiformes, Apodiformes. – Aquila 84: 9–36.

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. 1983. Lemming-remain from the Older Pleistocene of Southern Hungary (Villány, Somssich Hill 2.). – Fragmenta Mineralogica et Paleontologica 11: 55–60.

Jánossy, D. 1985. Wildvogelreste aus archaeologischen Grabungen in Ungarn (Neoliticum bis Mittelalter) [Wild bird remains from archaeological excavations in Hungary (from the Neoliticum to the Middle Ages)]. – Fragmenta Mineralogica et Paleontologica 12: 67–103. (in German)

Jánossy, D. 1986. Pleistocene Vertebrate faunas of Hungary. – Akadémiai Kiadó, Budapest & Elsevier, Amsterdam

Jánossy, D. 1987. Ältestpleistozäne vertebratenfauna von Beremend 15 (Sud-Ungarn) [Earliest Pleistocene vertebrate fauna of Beremend 15th (South Hungary)]. – Fragmenta Mineralogica et Paleontologica 13: 89–96. (in German)

Jánossy, D. 1992. Lower Pleistocene bird remains from Beremend (S-Hungary, Loc. 15. and 16.). – Aquila 99: 9–25.

Jánossy, D. 1995. A Late Miocene avifauna from Polgárdi, Western Hungary. – Acta Palaeornithologica, Courier Forschungsinstitut Senckenberg 181: 203–206.

Jurcsák, T. 1974. Prezenţa lui *Gyps fulvus* (Habl.) în cuaternarul României [The presence of *Gyps fulvus* (Habl.) in Romanian Queternar]. – Nymphaea 2: 169–184. (in Romanian)

Jurcsák, T. & Kessler, E. 1986. Evoluţia avifaunei pe teritoriul României (I) [Evolution of the avifauna in the territory of Romania (I)]. – Crisia (16): 577–615. (in Romanian with English Summary)

Jurcsák, T. & Kessler, E. 1988. Evoluţia avifaunei pe teritoriul României (III) [Evolution of avifauna on the territory of Romania (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. 1974c Avifauna postglaciară de la Cuina Turcului, Cazanele Mari, România [Postglacial avifauna from Cuina Turcului, Cazanele Mari, România]. – Tibiscus 11: 113–122. (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 [Postglaciale avifauna from Vadu Crişului, Bihor County]. – Tibiscus 14: 255–260. (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. 1985. Contribuţii noi la studiul avifaunelor cuaternare din România [New contributions to the study of Quaternary bird faunas in Romania]. – Crisia 15: 485–491. (in Romanian)

Kessler, J. 2009. Új eredmények a Kárpát-medence neogén és negyedidőszaki madár-világához, I. [New results with regard to the Neogene and Quaternary avifauna of the Carpathian Basin. Part I.]. – Földtani Közlöny 139(1): 67–82. (in Hungarian with English Summary)

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. 1954. Befejező jelentés a csákvári barlang őslénytani feltárásáról [Concluding report on the palaeontological exploration of Csákvár Cave]. – A Magyar Állami Földtani Intézet Évi Jelentése az 1952 évről, pp. 37–69. (in Hungarian)

Lambrecht, K. 1912a A borsodi Bükk fossilis madarai (Fossile Vögel des Borsoder Bükkgebirges) [Fossil birds of the Bükk Mountains from Borsod]. – Aquila 19: 270–287. (in Hungarian and German)

Lambrecht, K. 1912b 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 [Recent 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 pleistocénből [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. 1929. Mezozoische und tertiäre Vogelreste aus Siebenburgen [Mezozoic and Tertiary bird remains from Transylvania]. – In: Csiki, E. (ed.) X. Congres International de Zoologie, pp. 1262–1275. (in German)

Lambrecht, K. 1933. Handbuch der Palaeornithologie [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, 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 Northwest Croatia]. – Rad Hazu knj. 371: 245–265. (in Croatian)

Malez, V. 1973. Fosilne ptice Jugoslavije [Fossil birds from Yugoslavia]. – Unpublished Dissertation, Zagreb University (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]. – 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)

Mlikovskỳ, J. 1998. Early Pleistocene birds of Deutsch-Altenburg, Austria. – Acta Societatis Zoologicae Bohemicae 62: 135–141.

Mlikovskỳ, J. 2002. Cenozoic birds of the World, Part 1., Europe. – Ninox Press, Praha

Mlikovskỳ, J. 2009. Middle Pleistocene birds of Hundsheim, Austria. – Journal of the National Museum (Prague), Natural History Series 177(7): 69–82.

Mottl, M. 1938. Faunen, Flora und Kultur des ungarische Solutréen [Fauna, flora and culture of the Hungarian Solutréen]. – Quartär 1: 36–54. (in German)

Mottl, M. 1941. Die Interglazial- und Interglazialzeiten im Lichte der Ungarischen Saugetierfauna [Interglacial and interglacial times in the light of Hungarian mammalian fauna]. – Mitteilungen aus dem Jahrbucke der Königlich Ungarischen Geologischen Anstalt 35: 13–39. (in German)

Olson, S. L. 1985. The fossil record of birds. – Avian Biology 7: 80–252.

Olson, S. L. & Rasmussen, P. C. 2001. Miocene and Pliocene biords from the Lee Creek Mine North Carolina. – In: Ray, C. E. & Bohaska, D. J. (eds.) Geology and Paleontology of the Lee Creek Mine, North Carolina, III. Smithsonian Contributions to Paleobiology 90: 233–365.

Pike-Tay, A., Bartosiewicz, L., Gál, E. & Whitle, A. 2004. Body part representation and seasonility: sheep/goat, bird and fish remains from Early Neolitic Ecsegfalva 23 SE Hungary. – Journal of Taphonomy 2(4): 221–246.

Rabi, M. & Botfalvi, Z. 2008. A preliminary report on the Late Oligocene vertebrate fauna from Máriahalom, Hungary. – In: Galácz, A. (ed.) 125th Anniversary of the Department of Paleontology at Budapest University – A Jubilee Volume Hantkeniana 6: 177–185.

Randall, Z. S. 2012. https://www.floridamuseum.ufl.edu/florida-vertebrate-fossils/species/pandion-lovensis/

Rasmussen, D. T., Olson, S. L. & Simons, E. L. 1987. Fossil Birds from the Oligocene Jebel Qatrani Formation, Fayum Province, Egypt. – Smithsonian Contributions to Paleobiology 62: 1–20.

Róth, S. 1881. Szepesmegye néhány barlangjának leirása [Descriptions 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)

Tyrberg, T. 1998. Pleistocene birds of the Palearctic: a catalogue. – Cambridge, Mass.: Nuttall Ornithological Club [Publications of the Nuttall Ornithological Club, No. 27.]

Warter, S. L. 1976. A New Osprey from theMiocene of California (Falconiformes, Pandionidae). – In: Olson, S. L. (ed.) Collected Papers in Avian Paleontology Honoring the 90th Birthday of Alexander Wetmore. – Smithsonian Contributions to Paleobiology 27: 133–139.

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)

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Exploratory analyses of migration timing and morphometrics of the European Robin *(Erithacus rubecula)*

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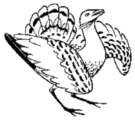

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Abstract Ornithological studies often rely on long-term bird ringing data sets as sources of information. However, basic descriptive statistics of raw data are rarely provided. In order to fill this gap, here we present the sixth item of a series of exploratory analyses of migration timing and body size measurements of the most frequent passerine species at a ringing station located in Central Hungary (1984–2017). First, we give a concise description of foreign ring recoveries of the European Robin in relation to Hungary. We then shift focus to data of 40,128 ringed and 11,231 recaptured individuals with 24,056 recaptures (several years recaptures in 313 individuals) derived from the ringing station, where birds have been trapped, handled and ringed with standardized methodology since 1984. Timing is described through annual and daily capture and recapture frequencies and their descriptive statistics. We show annual mean arrival dates within the study period and present the cumulative distributions of first captures with stopover durations. We present the distributions of wing, third primary, tail length and body mass, and the annual means of these variables. Furthermore, we show the distributions of individual fat and muscle scores, and the distributions of body mass within each fat score category. We distinguish the spring and autumn migratory periods and age groups (i.e. juveniles and adults). Our aim is to provide a comprehensive overview of the analysed variables. However, we do not aim to interpret the obtained results, merely to draw attention to interesting patterns that may be worth exploring in detail. Data used here are available upon request for further analyses.

Keywords: Ócsa Bird Ringing Station, wing, third primary, tail length, body mass, fat, muscle, bird banding, capture-recapture, long term data, meta-analyses, Robin Redbreast

Összefoglalás Madártani tanulmányokban gyakran elemeznek hosszútávú madárgyűrűzési adatsorokat, de az alapvető leíró statisztikák és exploratív elemzések általában nem hozzáférhetőek. E hiányt pótolandó, cikksorozatot indítottunk, melyben egy közép-magyarországi gyűrűző állomáson leggyakrabban előforduló énekesmadár fajok vonulás időzítésének és testméreteinek exploratív elemzéseit közöljük (1984–2017). A sorozat hatodik tagjaként szolgáló jelen cikkben először áttekintjük a vörösbegy magyar gyűrűs külföldi és külföldi gyűrűs magyarországi megkerüléseit, majd rátérünk a faj egy magyarországi, 1984 óta standard módszerekkel dolgozó gyűrűzőállomásról származó 40 128 gyűrűzött és 11 231 visszafogott egyedétől (összesen 24 056 visszafogási esemény, 313 esetben több évből) származó adatainak elemzésére. Az időzítés és a fogásszám jellemzésére a napi és évi fogás és visszafogás gyakoriságokat használtuk. Ábrázoltuk az évenkénti átlagos érkezési időket és azok változását. Az éven belüli időzítést az első megfogások kumulatív eloszlásával ábrázoljuk feltüntetve a tartózkodási időket is. Közöljük a szárnyhossz, a harmadik evező hossz, a farokhossz és testtömeg leíró statisztikáit. Ábrázoljuk ezen változók éves átlagait, a zsír- és izomkategóriák gyakorisági eloszlását, valamint a testtömegek eloszlását zsírkategóriák szerinti bontásban. Az elemzésben elkülönítjük a vonulási (tavasz, ősz) időszakokat és a korcsoportokat (fiatal, öreg). Célunk a vizsgált változók átfogó bemutatása és a bennük található mintázatok feltárása volt az eredmények interpretálása nélkül. Kérésre a cikkhez felhasznált adatsort rendelkezésre bocsátjuk.

Kulcsszavak: Ócsai Madárvárta, szárnyhossz, harmadik evező hossza, farokhossz, testtömeg, zsír, izom, madárgyűrűzés, hosszútávú adatsor, meta-analízis

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Introduction

Bird ringing or banding is one of the principal and oldest methods in use to study various aspects of avian populations (Robinson *et al.* 2009). Overwhelming amount of data has been collected by professional research entities and within citizen science projects Cooper *et al.* 2014) in over a century of bird ringing, and has been used excessively in a diverse array of disciplines. However, compared to the amount of data available throughout the world, concise descriptive information on measured parameters suitable for meta- or comparative analyses is sporadically available (Gienapp *et al.* 2007, Harnos *et al.* 2015). Though purely descriptive studies are often hard to publish within the framework of current hypothesis-focused science, we feel that such studies may well play an outstanding role in generating new hypotheses. Therefore, it is essential that descriptive studies apply the most appropriate statistical methodologies (Harnos *et al.* 2015, 2016, 2017). The bulk of currently available data is often collected at permanent, long-term ringing stations where large amount of individuals of various species are trapped simultaneously (Csörgő *et al.* 2016). These projects generally apply standardized methodologies in trapping, handling and data collection, thus information derived from these sites is suitable for location-wise comparisons (Schaub & Jenni 2000, Marra *et al.* 2004, Schaub *et al.* 2008, Tøttrup *et al.* 2010).

The civil interest towards nature can be well matched with serious, scientific work. Many scientific research is based on the important work of volunteers, ”civilians” in data collection (citizen science, Miller-Rushing *et al.* 2008, Cooper *et al.* 2014).

Here we present exploratory and descriptive statistics on the migration timing and morphometrics of the European Robin *(Erithacus rubecula)* between 1984–2017 from a

Central European ringing station (Ócsa Bird Ringing Station, Hungary, see Csörgő *et al.* 2016 in English and Csörgő & Harnos 2018 in Hungarian for details).

The Robin is a small-sized omnivorous passerine of the Muscicapidae family (Collar 2018). The plumage of the nominate race is lined with grey, olive-brown upperparts and whitish belly, the chest, throat and face are red-brown to orange. Juveniles are markedly different, having spotted brown and white cryptic colouration, with gradually appearing patches of orange (Svensson 1992, Cramp 1988, Demongin 2016). The species shows little sexual dimorphism in plumage colour and body size (Pettersson & Lindholm 1983, Cuadrado 1991, Madsen 1997, Pérez-Tris *et al.* 2000, Rosińska 2007, Rosińska & Adamska 2007, Jovani *et al.* 2012, McCollin *et al.* 2015).

The Robin is polytypical with 9 described subspecies, namely *Erithacus rubecula rubecula*, *E. r. melophilus*, *E. r. witherbyi*, *E. r. tataricus*, *E. r. valens*, *E. r. caucasicus*, *E. r. hyrcanus*, *E. r. superbus* and *E. r. marionae* (Gill & Donsker 2017). The subspecies are quite similar in their appearance, with minor variations in plumage colouration and biometrics (Cramp 1988, Svensson 1992, Demongin 2016). The breeding distribution ranges across much of the boreal, temperate and Mediterranean zones of the Western Palaearctic and in Mediterranean North Africa (Cramp 1988). The nominate subspecies occupies the majority of the breeding range. Migration strategies of subspecies may be markedly different (see below) (Cramp 1988, Adriaensen & Dhondt 1990, Fennessy & Harper 2002).

Its habitat varies from deciduous and coniferous forest. It requires light or medium cover moist habitats, farmland hedges, gardens and parks but avoid the densest woodland (Cramp 1988, Mead 1997).

The Robin is classified as Least Concern in the IUCN Red List, the European population trends is increasing (BirdLife International 2017). Many individuals are poached for food in the Mediterranean Basin in winter (Collar 2018). Severe, hard winters may drive population fluctuations among residents in Britain (Marchant *et al.* 1990, Mead 1997). In Italy, large part of the recoveries are related to human activities, predominantly hunting (Spina & Volponi 2009). The wintering range of the bird is compressing in the western Mediterranean Basin (Fandos & Tellería 2017).

Their mating system is typically monogamous, however some studies found low frequency bigamy (Cramp 1988). The species is single-brooded in northern regions of its range, elsewhere it is double or rarely triple brooded (Cramp 1988). The Robin is territorial in the breeding area and also during wintering (Cramp 1988, Cuadrado 1997, Tobias 1997, Tobias & Seddon 2000). Breeding occurs from February to early July in general, from the end of April to late July in Central Europe, from mid-May in the northern and from mid-April in the southern part of Russia (Cramp 1988, Collar 2018).

Robins are nocturnal migrants and typically travel in short bursts and rest for several days between migration flights (Cramp 1988, Collar 2018).

Migration strategies may be markedly different among subspecies, within subspecies' breeding populations and between individuals of the same population (Cramp 1988, Adriaensen & Dhondt 1990, Fennessy & Harper 2002). Korner-Nievergelt *et al.* (2014) divided Europe into four regions: (1) Scandinavia, the Baltic countries, Belarus and North East Russia, where the Robin is a breeding or migratory bird, but it does not overwinter; (2) the central part of Europe including the British Isles, and the band from the Low Countries to Romania, Moldavia and Ukraine, which is both a breeding and a wintering area; (3) southern Europe; and (4) edge of northern Africa. The last two parts are also breeding areas and important wintering sites for the birds originating from northern and central Europe.

Sedentary individuals typically occur in urban breeding habitats and on temperate islands, while other populations may range from obligate short/medium range migrants to various degree of partial migration. In general, populations east of line connecting Norway and Central Europe are obligatory migrants, moving southward to the Mediterranean Basin, Black Sea hinterland, South Caspian, Mesopotamia and Gulf region. Birds west of line from Germany to Balkans are partially migratory or largely resident (Collar 2018). The migration strategy is probably genetically determined (Biebach 1983).

Robins from Fennoscaninavia and the Baltic countries migrate mainly through Denmark during autumn and continue south-west towards Western Europe and North-West Africa (Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008, Valkama *et al.* 2014). Main migratory pathway of the Finnish birds follows both coasts of the Baltic Sea, crosses Central Europe in a rather wide belt ending as far as Morocco and Algeria. Adult birds are slightly ahead than the young (Valkama *et al.* 2014). Danish birds have been recovered in a rather narrow zone through the Netherlands, Belgium, western Germany, France, Spain and Portugal (Bønløkke *et al.* 2006). The recovery pattern suggest that nearly all Robins migrating through the south coast of the Baltic see are moving west-southwest and are originated from Scandinavia and western Russia (Ehnbom *et al.* 1993, Remisiewicz *et al.* 1997, Fransson & Hall-Karlsson 2008, Valkama *et al.* 2014). Minor proportion of the Fennoscandian birds migrate to the south-southest (Remisiewicz *et al.* 1997, Valkama *et al.* 2014). Based on orientation tests using Busse's method (Busse 1995) in Poland, over 30% of tested birds use the eastern way. Probably due to the lack of ringing activity, recaptures are missing from this area (Busse *et al.* 2001, Ściborska & Busse 2004, Rosińska & Adamska 2007). Robins were studied with the same method for directional preferences during autumn migration in southern Poland. More than 60% of the tested birds showed reversed (northern) headings, probably because the Carpathian mountains are potential barriers for this species (Adamska & Filar 2005). Most German breeders are migratory, and most of the birds passing through Germany originate from North, North-East and lot of northern birds winter in Germany (Bairlein *et al.* 2014). In central Europe including the Czech Republic, Slovakia and Hungary and Croatia the Robin is a common breeder and there are a lot of migrants coming from Fennoscandinavia, Poland and the western part of Russia (Klvaňa 2008, Gyurácz & Csörgő 2009, Budinski 2013). Birds from Bohemia prefer the south-western direction, most recoveries were made in Switzerland, France and the Iberian Peninsula. The majority of the birds from Moravia and Slovakia head more to the south (Appenine Peninsula) and to south-east (Balkan Peninsula) (Klvaňa 2008). Birds passing through Croatia were recaptured in Italy and Tunisia (Budinski 2013). Italy is a crossroad for this species. They come from Fennosscandinavia, the Baltic areas, Central and Eastern Europe. The majority of the autumn recoveries are in the Alpine area, in Emilia Romanque, Tuscany and Sardinia. Robins ringed in Italy are concentrated in the south-western Mediterranean and some in North Africa (Spina & Volponi 2009). Robins prefer the south-south-eastern direction (34%) in northern Italy towards the Apennine Peninsula based on orientation studies (Adamska & Rosińska 2006).

The dynamics of the migration depends on the place of origin and the target area. Most birds leave Sweden in September, adults and juveniles in the same time. Their mean position is in September is South Denmark, and they reach their wintering quarters in West and South-West Europe in November (Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008). Autumn migration in Finland starts in September-October, the median is at the end of September, beginning of October. Adults' median date is in September in the latitude of South Sweden and the Baltic states, in October in South-West Germany, in November in South France. Adult birds are slightly ahead than the young. Juveniles are only in Denmark in October (Valkama *et al.* 2014). Local Belgian populations start their migration in the second half of August, the trans-migrant northern birds pass through the country from mid-September until mid-November, in high numbers in the first half of October (Adriaensen 1987). Autumn passage on the Polish Baltic coast lasts from mid-August to early November peaking late September and October. Passage in south appears to occur slightly later than in north, and also slight tendency for adults to pass later than juveniles. Adult females arrive later than adult males (Polakowski & Jankowiak 2012). In Germany autumn migration lasts from late August to mid-November, peak in late September, early October (Bairlein *et al.* 2014). The passage between September and November with a peak in October is observed in the Italian Alps. On the Apennine Peninsula, the earliest foreign birds can be detected in late August, the most intensive period is in October and the migration ends in November (Schubert *et al.* 1986, Bottoni *et al.* 1991, Spina & Volponi 2009). In Iberia the autumn migration period lasts from September to November with a main peak in October, and the birds reach North Africa from late September (Cramp 1988, Remisiewicz 2001). Birds migrating to the Balkan Peninsula travel later than those migrating to other parts of the wintering range (Remisiewicz 2002). Birds migrating later in the season stay for winter in the more northern regions (Remisiewicz 2001).

The species shows a typical leap-frog migration strategy. 48% of the Scandinavian birds winter in North Africa, and only 18% appears in Central Europe. However the proportion of Central European individuals in North Africa is only 31%, 34% of the birds are resident (Korner-Nievergelt *et al.* 2014). Birds breeding on the Apennine Peninsula winter in Marocco and Algeria (Adamska & Rosińska 2006, Spina & Volponi 2009).

The species has a week population level migratory connectivity. The wintering sites of Finnish, Swedish, Danish birds can be found from Great-Britain, South Finland, South Sweden through south-western Europe and North-Africa to the Balkan Peninsula (Remisiewicz *et al.* 1997, Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008, Klvaňa 2008, Spina & Volponi 2009, Gyurácz & Csörgő 2009, Bairlein *et al.* 2014, Valkama *et al.* 2014). Like in the northern European populations the main wintering grounds of Robins ringed in Poland, Germany and Czech Republic are the Iberian Peninsula, southern and western France, the Baleari Islands, Algeria and Morocco, northern Italy, Sardinia, Corsica and also the Balkans (Remisiewicz *et al.* 1997, Klvaňa 2008, Bairlein *et al.* 2014).

Although, the migratory connectivity is very week, exceptions may exist on specific parts of the migratory route. Robins ringed at Ottenby Bird Observatory were recovered east of Robins ringed at Fasterbo, indicating parallel migrations to wintering area (Fransson & Hall-Karlsson 2008). From biometric measurements it has turned out, that Robins from the two sites (Falsterbo, Ottenby) use different migration strategies, Falsterbo Robins are ”short-stage migrants”, travelling over land, while the Ottenby Robins are ”long-stage migrants” (Pettersson & Hasselquist 1985, Karlsson *et al.* 1988, Sandberg *et al.* 1988, Åkesson *et al.* 1992).

The resident males' survival was higher (50%) than the survival of migrants (17%) in Belgium. Resident and migratory birds were habitat separated (migratory males in woodland, resident males in gardens and parks, all females were migratory, Adriaensen & Dhondt 1990).

The Iberian Peninsula is an important wintering site for the Robins arriving from a very large area (Campos *et al.* 2011b). Biometry of birds arriving from north and local individuals is different (Domínguez *et al.* 2007). Sexes show strong latitudinal segregation (there are more females in south, Catry *et al.* 2004). The males are dominant over the females (Campos *et al.* 2011a). Maintenance of winter territories has not only feeding, but even more anti-predation benefits (Cuadrado 1997).

Strong site attachment and site fidelity were proved experimentally in Italian studies. Adult Robins have a stronger site attachment and homing success than juveniles. Adult birds were better homers than sub-adults, but no significant differences were observed between males and females. Subadults become site-attached during autumn and early winter at their first season on the wintering ground (Benvenuti & Ioalè 1980, 1983, Ioalè & Benvenuti 1983).

First signs of return passage are in early February with increasing numbers along coasts of Algeria and Morocco (Cramp 1988). The spring migration could start in early January, but mostly in midd-February, first the breeding population of Apennine Peninsula arrives in this time (Spina & Volponi 2009). The passage through this area begins in mid-March and ends at the beginning of May peaking between the last week of March and the third week of April. Spring migration lasts from March to April in northern Spain (Arizaga *et al.* 2010). The obligatory migrant individuals originated from the British Isles arrive back at the end of March. This population migrates along the coast of the Atlantic Ocean, in the case of the other populations the general bearing is north-east (Fennessy & Harper 2002).

The first individuals arrive to their breeding site in Central Europe in early March and the migration peaks mainly in April (Hubálek 2005, Klvaňa 2008, Gyurácz & Csörgő 2009, Bairlein *et al.* 2014). The Robins arrive to the northern breeding areas from the end of March to the end of May, the yearly peaks are between mid-April and mid-May (Sokolov *et al.* 1998, Biaduń *et al.* 2011, Valkama *et al.* 2014). The Belgian and the Danish birds depart from mid-March to early May with a peak in the first half of April (Adriaensen 1987, Bønløkke *et al.* 2006). Robins depart in March from the wintering quarters and reach the North Sea in April, the average is in mid-April in Germany (Hüppop & Hüppop 2003). The first Robins arrive in Sweden in mid-March, the mean arrival time in South Sweden is in the second half of April (Stervander *et al.* 2005) and the birds reach their breeding sites in May (Fransson & Hall-Karlsson 2008). Finnish birds have similar phenology (Valkama *et al.* 2014). Birds do not reach the Urals until early May (Cramp 1988).

The average stopover time in spring was shorter than that in autumn in the central pre-Alps of Italy (Bottoni *et al.* 1991). In spring, European Robins selected optimal wind condition to start a new flight, while in autumn they departed under moderately unfavourable winds on the Courish Spit (Eastern Baltic; Bulyuk & Tsvey 2006). The wind condition may effect the timing, accordingly the stopover duration may vary in a broader interval, between 1 and 19 days (Bulyuk & Tsvey 2013). In spring, Robins presumably use the same routes as in autumn with no detected indication of loop migration (Cramp 1988, Remisiewicz *et al.* 1997, Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008, Bairlein *et al.* 2014).

The migration timing of Robins did not change markedly in the last decades in autumn in Poland (Nowakowski *et al.* 2005). The mean spring passage time has become earlier in North Europe (Sokolov *et al.* 1998, Hüppop & Hüppop 2003, 2011, Stervander *et al.* 2005, Tøttrup *et al.* 2006, Valkama *et al.* 2014). The NAO index had no significant effect on arrival time, however the mean temperature had (Hüppop & Hüppop 2003), the decline of the mean temperature in February shifted later the spring arrival (Biaduń *et al.* 2011).

The migratory distance of north-eastern birds decreased during the past decades due to the north-eastwards shift in the wintering grounds, while the proportion of residents increased (Remisiewicz 2001, 2002, Tøttrup *et al.* 2006, Tellería 2015). This distance is more or less independent of the yearly weather. Partial and short distance migrants only slightly shifted their wintering grounds, but their migration distance changes with the winter temperature (Ambrosini *et al.* 2016).

In Hungary all of the breeding and trans-migrant individuals belong to the nominate subspecies (Gyurácz & Csörgő 2009). The Hungarian breeding population is estimated to 306,000–409,000 pairs showing a moderate increase recently (Szép *et al.* 2012). The species is protected in Hungary (BirdLife Hungary 2018). Robin is one of the most common migrants from March to mid-April in spring and from September until mid-November in autumn (Antli & Németh 1998, Hadarics & Zalai 2008, Gyurácz & Csörgő 2009, Gyimóthy *et al.* 2011b). The autumn migration has one wave, the breeding population depart until the middle of September and use south-western and south-eastern ways to the wintering areas (BirdLife Hungary 2018). Autumn passage migrants in Hungary originate mainly from Slovakia, Poland, Ukraine, southern Scandinavia, Baltic States and north-western Russia. Compared to the high number of ringed birds from north of Hungary, there were only a few northern recoveries *(Figure 1)*. For example, there were 691,134 captures (more than 20,000 per year) with 2438 recaptures within Sweden up to 2003, 373,258 captures (6-8000 per year) with 1147 foreign recoveries in Finland. The species uses a south-western fly-way west to the Carpathian basin (Fransson & Hall-Karlsson 2008, Valkama *et al.* 2014). More than 60% of the birds showed northern headings that we called "reversed directions" in Poland, meaning that the Carpathians are potential barriers for this species (Adamska & Filar 2005). On the other hand, birds originating from eastern breeding sites use eastern routes. Recoveries are mainly from Italy, but Hungarian ringed birds have also been recaptured in Spain, France and Algeria (Gyurácz & Csörgő 2009, BirdLife Hungary 2018). Probably they also winter in Morocco (Hornok *et al.* 2012). The majority of the Hungarian breeding birds leave the Carpathian Basin and use south-western (and winters in the Apennine Peninsula and on the surrounding islands) and south-eastern ways to the wintering area by mid-September (BirdLife Hungary 2018). Autumn passage migration peaks in late September to early October in Hungary (Gyurácz *et al.* 2008, Gyimóthy *et al.* 2011b). The stopover duration is 4–9 days on average (Gyimóthy *et al.* 2011b). The habitat quality influences the the dynamics and the age distribution on different ringing stations of Hungary (Gyimóthy *et al.* 2011b). Northern individuals arrive at the end of autumn migration according to studies of wing-length, body mass and fat reserves (Gyimóthy *et al.* 2011a). The spring migration in Hungary lasts from the beginning of March to the end of April, and the passage is faster than in autumn. The peak of the migration is between late March and early April (Gyurácz & Csörgő 2009, BirdLife Hungary 2018).

The Robin is an abundant passage migrant and may sporadically breed and overwinter at the Ócsa Bird Ringing Station, the source of data analysed in this paper.

Our aim is to provide a comprehensive overview of migration timing, body size measurements and inter-annual changes in these variables. Hopefully, these patterns will help formulate research questions and provide information for further higher level analyses. However, we do not aim to interpret the obtained results, merely draw attention to interesting patterns, that may be worth exploring in detail.

Materials and methods

Bird ringing data

The Ócsa Bird Ringing Station is situated in Central Hungary (N47.2970, E19.2104) in the Duna-Ipoly National Park in the immediate vicinity of Ócsa town. The study site is characterized by a post-glacial peat bog with a mosaic of habitats including open water surfaces, reedbeds, bushy vegetation and forests. It is situated in a humid continental transitional climate zone (for further details see Csörgő *et al.* 2016, ocsabirdringing.org). Birds were trapped with standard mistnets placed at standard locations throughout the study period. Trapping effort is seasonal and changed over the years (see Csörgő *et al.* 2016 for details).

The day of the year of first capture in spring and in autumn were considered as arrival (migration) timing of individual birds. Stopover duration was calculated as the difference of within season last and first captures excluding within day recaptures. Biometric measurements were taken following strictly standardized methods (Szentendrey *et al.* 1979, EURING 2015). Only data of the first captures were used in the analysis. We distinguished first calendar year birds (juveniles) from adults upon plumage characteristics (Cramp 1988, Svensson 1992, Demongin 2016), and we present all results according to these groups. We present data for spring and autumn migratory seasons separately; birds caught after the 70th and before the 110th day of the year were considered to be spring migrants and birds caught after the 230th and before the 310th day of the year were considered to be autumn migrants. A total of 40,128 were captured and ringed between March and November; 14,162 in spring and 3,330 adults and 19,378 juveniles in autumn (the rest of the birds was not aged) in the study period of 1984–2017. This total value constitutes cca. 17.8% of the 224,393 European Robins ringed in Hungary in this period.

Statistical methods

To describe daily and yearly capture frequencies and the cumulative distribution of the date of first captures with recaptures, we used the functions of the `ringR` package (Harnos *et al.* 2015). Descriptive tables (mean, median, standard deviation (SD), minimum (min), maximum (max) values and sample size (N)) on the timing of migration, stopover duration, the length of wing, third primary and tail, and body mass were created by the `data.table` package (Dowle *et al.* 2013). The annual mean values of timing, body mass, wing-, third primary and tail lengths are plotted against time (year) on scatterplots. Loess smooth lines were fitted to highlight trends (Cleveland *et al.* 1992). The distribution of the same variables were represented with histograms and overlaid smoothed histograms. Boxplots were used to show the body mass distributions by fat score categories. Fat and muscle score frequencies are shown using barplots. We distinguished seasons and age groups throughout the analyses. For more details on the analysis, please visit ocsabirdringing.org. All analyses were carried out in R 3.4.0 (R Core Team 2017).

Results

A total of 153 foreign recaptures were recorded between 1951 and 2017 in relation to Hungary *(Figure 1)*. Annual capture and recapture frequencies at the study site are shown in *Figure 2*. Within-year capture and recapture frequencies, together with cumulative distribution of individual first and last captures are depicted in *Figure 3*, while their respective descriptive statistics are presented in *Table 1–2*. Changes in annual mean arrival dates throughout the study period and the distribution of within-year migration timing

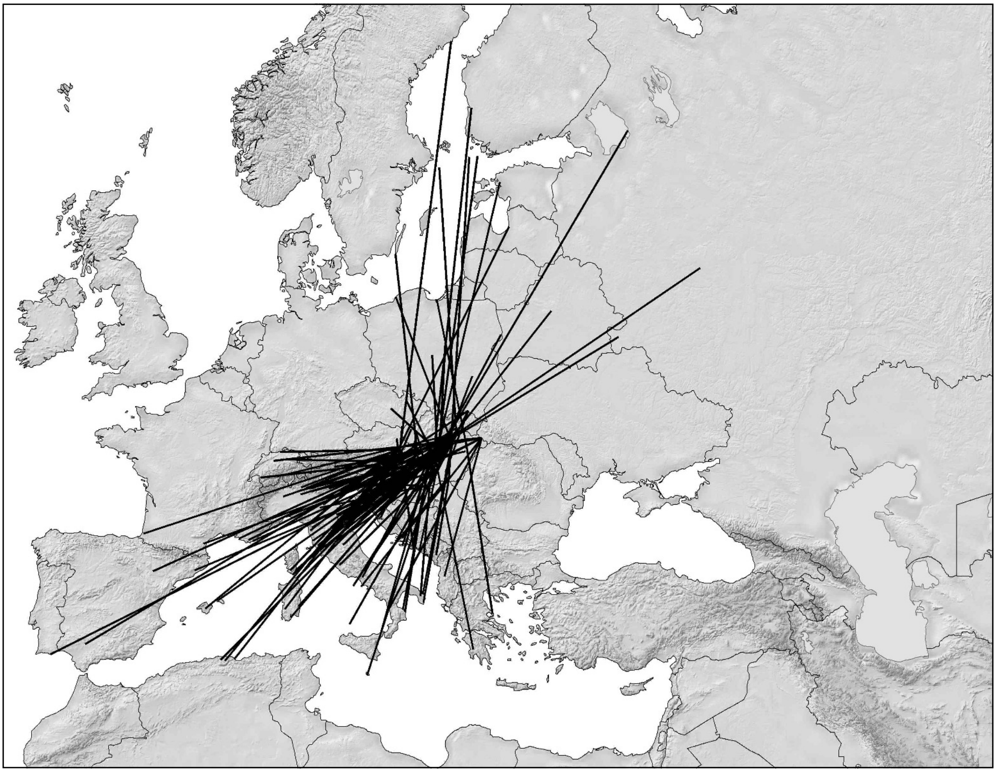

Figure 1. Foreign ring recoveries of European Robins. The data of birds ringed in Hungary and recovered abroad and the birds ringed abroad and recovered in Hungary are depicted

1. ábra Magyarországon jelölt és külföldön megkerült, illetve külföldön jelölt és Magyarországon megfogott vörösbegyek

according to season and age are presented in *Figure 4*. The trend of annual mean wing lengths and the distribution of wing length measurements according to season and age are shown in *Figure 5*, while their respective descriptive statistics are presented in *Table 3*.

Third primary length *(Figure 6*, *Table 4)*, tail length *(Figure 7*, *Table 5)* and body mass *(Figure 8*, *Table 6)* are presented in a similar fashion. Body mass in relation to season and age and fat scores are visualized with boxplots in *Figure 9*. Finally, the distribution of fat and muscle scores grouped by season and age can be found in *Figure 9 b,d,f* and *Figure 10*.

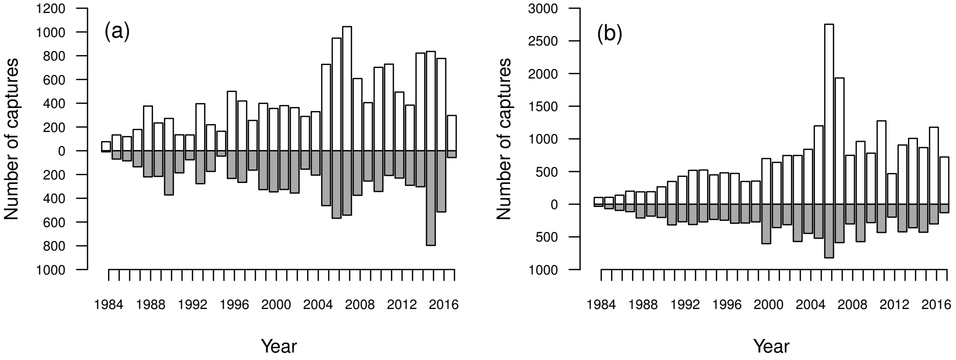

Figure 2. Annual capture (white bars) and recapture (grey bars) frequencies in spring (a), and in autumn (b)

2. ábra Éves fogás (fehér oszlopok) és visszafogás (szürke oszlopok) gyakoriságok tavasszal (a) és ősszel (b)

Table 1. Descriptive statistics of migration timing (day of the year)
1. táblázat A vonulás időzítés (év napja) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	89.0	89	8.5	70	110	14162
autumn	adult	277.6	278	12.5	231	310	3330
autumn	juvenile	272.5	273	16.3	230	310	19378

Table 2. Descriptive statistics of stopover duration (day)
2. táblázat A tartózkodási idő (nap) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	5.6	4	5.1	1	35	3582
autumn	adult	4.9	3	5.0	1	40	537
autumn	juvenile	5.9	4	5.7	1	75	3800

Table 3. Descriptive statistics of wing length (mm)
3. táblázat A szárnyhossz (mm) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	72.5	72	2.1	65	80	13493
autumn	adult	72.8	73	2.1	66	79	3214
autumn	juvenile	72.3	72	2.0	65	79	18744

Table 4. Descriptive statistics of third primary length (mm)
4. táblázat A harmadik evező hosszának (mm) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	54.3	54	1.8	46	62	12633
autumn	adult	54.2	54	1.8	48	60	3100
autumn	juvenile	54.1	54	1.8	48	62	17795

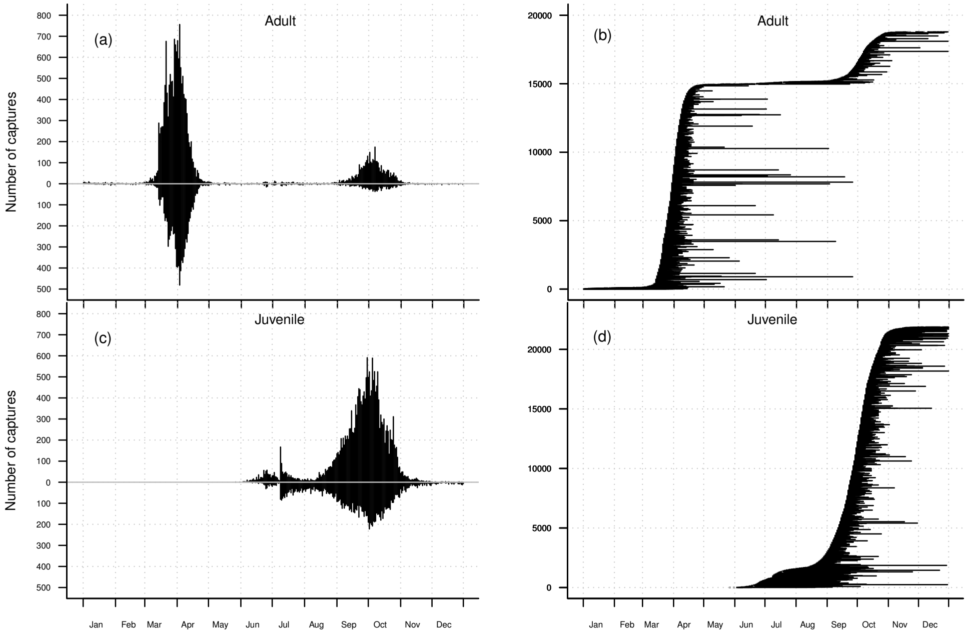

Figure 3. Within-year capture (black bars) and recapture (grey bars) frequencies (a, c) and cumulative distributions of individual first capture dates (b, d) according to age groups (horizontal lines: stopover durations)

3. ábra Éven belüli fogás (fekete oszlopok) és visszafogás (szürke oszlopok) gyakoriságok (a, c) és az egyedek első megfogási idejének kumulatív eloszlása (b, d) korcsoportonként (vízszintes vonalak: tartózkodási idők)

Table 5. Descriptive statistics of tail length (mm)
5. táblázat A farokhossz (mm) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	60.2	60	2.5	51	68	13356
autumn	adult	60.3	60	2.6	52	69	3169
autumn	juvenile	60.0	60	2.6	51	69	18469

Table 6. Descriptive statistics of body mass (g)
6. táblázat A testtömeg (g) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	15.9	15.9	1.2	11.7	22.7	13947
autumn	adult	16.3	16.2	1.4	11.9	22.3	3297
autumn	juvenile	16.1	15.9	1.3	11.6	23.7	19155

Migration timing

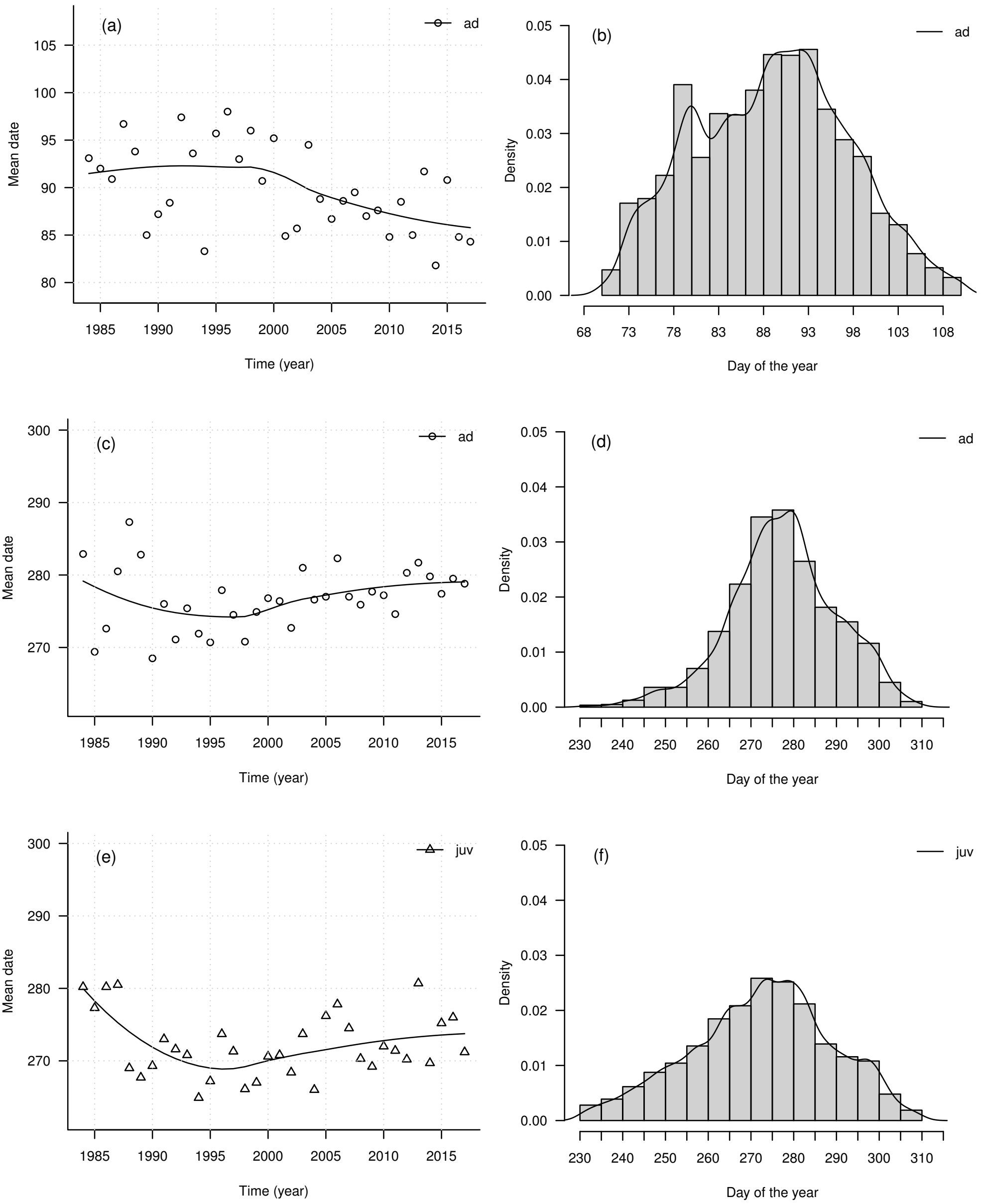

Figure 4. Annual mean migration timing (day of the year) throughout the study period and histograms/smoothed histograms of timing in spring (a–b) and in autumn (c–f)

4. ábra Az éves átlagos vonulás időzítés (év napja) a vizsgálati időszakban és az időzítés hisztogramja/simított hisztogramja tavasszal (a–b) és ősszel (c–f)

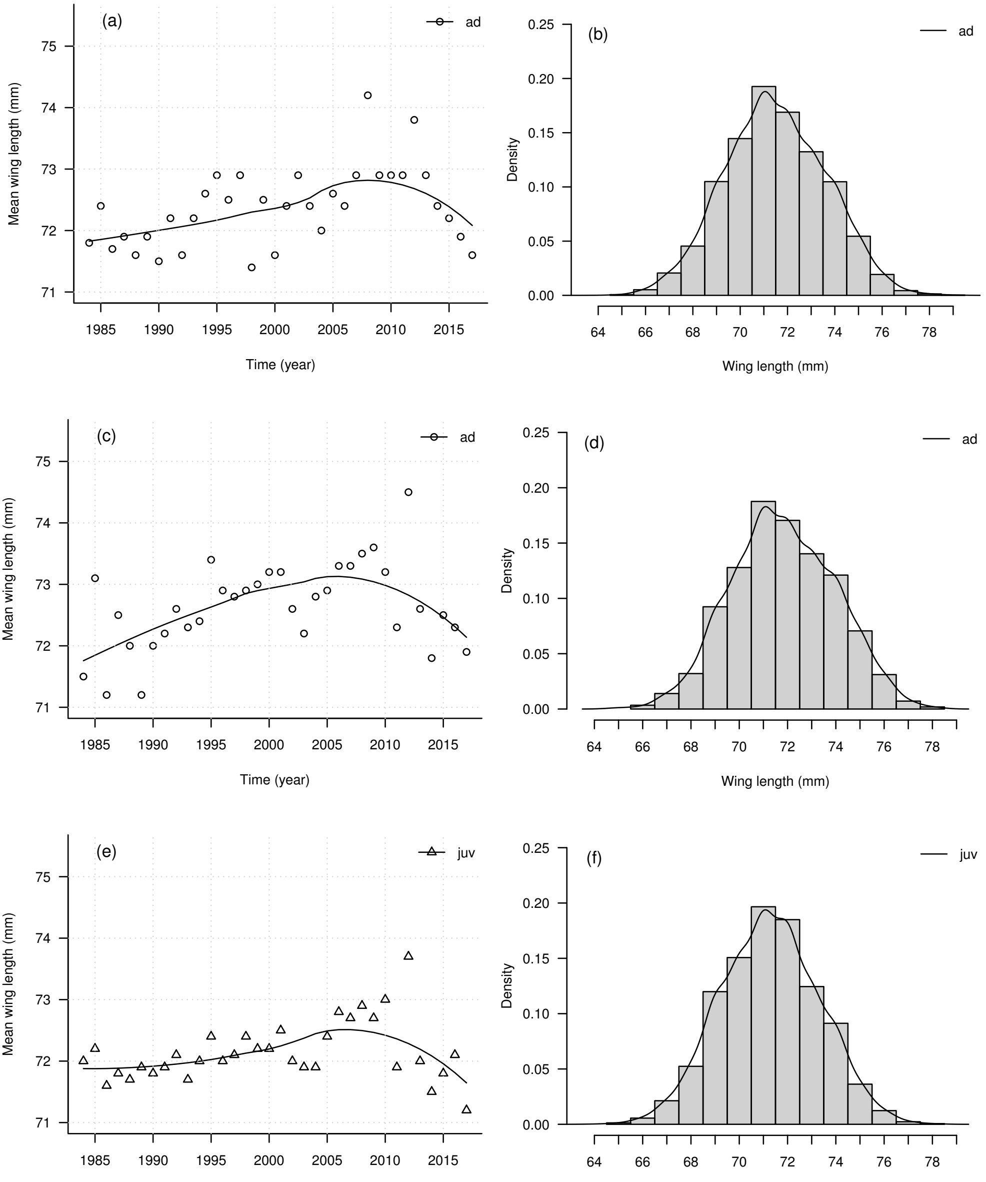

Figure 5. Annual mean wing length (mm) throughout the study period and histograms/smoothed histograms of wing length in spring (a–b) and in autumn (c–f)

5. ábra Az éves átlagos szárnyhossz (mm) a vizsgálati időszakban és a szárnyhossz hisztogramja/simított hisztogramja tavasszal (a–b) és ősszel (c–f)

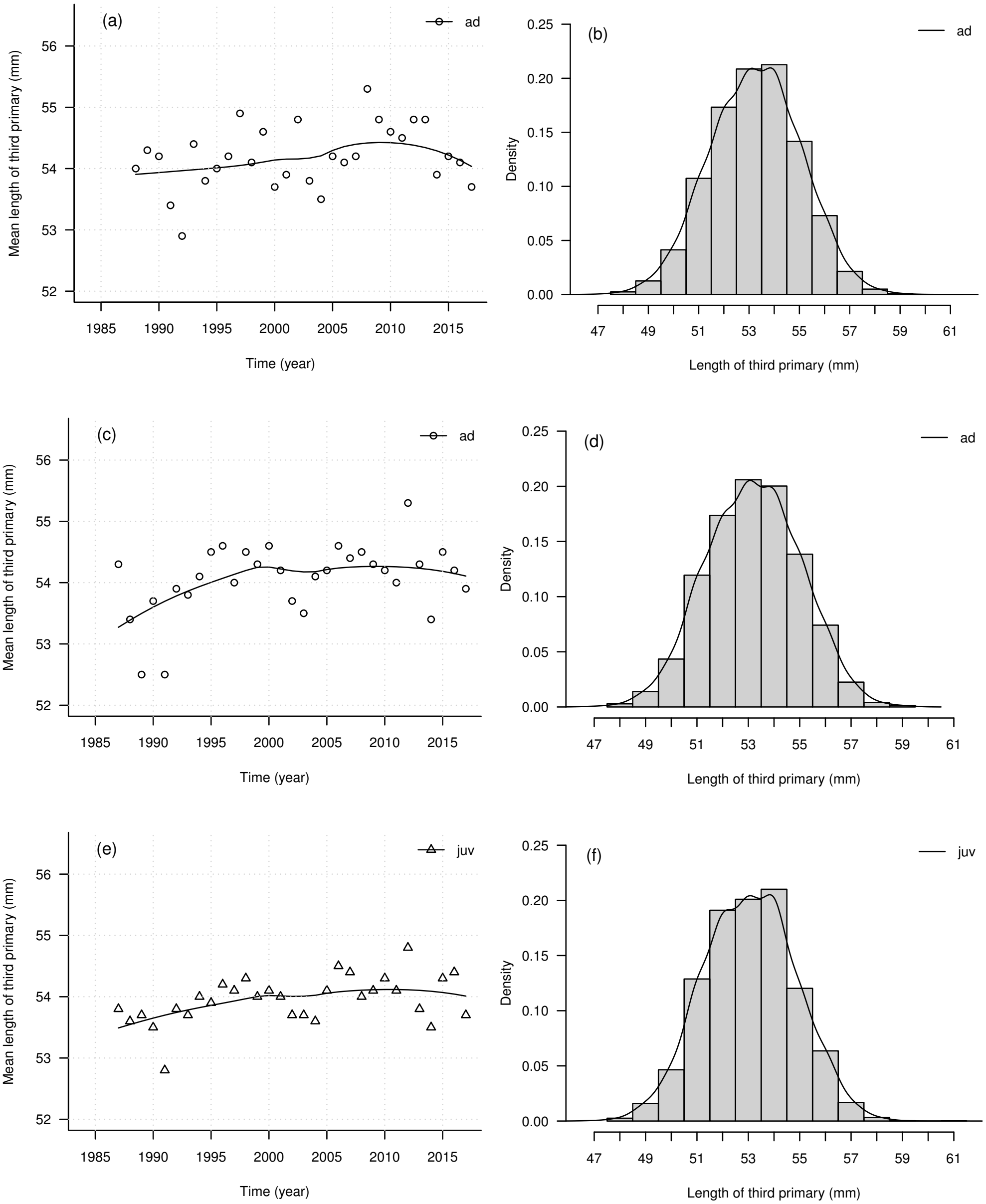

Figure 6. Annual mean third primary length (mm) throughout the study period and histograms/smoothed histograms of third primary length in spring (a–b) and in autumn (c–f)

6. ábra Az éves átlagos harmadik evező hossz (mm) a vizsgálati időszakban és a harmadik evező hosszának hisztogramja/simított hisztogramja tavasszal (a–b) és ősszel (c–f)

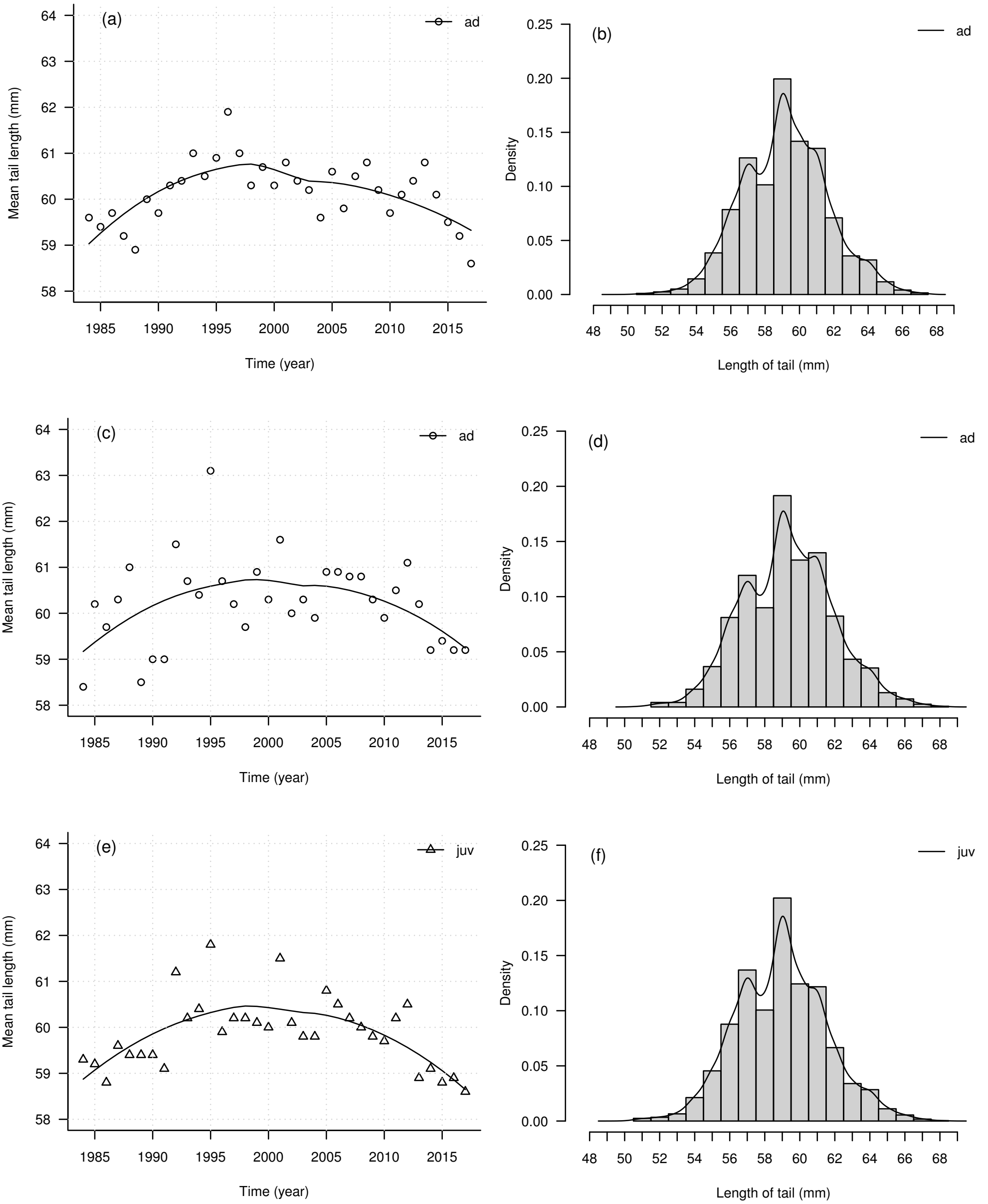

Figure 7. Annual mean tail length (mm) throughout the study period and histograms/smoothed histograms of third primary length in spring (a–b) and in autumn (c–f)

7. ábra Az éves átlagos farokhossz (mm) a vizsgálati időszakban és a farokhossz hisztogramja/simított hisztogramja tavasszal (a–b) és ősszel (c–f)

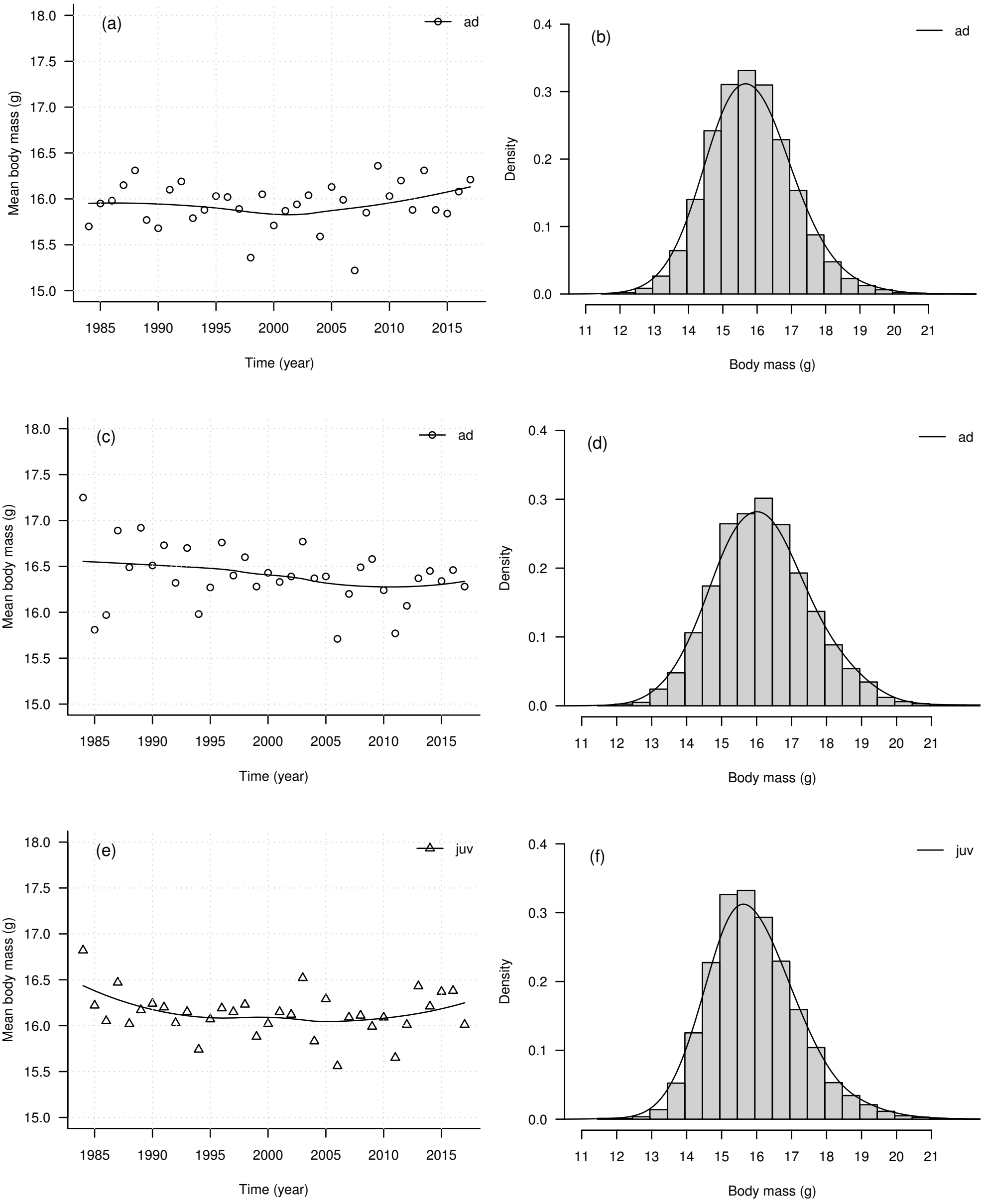

Figure 8. Annual mean body mass (g) throughout the study period and histograms/smoothed histograms of body mass in spring (a–b) and in autumn (c–f)

8. ábra Az éves átlagos testtömeg (g) a vizsgálati időszakban és a testtömeg hisztogramja/simított hisztogramja tavasszal (a–b) és ősszel (c–f)

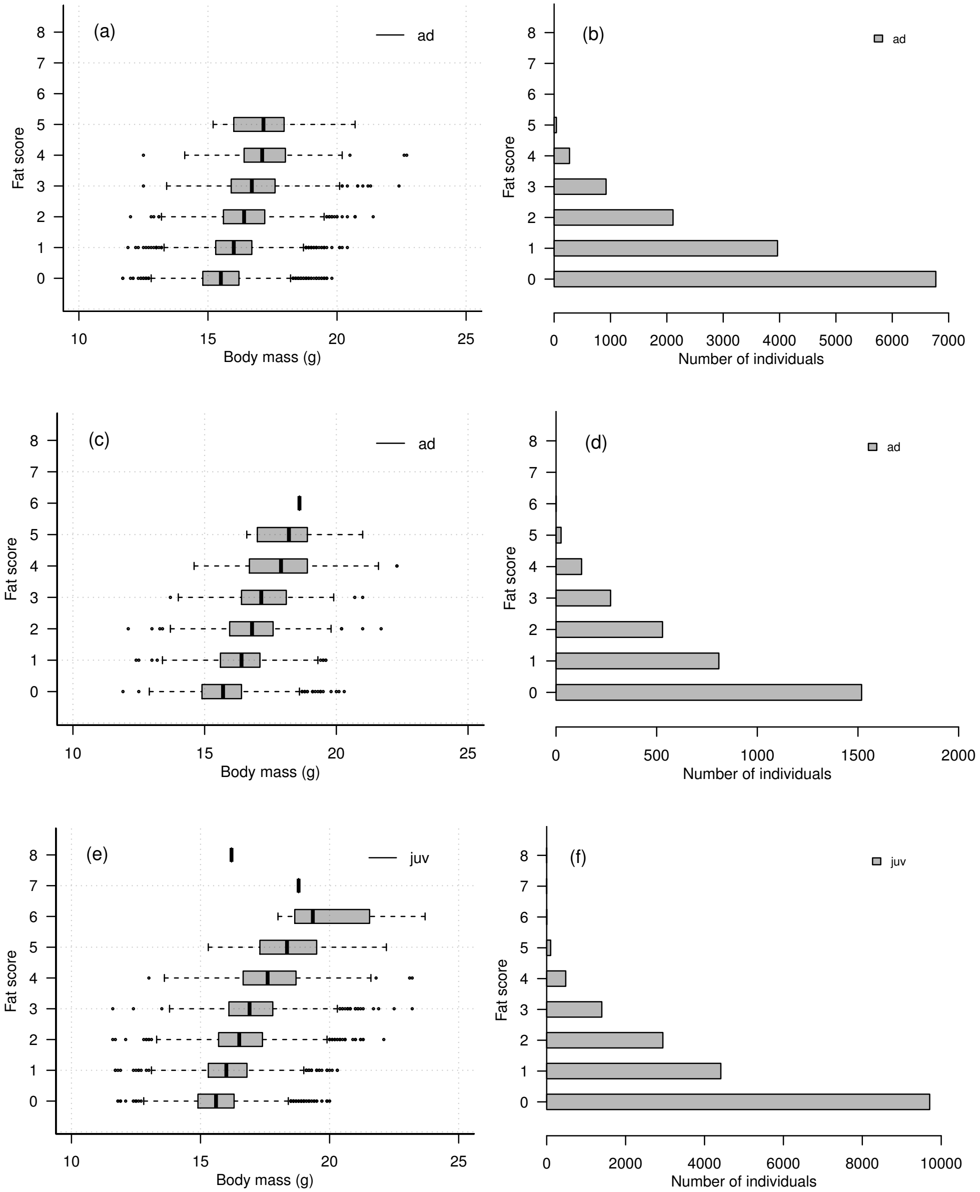

Figure 9. Boxplots of body mass according to fat score, and fat score frequencies in spring (a–b) and in autumn (c–f)

9. ábra A testtömeg boxplot-ja zsírkategóriánként és a zsírkategóriák gyakoriságai tavasszal (a–b) és ősszel (c–f)

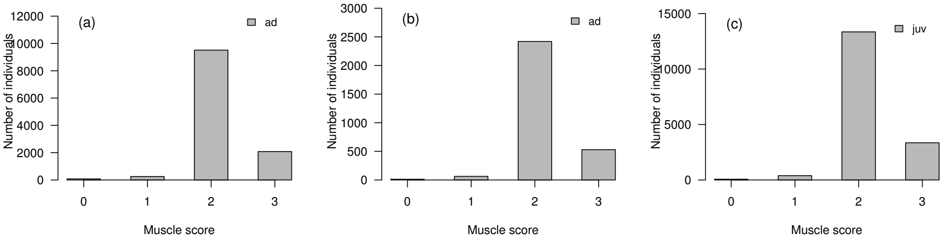

Figure 10. Muscle score frequencies in spring (a) and in autumn (b–c)
10. ábra Izom kategória gyakoriságok tavasszal (a) és ősszel (b–c)

Discussion

The exploratory analyses of timing and morphometrics of the Robin revealed several patterns of interest. Apparently, there is considerable variation in inter-annual capture and recapture frequencies *(Figure 2 a,b)* with an growing trend *(Figure 2 a)* in both seasons probably due to the increased capture effort end extended working seasons after 2001 (Csörgő *et al.* 2016). Beyond this increase, the number of captured birds is highly variable, probably due to the variability in the number of trans-migrants in different years. The stopover durations are similar in all cases, only the juveniles stay 1 day longer than the adults in autumn *(Figure 3 b,d, Table 2).*

The birds appear in greater numbers in both seasons, but the amount of juveniles greatly exceeds the amount of the adults in autumn, and there are four times more adults in spring than in autumn, which can be a result of potential local loop migration. The existence of a few captures of all age groups during the breeding season corroborates that there is a small local breeding population at the study site *(Figure 3 a,b).*

The spring migration timing appears to be more or less constant before 2000 and slightly decreasing after *(Figure 4 a)*, the autumn timing hits a bottom in the middle of the 1990's, than it slightly increasing. Both trends after 2001 are probably due to the extended working seasons (Csörgő *et al.* 2016). Timing of the adults is a bit delayed compared to that of the juveniles in the autumn *(Figure 4 c,e)*. The distribution of arrival timing in spring has two peaks and the distributions are broadened at larger values in case of autumn timings. Both cases are probably the result of the previously mentioned changed working seasons *(Figure 4 b,d,f)*. There are apparent increasing trends over the years both in the wing length and in the third primary length of the birds, which can be the result of the extended working seasons, since usually larger birds arrive earlier in spring and leave later in autumn *(Figures 5–6 a,c,e).*

Tail length seems to peak around the late 1990's, although with a considerable inter-annual variation *(Figure 7 a,c,e)*. The mean body mass is more or less constant over the years *(Figure 8 a)*, however a slight decreasing trend can be observed during the autumn season in case of the adult birds *(Figure 8 c,d).*

The biometric variables except the slight bimodality of the tail length have unimodal distribution indicating that there is no considerable size difference between the sexes *(Figure 5–8 a,c,e)*.

The fat score distributions suggest that the birds can accumulate fat reserves, and it is more pronounced in spring than in autumn *(Figure 9)*. Muscle score distributions suggest that the birds also build their muscles in both seasons *(Figure 10)*.

Our results show that comprehensive exploratory analyses may reveal intriguing patterns, which may be investigated in more detail in the future. However, we emphasize that although the temporal extent of the data reported here is considerably large, all information presented here derives from a single location and thus has to be interpreted accordingly. Nonetheless, we hope that our results will help researchers conducting comparative or meta-analyses with baseline data and may also encourage others to report their data in a similar fashion. We also seek cooperation with interested parties and are willing to share all data reported here. Please contact the corresponding author for details.

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References

Adamska, K. & Filar, M. 2005. Directional preferences of the Chiffchaff *(Phylloscopus collybita)* and the Robin *(Erithacus rubecula)* on autumn migration in the Beskid Niski Mountains (S Poland). – Ring 27(2): 159–176. DOI: 10.2478/v10050-008-0017-y

Adamska, K. & Rosińska, K. 2006. Directional preferences of the Robin *(Erithacus rubecula)* and the Blackcap *(Sylvia atricapilla)* during autumn migration at Arosio (N Italy) in 2005. – Ring 28(2): 101–111. DOI: 10.2478/v10050-008-0032-z

Adriaensen, F. 1987. The timing of Robin migration in Belgium as shown by ringing recoveries. – Ringing & Migration 8(1): 43–55. DOI: 10.1080/03078698.1987.9673901

Adriaensen, F. & Dhondt, A. 1990. Population dynamics and partial migration of the European Robin *(Erithacus rubecula)* in different habitats. – Journal of Animal Ecology 59: 1077–1090. DOI: 10.2307/5033

Åkesson, S., Karlsson, L., Pettersson, J. & Walinder, G. 1992. Body composition and migration strategies: a comparison between Robins *(Erithacus rubecula)* from two stop-over sites in Sweden. – Vogelwarte 36: 188–195.

Ambrosini, R., Cuervo, J. J., Feu, C., Fiedler, W., Musitelli, F., Rubolini, D., Sicurella, B., Spina, F., Saino, N. & Møller, A. P. 2016. Migratory connectivity and effects of winter temperatures on migratory behaviour of the European Robin *Erithacus rubecula*: a continent-wide analysis. – Journal of Animal Ecology 85(3): 749–760. DOI: 10.5061/dryad.5fn37

Antli, I. & Németh, C. 1998. Madárvonulás-dinamikai vizsgálatok vörösbegy *(Erithacus rubecula)* populációin a Soproni-dombvidék tájegység területén [Migration dynamics of Robin *(Erithacus* *rubecula)* in the Sopron-hills, Western Hungary]. – Ornis Hungarica 8: 153–162. (in Hungarian with English Summary)

Arizaga, J., Alonso, D. & Barba, E. 2010. Patterns of migration and wintering of Robins *Erithacus rubecula* in northern Iberia. – Ringing & Migration 25(1): 7–14. DOI: 10.1080/03078698.2010.9674408

Bairlein, F., Dierschke, J., Dierschke, V., Salewski, V., Geiter, O., Hüppop, K., Köppen, U. & Fiedler, W. 2014. Atlas des Vogelzugs [Bird Migration Atlas]. – AULA-Verlag, chap. Robin *(Erihacus rubecula)*. pp. 467–470. (in German with English Summary)

Benvenuti, S. & Ioalè, P. 1980. Homing experiments with birds displaced from their wintering ground. – Journal of Ornithology 121(3): 281–286. DOI: 10.1007/bf01647618

Benvenuti, S. & Ioalè, P. 1983. Age differences in the dispersal behaviour of Robins *Erithacus rubecula* studied by counting wing spots. – Ringing & Migration 4(4): 237–242.

Biaduń, W., Kitowski, I. & Filipiuk, E. 2011. Study on the first arrival date of spring avian migrants to Eastern Poland. – Polish Journal of Environmental Studies 20(4): 843–849.

Biebach, H. 1983. Genetic determination of partial migration in the European Robin *(Erithacus rubecula)*. – The Auk 100(3): 601–606.

BirdLife Hungary 2018. Magyarország madarai: Vörösbegy [Birds of Hungary: the European Robin]. – Magyar Madártani és Természetvédelmi Egyesület [BirdLife Hungary]. URL: http://www.mme.hu/magyarorszagmadarai/madaradatbazis-erirub, downloaded on 30 April 2018. (in Hungarian)

BirdLife International2017. *Erithacus rubecula*. (amended version published in 2016) The IUCN Red List of Threatened Species 2017: e.T22709675A111058208. Downloaded on 08 June 2017. DOI: 10.2305/IUCN.UK.2014-2.RLTS.T22709675A62579610.en.

Bønløkke, J., Madsen, J. J., Thorup, K., Pedersen, K. T., Bjerrum, M. & Rahbek, C. 2006. Dansk trækfugleatlas [Danish Bird Migration Atlas]. – Rhodos, Humlebæk, pp. 595–599. (in Danish with English Summary)

Bottoni, L., Massa, R. & Fornasari, L. 1991. The migration of the Robin *Erithacus rubecula* in the central pre-Alps of Italy. – Ringing & Migration 12(1): 48–53. DOI: 10.1080/03078698.1991.9673985

Budinski, I. 2013. Crvendać, *Erithacus rubecula*, European Robin. – In: Kralj, J., Barišić, S., Tutiš, V. & Ćiković, D. (eds.) Atlas selidbaptica Hrvatske [Croatian Bird Migration Atlas]. – Croatian Academy of Sciences and Arts, Zagreb, pp. 162–163. (in Croatian with English Summary)

Bulyuk, V. N. & Tsvey, A. 2006. Timing of nocturnal autumn migratory departures in juvenile European Robins *(Erithacus rubecula)* and endogenous and external factors. – Journal of Ornithology 147(2): 298–309. DOI: 10.1007/s10336-005-0046-0

Bulyuk, V. N. & Tsvey, A. 2013. Regulation of stopover duration in the European Robin *Erithacus rubecula*. – Journal of Ornithology 154(4): 1115–1126. DOI: 10.1007/s10336-013-0981-0

Busse, P. 1995. New technique of a field study of directional preferences of night passerine migrants. – Ring 17(1–2): 97–116.

Busse, P., Gavrilov, V. M., Ivliev, V. & Nowakowski, J. K. 2001. Differentiation of directional preferences of some nocturnal migrants on autumn migration across the central and eastern Europe. – Ring 23(1): 119–130.

Campos, A. R., Catry, P., Ramos, J. & Robalo, J. 2011a Competition among European Robins *Erithacus rubecula* in the winter quarters: sex is the best predictor of priority of access to experimental food resources. – Ornis Fennica 88: 226–233.

Campos, A. R., Catry, P., Tenreiro, P., Neto, J. M., Pereira, A. C., Brito, R., Cardoso, H., Ramos, J. A., Bearhop, S. & Newton, J. 2011b How do Robins *Erithacus rubecula* resident in Iberia respond to seasonal flooding by conspecific migrants? – Bird Study 58(4): 435–442. DOI: 10.1080/00063657.2011.603291

Catry, P., Campos, A., Almada, V. & Cresswell, W. 2004. Winter segregation of migrant European Robins *Erithacus rubecula* in relation to sex, age and size. – Journal of Avian Biology 35(3): 204–209. DOI: 10.1111/j.0908-8857.2004.03266.x

Cleveland, W. S., Grosse, E. & Shyu, W. M. 1992. Local regression models. – In: Chambers, J. & Hastie, T. (eds.) Statistical Models in S. – Pacific Grove, California, pp. 309–376.

Collar, N. 2018. European Robin *(Erithacus rubecula)*. – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. & de Juana, E. (eds.) Handbook of the Birds of the World. – Lynx Edicions, Barcelona (http://www.hbw.com/node/58467 on 17 May 2018)

Cooper, C. B., Shirk, J. & Zuckerberg, B. 2014. The invisible prevalence of citizen science in global research: Migratory birds and climate change. – PLoS ONE 9(9): e106508. DOI: 10.1371/journal.pone.0106508

Cramp, S. 1988. Handbook of the Birds of the Western Palearctic, Vol. 5. – Oxford University Press, Oxford, pp. 596–616.

Csörgő, T. & Harnos, A. 2018. Az Ócsai Madárvárta működése és fontosabb kutatási eredményei – Természetvédelem és kutatás a Turjánvidék északi részén [The operation and selected research results of the Ócsa Bird Ringing Station – Conservation and research at the northern part of "Turjánvidék"]. – Rosalia 10: 929–960. (in Hungarian)

Csörgő, T., Harnos, A., Rózsa, L., Karcza, Zs. & Fehérvári, P. 2016. Detailed description of the Ócsa Bird Ringing Station, Hungary. – Ornis Hungarica 24(2): 91–108. DOI: 10.1515/orhu-2016-0018

Cuadrado, M. 1991. Wing length criteria for sex determination of Robins *Erithacus rubecula* wintering in southern Spain. – Ornis Svecica 1: 55–57.

Cuadrado, M. 1997. Why are migrant Robins *(Erithacus rubecula)* territorial in winter?: the importance of the anti-predatory behaviour. – Ethology Ecology & Evolution 9(1): 77–88. DOI: 10.1080/08927014.1997.9522904

Demongin, L. 2016. Identification guide to birds in the hand. – Beauregard-Vernon, pp. 245–246.

Domínguez, M., Barba, E., Cantó, J. L., López, G. M. & Monrós, J. S. 2007. Seasonal interchange of the European Robin *Erithacus rubecula* populations in an evergreen holm oak forest. – Acta Ornithologica 42(1): 15–21. DOI: 10.3161/000164507781646942

Dowle, M., Short, T. & Lianoglou, S. 2013. data.table: Extension of data.frame for fast indexing, fast ordered joins, fast assignment, fast grouping and list columns. – R package version 1.8.10; with contributions from Srinivasan, S., Lianoglou, A. & Saporta, R. URL: http://CRAN.R-project.org/package=data.table

Ehnbom, S., Karlsson, L., Ylvén, R. & Åkesson, S. 1993. A comparison of autumn migration strategies in Robins *Erithacus rubecula* at a coastal and an inland site in southern Sweden. – Ringing & Migration 14(2): 84–93. DOI: 10.1080/03078698.1993.9674049

EURING 2015. The EURING Exchange Code 2000 Plus. – The European Union for Bird Ringing, Thetford, UK. URL: http://www.euring.org/data_and_codes/euring_code_list/index.html

Fandos, G. & Tellería, J. L. 2017. Range compression of migratory passerines in wintering grounds of the Western Mediterranean: conservation prospects. – Bird Conservation International : 1–13. DOI: 10.1017/S0959270917000120

Fennessy, G. & Harper, D. 2002. European Robin *(Erithacus rubecula)*. – In: Wernham, C., Toms, M., Marchant, J., Clarke, J., Siriwardena, G. & Baillie, S. (eds.) The Migration Atlas: Movements of the Birds of Britain and Ireland. – T & AD Poyser, London, pp. 498–501.

Fransson, T. & Hall-Karlsson, S. 2008. Svensk Ringmärkningsatlas, Vol. 3. [Swedish Bird Ringing Atlas, Vol. 3.]. – Naturhistoriska Riksmuseet & Sveriges Ornitologiska Förening, Stockholm, pp. 56–61. (in Swedish with English Summary)

Gienapp, P., Leimu, R. & Merilä, J. 2007. Responses to climate change in avian migration time microevolution versus phenotypic plasticity. – Climate Research 35: 25–35. DOI: 10.3354/cr00712

Gill, F. & Donsker, D. E. 2017. IOC World Bird List (v 7.2.). DOI: 10.14344/IOC.ML.7.2. URL: www.worldbirdnames.org

Gyimóthy, Zs., Gyurácz, J., Bank, L., Bánhidi, P., Farkas, R., Németh, Á. & Csörgő. 2011a Wing-length, body mass and fat reserves of Robins *(Erithacus rubecula)* during autumn migration in Hungary. – Acta Zoologica Academiae Scientiarum Hungaricae 57(2): 203–218.

Gyimóthy, Zs., Gyurácz, J., Bank, L., Bánhidi, P., Farkas, R., Németh, Á. & Csörgő, T. 2011b Autumn migration of Robins *(Erithacus rubecula)* in Hungary. – Biologia 66(3):548–555. DOI: 10.2478/s11756-011-0039-9

Gyurácz, J., Bánhidi, P. & Gyimóthy, Z. 2008. A vörösbegy *(Erithacus rubecula)* vonuló populációinak élőhely-választása és vonulás-dinamikája az őszi vonulási időszakban [Habitat choice and dynamics of migrating populations of the Robin *(Erithacus rubecula)* during the autumn migration season]. – Ornis Hungarica 15–16: 25–34. (in Hungarian with English Summary)

Gyurácz, J. & Csörgő, T. 2009. Vörösbegy [European Robin]. – 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. 440–442. (in Hungarian with English Summary)

Hadarics, T. & Zalai, T. 2008. Nomenclator avium Hungariae – Magyarország madarainak névjegyzéke [An annotated list of the birds of Hungary]. – Magyar Madártani és Természetvédelmi Egyesület, Budapest, pp. 174–175. (in Hungarian)

Harnos, A., Csörgő, T. & Fehérvári, P. 2016. Hitchhikers' guide to analysing bird ringing data. Part 2. – Ornis Hungarica 24(1): 172–181. DOI: 10.1515/orhu-2016-0010

Harnos, A., Csörgő, T. & Fehérvári, P. 2017. Hitchhikers' guide to analysing bird ringing data. Part 3. – Ornis Hungarica 25(2): 141–156. DOI: 10.1515/orhu-2017-0020

Harnos, A., Fehérvári, P. & Csörgő, T. 2015. Hitchhikers' guide to analysing bird ringing data. Part 1. – Ornis Hungarica 23(2): 163–188. DOI: 10.1515/orhu-2015-0018

Hornok, S., Karcza, Zs. & Csörgő, T. 2012. Birds as disseminators of ixodid ticks and tick-borne pathogens: note on the relevance to migratory routes. – Ornis Hungarica 20(2): 86–89. DOI: 10.2478/orhu-2013-0010

Hubálek, Z. 2005. Co-fluctuation among bird species in their migration timing. – Folia Zoologica 54(1–2): 159–164.

Hüppop, O. & Hüppop, K. 2003. North Atlantic Oscillation and timing of spring migration in birds. – Proceedings of the Royal Society of London B: Biological Sciences 270(1512): 233–240. DOI: 10.1098/rspb.2002.2236

Hüppop, O. & Hüppop, K. 2011. Bird migration on Helgoland: the yield from 100 years of research. – Journal of Ornithology 152(1): 25. DOI: 10.1007/s10336-011-0705-2

Ioalè, P. & Benvenuti, S. 1983. Site attachment and homing ability in passerine birds. – Monitore Zoologico Italiano – Italian Journal of Zoology 17(3): 279–294. DOI: 10.1080/00269786.1983.10736429

Jovani, R., Avilés, J. M. & Rodríguez-Sánchez, F. 2012. Age-related sexual plumage dimorphism and badge framing in the European Robin *Erithacus rubecula*. – Ibis 154(1): 147–154. DOI: 10.1111/j.1474-919X.2011.01187.x

Karlsson, L., Persson, K., Pettersson, J. & Walinder, G. 1988. Fat-weight relationships and migratory strategies in the Robin *Erithacus rubecula* at two stop-over sites in south Sweden. – Ringing & Migration 9(3): 160–168. DOI: 10.1080/03078698.1988.9673940

Klvaňa, P. 2008. Červenka obecná, *Erithacus rubecula*, Červienka obyčajna, European Robin – In: Cepak, J., Klvaňa, P., Škopek, J., Schröpfer, L., Jelínek, M., Hořák, D., Formánek, J. & Zárybnický, J. (eds.) Atlas migrace ptáků České a Slovenské republiky [Chech and Slovak Bird Migration Atlas]. – Aventinum, Praha, pp. 368–371. (in Slovakian with English Summary)

Korner-Nievergelt, F., Liechti, F. & Thorup, K. 2014. A bird distribution model for ring recovery data: where do the European Robins go? – Ecology and Evolution 4(6): 720–731. DOI: 10.1002/ece3.977

Madsen, V. 1997. Sex-determination of continental European Robins *Erithacus r. rubecula*. – Bird Study 44(2): 239–244. DOI: 10.1080/00063659709461060

Marchant, J., Hudson, R., Carter, S. & Whittington, P. 1990. Population Trends in British Breeding Birds. – BTO, Tring

Marra, P. P., Francis, C. M., Mulvihill, R. S. & Moore, F. R. 2004. The influence of climate on the timing and rate of spring bird migration. – Oecologia 142(2): 307–315. DOI: 10.1007/s00442-004-1725-x

McCollin, D., Hodgson, J. & Crockett, R. 2015. Do British birds conform to Bergmann's and Allen's rules? An analysis of body size variation with latitude for four species. – Bird Study 62(3): 404–410. DOI: 10.1080/00063657.2015.1061476

Mead, C. 1997. *Erithacus rubecula*, Robin. – In: Hagemeijer, W. J. & Blair, M. J. (eds.) The EBCC atlas of European breeding birds: Their distribution and abundance. – T & AD Poyser, London, pp. 512–513.

Miller-Rushing, A. J., Primack, R. B. & Stymeist, R. 2008. Interpreting variation in bird migration times as observed by volunteers. – The Auk 125(3): 565–573. DOI: 10.1525/auk.2008.07005

Nowakowski, J. K., Remisiewicz, M., Keller, M., Busse, P. & Rowiński, P. 2005. Synchronisation of the autumn mass migration of passerines: a case of Robins *Erithacus rubecula*. – Acta Ornithologica 40(2): 103–115. DOI: 10.3161/068.040.0206

Pérez-Tris, J., Carbonell, R. & Tellería, J. L. 2000. Abundance distribution, morphological variation and juvenile condition of Robins, *Erithacus rubecula* (L.), in their Mediterranean range boundary. – Journal of Biogeography 27(4): 879–888. DOI: 10.1046/j.1365-2699.2000.00457.x

Pettersson, J. & Hasselquist, D. 1985. Fat deposition and migration capacity of Robins *Erithacus rubecula* and Goldcrests *Regulus regulus* at Ottenby, Sweden. – Ringing & Migration 6(2): 66–76. DOI: 10.1080/03078698.1985.9673859

Pettersson, J. & Lindholm, C. 1983. The sequential passage of different Robin *Erithacus rubecula* populations at Ottenby. – Ornis Fennica Suppl. 3: 34–36.

Polakowski, M. & Jankowiak, Ł. 2012. Timing of autumn migration and biometric characteristics of migrating populations of European Robin (*Erithacus rubecula* L., 1758) in north-eastern Poland. – Polish Journal of Ecology 60(4): 797–804.

R Core Team 2017. R: A Language and Environment for Statistical Computing. – R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/

Remisiewicz, M. 2001. The pattern of winter-quarters of Robins *(Erithacus rubecula)* migrating in autumn through the southern Baltic coast. – The Ring 23(1): 37–53.

Remisiewicz, M. 2002. The temporal pattern to Robin *Erithacus rubecula* migration: evidence from ringing recoveries. – Ardea 90(3): 489–502.

Remisiewicz, M., Nowakowski, J. & Busse, P. 1997. Migration pattern of Robin *(Erithacus rubecula)* on the basis of Polish ringing recoveries. – The Ring 19(1–2): 3–40.

Robinson, R. A., Julliard, R. & Saracco, J. F. 2009. Constant effort: Studying avian population processes using standardised ringing. – Ringing & Migration 24(3): 199–204. DOI: 10.1080/03078698.2009.9674392

Rosińska, K. 2007. Biometrics and morphology variation within sex-age groups of Robins *(Erithacus rubecula)* migrating through the Polish Baltic coast. – Ring 29(1–2): 91–106. DOI: 10.2478/v10050-008-0043-9

Rosińska, K. & Adamska, K. 2007. Biometrics variation and directional preferences of immature Robins *(Erithacus rubecula)* caught in northern Italy during autumn migration in 2005. – Ring 29(1–2): 107–120. DOI: 10.2478/v10050-008-0038-6

Sandberg, R., Pettersson, J. & Alerstam, T. 1988. Why do migrating Robins, *Erithacus rubecula*, captured at two nearby stop-over sites orient differently? – Animal Behaviour 36(3): 865–876. DOI: 10.1016/S0003-3472(88)80169-6

Schaub, M. & Jenni, L. 2000. Fuel deposition of three passerine bird species along the migration route. – Oecologia 122(3): 306–317. DOI: 10.1007/s004420050036

Schaub, M., Jenni, L. & Bairlein, F. 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. – Behavioral Ecology 19(3): 657–666. DOI: 10.1093/beheco/arn023

Schubert, M., Fedrigo, A. & Massa, R. 1986. Timing and pattern of the post-breeding migration of some species of passerines through Lombardy, Northern Italy. – Ringing & Migration 7(1): 15–22. DOI: 10.1080/03078698.1986.9673874

Ściborska, M. & Busse, P. 2004. Intra-seasonal changes in directional preferences of Robins *(Erithacus rubecula)* caught on autumn migration at Bukowo-Kopań ringing station (N Poland) in 1996. – Ring 26(1): 41–58. DOI: 10.2478/v10050-008-0061-7

Sokolov, L. V., Markovets, M. Y., Shapoval, A. P. & Morozov, Y. G. 1998. Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. – Avian Ecology and Behaviour 1(1): 1–21.

Spina, F. & Volponi, S. 2009. Atlante della migrazione degli uccelli in Italia, Vol. 2.: Passeriformi [Italian Bird Migration Atlas Vol. 2.: Passeriformes]. – Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Roma (Italy) ISPRA, pp. 146–155. (in Italian with English Summary)

Stervander, M., Lindström, Å., Jonzén, N. & Andersson, A. 2005. Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. – Journal of Avian Biology 36(3): 210–221. DOI: 10.1111/j.0908-8857.2005.03360.x

Svensson, L. 1992. Identification Guide to European Passerines. – Ugga, Stockholm, 4th ed., pp. 109–110.

Szentendrey, G., Lövei, G. & Kállay, Gy. 1979. Az Actio Hungarica madárgyűrűző tábor mérési módszerei [Measuring methods in the bird ringing camps of Actio Hungarica]. – Állattani Közlemények 66: 161–166. (in Hungarian)

Szép, T., Nagy, K., Nagy, Z. & Halmos, G. 2012. Population trends of common breeding and wintering birds in Hungary, decline of longdistance migrant and farmland birds during 1999–2012. – Ornis Hungarica 20(2): 13–63. DOI: 10.2478/orhu-2013-0007

Tellería, J. L. 2015. The decline of a peripheral population of the European Robin *Erithacus rubecula*. – Journal of Avian Biology 46(2): 159–166. DOI: 10.1111/jav.00451

Tobias, J. 1997. Food availability as a determinant of pairing behaviour in the European Robin. – The Journal of Animal Ecology 66(5): 629–639. DOI: 10.2307/5916

Tobias, J. & Seddon, N. 2000. Territoriality as a paternity guard in the European Robin, *Erithacus rubecula*. – Animal Behaviour 60(2): 165–173. DOI: 10.1006/anbe.2000.1442

Tøttrup, A. P., Rainio, K., Coppack, T., Lehikoinen, E., Rahbek, C. & Thorup, K. 2010. Local temperature fine-tunes the timing of spring migration in birds. – Integrative and Comparative Biology 50(3): 293–304. DOI: 10.1093/icb/icq028

Tøttrup, A. P., Thorup, K. & Rahbek, C. 2006. Changes in timing of autumn migration in North European songbird populations. – Ardea 94(3): 527–536. DOI: 10.1111/j.0908-8857.2006.03391.x

Valkama, J., Saurola, P., Lehikoinen, A., Lehikoinen, E., Piha, M., Sola, P. & Velmala, W. 2014. Suomen Rengastusatlas, Osa 2. [The Finnish Bird Ringing Atlas, Vol. 2.]. – Finnish Museum of Natural History and Ministry of Environment, Helsinki, pp. 396–403. (in Finnish with English Summary)

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Exploratory analyses of migration timing and morphometrics of the Thrush Nightingale *(Luscinia luscinia)*

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Abstract Ornithological studies often rely on long-term bird ringing data sets as sources of information. However, basic descriptive statistics of raw data are rarely provided. In order to fill this gap, here we present the seventh item of a series of exploratory analyses of migration timing and body size measurements of the most frequent Passerine species at a ringing station located in Central Hungary (1984–2017). First, we give a concise description of foreign ring recoveries of the Thrush Nightingale in relation to Hungary. We then shift focus to data of 1138 ringed and 547 recaptured individuals with 1557 recaptures (several years recaptures in 76 individuals) derived from the ringing station, where birds have been trapped, handled and ringed with standardized methodology since 1984. Timing is described through annual and daily capture and recapture frequencies and their descriptive statistics. We show annual mean arrival dates within the study period and present the cumulative distributions of first captures with stopover durations. We present the distributions of wing, third primary, tail length and body mass, and the annual means of these variables. Furthermore, we show the distributions of individual fat and muscle scores, and the distributions of body mass within each fat score category. We present data only for the autumn migratory period since there were only 27 spring captures in the study period. We distinguish the age groups (i.e. juveniles and adults) in the analyses. Our aim is to provide a comprehensive overview of the analysed variables. However, we do not aim to interpret the obtained results, merely to draw attention to interesting patterns that may be worth exploring in detail. Data used here are available upon request for further analyses.

Keywords: Ócsa Bird Ringing Station, wing, third primary, tail length, body mass, fat, muscle, bird banding, capture-recapture, long term data, meta-analyses, migratory connectivity, Sprosser

Összefoglalás Madártani tanulmányokban gyakran elemeznek hosszútávú madárgyűrűzési adatsorokat, de az alapvető leíró statisztikák és exploratív elemzések általában nem hozzáférhetőek. E hiányt pótolandó, cikksorozatot indítottunk, melyben egy közép-magyarországi gyűrűző állomáson leggyakrabban előforduló énekesmadár fajok vonulás időzítésének és testméreteinek exploratív elemzéseit közöljük (1984–2017). A sorozat hetedik tagjaként szolgáló jelen cikkben először áttekintjük a nagy fülemüle magyar gyűrűs külföldi és külföldi gyűrűs magyarországi megkerüléseit, majd rátérünk a faj egy magyarországi, 1984 óta standard módszerekkel dolgozó gyűrűzőállomásról származó 1138 gyűrűzött és 547 visszafogott egyedétől (összesen 1557 visszafogási esemény, 76 esetben több éves) származó adatainak elemzésére. Az időzítés és a fogásszám jellemzésére a napi és évi fogás és visszafogás gyakoriságokat használtuk. Ábrázoltuk az évenkénti átlagos érkezési időket és azok változását. Az éven belüli időzítést az első megfogások kumulatív eloszlásával ábrázoljuk feltüntetve a tartózkodási időket is. Közöljük a szárnyhossz, a harmadik evező hossz, a farokhossz és testtömeg leíró statisztikáit. Ábrázoljuk ezen változók éves átlagait, a zsír- és izomkategóriák gyakorisági eloszlását, valamint a testtömegek eloszlását zsírkategóriák szerinti bontásban. Csak az őszi fogásokra közlünk elemzéseket, mivel összesen 27 tavaszi fogás volt a vizsgálati időszakban. A korcsoportokat (fiatal, öreg) megkülönböztetjük. Célunk a vizsgált változók átfogó bemutatása és a bennük található mintázatok feltárása volt az eredmények interpretálása nélkül. Kérésre a cikkhez felhasznált adatsort rendelkezésre bocsátjuk.

Kulcsszavak: Ócsai Madárvárta, szárnyhossz, harmadik evező hossza, farokhossz, testtömeg, zsír, izom, madárgyűrűzés, hosszútávú adatsor, meta-analízis, vonulási kapcsoltság

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Introduction

Bird ringing or banding is one of the principal and oldest methods in use to study various aspects of avian populations (Robinson *et al.* 2009). Overwhelming amount of data has been collected by professional research entities and within citizen science projects Cooper *et al.* 2014) in over a century of bird ringing, and has been used excessively in a diverse array of disciplines. However, compared to the amount of data available throughout the world, concise descriptive information on measured parameters suitable for meta- or comparative analyses is sporadically available (Gienapp *et al.* 2007, Harnos *et al.* 2015). Though purely descriptive studies are often hard to publish within the framework of current hypothesis-focused science, we feel that such studies may well play an outstanding role in generating new hypotheses. Therefore, it is essential that descriptive studies apply the most appropriate statistical methodologies (Harnos *et al.* 2015, 2016, 2017). The bulk of currently available data is often collected at permanent, long-term ringing stations where large amount of individuals of various species are trapped simultaneously (Csörgő *et al.* 2016). These projects generally apply standardized methodologies in trapping, handling and data collection, thus information derived from these sites is suitable for location-wise comparisons (Schaub & Jenni 2000, Marra *et al.* 2004, Schaub *et al.* 2008, Tøttrup *et al.* 2010).

The civil interest towards nature can be well matched with serious, scientific work. Many scientific research is based on the important work of volunteers, ”civilians” in data collection (citizen science, Miller-Rushing *et al.* 2008, Cooper *et al.* 2014).

Here we present exploratory and descriptive statistics on the migration timing and morphometrics of the Thrush Nightingale *(Luscinia luscinia)* between 1984–2017 from a Central European ringing station (Ócsa Bird Ringing Station, Hungary, see Csörgő *et al.* 2016 in English and Csörgő & Harnos 2018 in Hungarian for details).

The Thrush Nightingale is a sexually monomorphic, omnivorous, medium-sized species of the Muscicapidae family (Collar 2018). The upper parts are typically dark olivaceous grey-brown, the tail is dull rufus-brown, the breast is brown, almost invariably mottled grey. The great-covers and tertials of adults are uniform brown. The juveniles' feathers are spotted until the postjuvenile moult. Thrush Nightingales are typically darker than Nightingales *(L. megarhynchos)*. Post-moult juveniles are similar to adults, but tips of tertials and greater covers retain pale spots (Cramp 1988, Svensson 1992, Demongin 2016). The plumage of sexes are similar, but the males are slightly darker and larger than females, and have more prominent grey mottling on breast. The exact sexing is only possible in hand, using the incubation patch of breeding adults (Dittberner & Dittberner 1989, Svensson 1992, Demongin 2016).

The Thrush Nightingale is a monotypical species with an extensive breeding range from Norway, Denmark, Germany, Poland, to central Asia, covering the temperate and continental climate zones, complementing the more southerly and westerly distribution of the Nightingale (Cramp 1988, Tucker & Heath 1994, Bogucki & Sorjonen 1997, Collar 2018). The Thrush Nightingale and the Nightingale are two ecologically and morphologically similar, closely related sister species (Sorjonen 1986, Reifová *et al.* 2011a). In a narrow zone from Denmark to the Balkans the Thrush Nightingale is sympatric with the Nightingale (Storchová *et al.* 2010). Both species have similar ecological requirements but partial habitat segregation has been observed in sympatry (Ranoszek 2001). The divergence in bill size most likely reflects segregation of feeding niches between the species in sympatry (Reifová *et al.* 2011b). The two species diverged approximately during the Pleistocene (1.8 Mya) (Storchová *et al.* 2010). Despite the close relationship and similarities of the sister species, their migratory strategies are remarkably different (Hahn *et al.* 2016, Csörgő *et al.* 2017). The hybridisation of the two species is relatively common in the overlapping breeding areas (Reifová *et al.* 2011b). The hybrid males are fertile and can reproduce with either of the parental species (Becker 1995, Reifová *et al.* 2011a). The two species are isolated by incomplete prezygotic isolation and female hybrid sterility (Kverek *et al.* 2008, Reifová *et al.* 2011a). The F1 birds have intermediate wing formula (Becker 2007, Kováts *et al.* 2013, Demongin 2016).

The Thrush Nightingale is classified as Least Concern in the IUCN Red List (BirdLife International 2018). After a largely stable population between 1970–1990, it has increased in Denmark, Poland, Norway, Finland and Estonia, and some range expansion has occurred in Sweden. The species has occupied urban areas, parks and cemeteries. Warmer springs have allowed new breeders to increase density and range (Bogucki & Sorjonen 1997). These increases proved a longer-term spread to the west and north (Tucker & Heath 1994, Valkama *et al.* 2014). The Swedish population changed from cca. 15,000 breeding pairs in the 1970's to cca. 20,000–50,000 pairs in the 1980's (Bogucki & Sorjonen 1997). The Finnish population size was about 200 pairs during the early 1950's (Merikallio 1958) and increased to around 8000 pairs during the early 1980's (Hildén & Koskimies 1984), and to 15,000–20,000 pairs for the late 1990's (Bogucki & Sorjonen 1997). The number of breeding occurrences also increased in eastern Germany in the early 1990's (Becker 1995). The long-term Pan-European trend showed a 9% population increase between 1980–2009, which means a 0.3% mean annual rate of change (Vickery *et al.* 2014). Number of vagrants greatly increased in Britain during the twentieth century in association with changes in population size or distribution (Newton 2008). In the meantime, number of birds decreased in Sweden based on point count and ringing data between 1980 and 1999 (Karlsson *et al.* 2005) and in Denmark (point-count census data) between 1976 and 2005 (Heldbjerg & Fox 2008).

The species is protected on the breeding area, but the situation is different on its migratory route. For example, beyond the 3.3 million Quails *(Coturnix coturnix)*, 0.5 million other birds were captured and killed in North Sinai during the 45 days of peak migration in 2012 in autumn and near 50,000 of them were Thrush Nightingales (Eason *et al.* 2016). The ratio of killed birds among the recoveries is decreasing (Fransson & Hall-Karlsson 2008).

The Thrush Nightingale inhabits more continental areas complementing the distribution of the Nightingale. Its preferred habitat is dense, damp thickets, often riverine or swampy, forest-edges with good ground cover (nettles and bramble). They occupy variable, densely vegetated habitats from lowland riverine woodland, edges of broad-leaved woodlands to bushland, managed open woodlands (young deciduous trees), suburban habitats and gardens (Cramp 1988, Tucker & Heath 1994, Bogucki & Sorjonen 1997).

Their mating system is social monogamy. Only the females incubate, but both parents feed the offspring. The pair-bond breaks down at the end of breeding season (Cramp 1988).

The Thrush Nightingale – mainly males – has a high breeding site fidelity (Cramp 1988, Becker 2007). In Czech Republic only 2% out of 351 adults have been found more than 10 km away, and 91.2% of juveniles settled less than 10 km from the natal site (Kverek *et al.* 2008). The median dispersal distance for birds ringed as nestlings is 2 km (0–220) and for breeding adults 0 km (0–51) in Finland (Valkama *et al.* 2014).

After breeding the complete moult of adults takes around 30–35 days, which is faster than in case of Nightingales (cca. 45 days) (Ginn & Melville 1983, Svensson 1992, Jenni & Winkler 1994).

The Thrush Nightingale is a long distance migratory bird with a typical funnel-shaped migratory pattern. Birds from the whole breeding distribution converge to a relatively narrow wintering zone in East-Africa (Cramp 1988).

Despite the large European population (3,7000,000–6,900,000 breeding pairs) (BirdLife International 2004), the number of ringed birds is relatively small, and thus the number of recoveries is also small (3831 ringed birds with 15 foreign recoveries up to 2002 in Denmark, 14,245 ringed birds up to 2003 with a mean of cca. 400 in the recent years and 14 foreign recoveries in Sweden, 11,608 ringed birds with 14 foreign recoveries up to 2012 in Finland) (Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008, Valkama *et al.* 2014). Ringing work is intense only in the western edge of its distribution, most birds breed east to this area (BirdLife International 2018). Even though the Thrush Nightingale is one of the most common Palaearctic passerine on the north-eastern side of the Ngulia ridge, in the West Tsavo National Park in south-east Kenya during November and December on the narrowest part of the funnel, where several hundreds of birds are ringed daily (Pearson & Backhurst 1976), there were only one Swedish and one Finnish recoveries (Fransson & Hall-Karlsson 2008, Valkama *et al.* 2014).

From the western breeding areas the species migrates to south-east direction in autumn. It is very common in the Eastern Mediterranean in during the postbreeding migration (Cramp 1988, Alerstam 2006), also the Appenine Peninsula can be a refuelling site for them (Stach *et al.* 2012), but the more eastern sites (Balkan area) are probably more important, since there are a relatively small number of ringed birds in Italy during autumn migration (Spina & Volponi 2009).

Recoveries in Denmark indicate that migrants from Sweden and Finland pass Denmark (Bønløkke *et al.* 2006), and the Swedish birds pass Germany. Birds ringed in Germany were recovered in Hungary and in north Italy (Bairlein *et al.* 2014). The Thrush Nightingale migrates with a strong concentration of recoveries in Egypt (Fransson *et al.* 2005, Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008, Bairlein *et al.* 2014).

The species leaves the breeding areas from early August to mid- or late September (Cramp 1988). The migration interval is quite wide, meanwhile the migration of individuals may be quick. For example, there were recoveries in Finland at the beginning of August, and in the meantime a bird with Finnish ring was found in on the 12th of August in Egypt (Valkama *et al.* 2014). While one Danish bird was recovered in Hungary in August, two others were recovered in Austria and in Egypt in September (Bønløkke *et al.* 2006).

The small set of ringing data has a peak in the second decade of August in Italy (Spina & Volponi 2009). Thrush Nightingales pass through Cyprus from mid-August to October with a peak in late August and September, through Egypt from mid-August to mid-October with a peak in late August to mid-September, through Ethiopia from the second week of September to early November and through central Sudan around the Nile system in August – November with a peak from late September. Movement into Kenya begins at the end of October peaking from 10th of November to 10th of December (Pearson & Backhurst 1976, Hogg *et al.* 1984, Cramp 1988, Yohannes *et al.* 2009b).

The Thrush Nightingale tracks vegetation greenness and the peaks of insect abundance occurring after rains throughout their annual cycle, adjusting the timing and direction of migratory movements with seasonal changes in resource availability over Europe and Africa. The species stops several times for longer time periods during autumn migration. The birds probably spend three-four weeks in southern Europe (Appenine and Balkan Peninsulas), then they spend up to 2 months (or a few of them even may stay for the whole winter) in green areas of eastern Sudan and western Ethiopia, then they break their journey in the east Kenyan bushland from late November to late December. They move between consecutive staging areas even within the wintering region in Africa to match seasonal variation in regional climate (Pearson & Lack 1992, Stach *et al.* 2012, Thorup *et al.* 2017).

The migration speed is cca. 120 km/day in Europe, and 140 km/day while the birds cross the desert, only cca. 20 km/day in north-east and east Africa in autumn (Yohannes *et al.* 2009a).

Some of the individuals winter in southern Ethiopia, but most of them winter south of the Equator (Kenya, Tanzania, Malawi, Zimbabwe, Mozambique, Namibia, Botswana, South Africa (Cramp 1988). Main arrival in southern Africa starts at late November (Cramp 1988, Bønløkke *et al.* 2006).

The body mass of the species decreases continuously in autumn from Europe (cca. 28 g) to the Equator (cca. 22 g) (Yohannes *et al.* 2009a,b). The body mass of Thrush Nightingales killed at Bahig on the Egyptian coast in autumn was 24.4 g with 5.2 g fat mass on average (Moreau & Dolp 1970). The deposited tissue consisted of 82% fat and 18% wet protein (Klaassen *et al.* 1997).

The species leaves the winter quarter in March, early April. Passage through Kenya lasts from late March until the 3rd week of April. They are present in Jordan, Israel, Syria, Lebanon from mid-April to early May. The birds arrive to the breeding site from mid-April in Romania and in early May in Germany and Sweden (Cramp 1988). The migration period is quite wide, and individual birds move quite fast similarly to the autumn migration. For example, there were Finnish birds at the end of April in Egypt, and there were migrating birds in Finland at the beginning of May (Valkama *et al.* 2014).

The species has an anti-clockwise loop migration (Klvaňa *et al.* 2018). The autumn migration route leads on the eastern side of the Nile and the Victoria-lake in Kenya, but the spring migration follows an even more eastern route in Africa, associated with the more humid conditions on the eastern coast (Pearson & Lack 1992, Tøttrup *et al.* 2012). A bird ringed in Sweden was recovered in Yemen (Fransson & Hall-Karlsson 2008), other two birds ringed in Finland were recovered in Lebanon (Valkama *et al.* 2014), and one Hungarian bird was recovered in Israel in spring (BirdLife Hungary 2018). The species is very rare in spring in Italy indicating also the more eastern route back to the breeding area (Spina & Volponi 2009).

During spring, their speed is cca. 80 km/day in East Africa, 230 km/day above the desert, and 80 km/day in Europe (Yohannes *et al.* 2009a).

Probably due to climate change, the whole migration wave advanced on the island of Christiansø, in the Baltic Sea in spring from 1976 to 1997 (Tøttrup *et al.* 2006) and the first-arrival days advanced during 1950 to 2012 at Ottenby, Sweden (Tøttrup *et al.* 2012). The actual weather situation also influences the migration, for example the arrival time at Ottenby of the species was delayed in an exceptionally drought year in north-east Africa in 2011 (Tøttrup *et al.* 2012). Arrival to Vilnius (Estonia) is negatively correlated with precipitation and positively correlated with atmospheric pressure (Zalakevicius *et al.* 2006).

The species is protected in Hungary (BirdLife Hungary 2018). The Thrush Nightingale was formerly common breeder species in the north-eastern part of Hungary (Farkas 1954), but in the second half of 20th century it has became a rare breeder in remnant patches of willow-poplar groves and willow bushes (Schmidt 1973). Recently the species was extinct from the site of the Felső-Tisza (and probably from its surroundings) and only interspecific hybrids with the Common Nightingale can be found. A strong evidence for a new haplotype group of Szatmár-Bereg was found, which had *L. megarhynchos* morphology but of *L. luscinia*' mtDNA (Ács & Kováts 2013). Currently 7% of the population of Nightingale were interspecific hybrids. The morphological character displacements and the proportion of hybrids refer a stable hybrid population (Kováts *et al.* 2013, Kováts & Harnos 2015).

Some birds recovered in Hungary have been ringed at the most western part of the breeding area: in Sweden, Germany, Finland, and birds ringed in Hungary were recaptured on the breeding areas (Csörgő & Kováts 2009, BirdLife Hungary 2018). These birds mostly fly from north-east to south-west direction in autumn. Two individuals ringed in Hungary were recovered in the following years in North-East (Belarus) indicating that the Carpathian Basin is in connection with a much wider zone. Birds ringed westward have typically been recovered in the western area of the country *(Figure 2)*. There were more several-year recoveries (76 birds (6.7%) in the study period at Ócsa). The pattern of recaptures and the high number of several-year recoveries are also signs of strong connectivity, which is atypical in case of long distance migrants (Finch *et al.* 2017).

The Thrush Nightingale is a regular, but not common migrant from late April until mid-May in spring, the peak is at the end of April, early May. Much more birds use the Carpathian Basin in the post breeding migration. The first specimens are usually captured at the beginning of August and the last ones in late September, early October peaking in mid-August. (Csörgő & Lövei 1986, 1995, Hadarics & Zalai 2008, Csörgő & Kováts 2009).

Many birds caught in two ringing stations near Budapest (Budakeszi and Ócsa) showed intensive increase in body mass during migration. The average body mass is cca. 25 g before the 20th of August, and it is near 30 g in the third pentad of September (Csörgő & Lövei 1986). 40% of the birds are recaptured at site within season with increasing body masses proving that the Ócsa area is used for stopover and pre-migratory fattening, so the fattest birds (some of them were more than 30 g) are able to reach Egypt without stopover (Csörgő & Lövei 1995). Contrarily, only 1% of the birds were recaptured (without several-year recaptures) in Szalonna, on a third ringing station of East Hungary. Here the individuals were in a relatively poor condition, indicating that birds only rest at that site. Here, within the 22 years of study (1989–2010), the median date of autumn migration of Thrush Nightingales shifted 8 days earlier (Kováts 2012). In the same time period, the arrival times also shifted earlier at Ócsa (see later in this paper).

Thrush Nightingales are regular, but not common passage migrants at the Ócsa Bird Ringing Station (regular in autumn, rare in spring as a sign of loop migration), the source of data analysed in this paper. Our aim is to provide a comprehensive overview of migration timing, body size measurements and inter-annual changes in these variables. Hopefully, these patterns will help formulate research questions and provide information for further higher level analyses. However, we do not aim to interpret the obtained results, merely draw attention to interesting patterns, that may be worth exploring in detail.

Materials and methods

Bird ringing data

The Ócsa Bird Ringing Station is situated in Central Hungary (N47.2970, E19.2104) in the Duna-Ipoly National Park in the immediate vicinity of Ócsa town. The study site is characterized by a post-glacial peat bog with a mosaic of habitats including open water surfaces, reedbeds, bushy vegetation and forests. It is situated in a humid continental transitional climate zone (for further details see Csörgő *et al.* 2016, ocsabirdringing.org). Birds were trapped with standard mistnets placed at standard locations throughout the study period. Trapping effort is seasonal and changed over the years (see Csörgő *et al.* 2016 for details).

The day of the year of first capture in autumn were considered as arrival (migration) timing of individual birds. Stopover duration was calculated as the difference of within season last and first captures excluding within day recaptures. Biometric measurements were taken following strictly standardized methods (Szentendrey *et al.* 1979, EURING 2015). Only data of the first captures were used in the analysis. We distinguished first calendar year birds (juveniles) from adults upon plumage characteristics (Cramp 1988, Svensson 1992, Demongin 2016), and we present all results according to these groups. We present data only for the autumn migratory season due to the almost total lack of spring migrants; birds caught after the 190th and before the 280th day of the year were considered to be autumn migrants. A total of 1138 Thrush Nightingales were captured and ringed between March and November; 27 adults in spring and 190 adults and 895 juveniles in autumn (the rest of the birds were not aged) in the study period of 1984–2017. This total value constitutes cca. 14.4% of the 3783 Thrush Nightingales ringed in Hungary in this period. Beyond the ringed individuals, there were 547 recaptured individuals with 1557 recaptures (76 several-year recaptures).

Statistical methods

To describe daily and yearly capture frequencies and the cumulative distribution of the date of first captures with recaptures, we used the functions of the `ringR` package (Harnos *et al.* 2015). Descriptive tables (mean, median, standard deviation (SD), minimum (min), maximum (max) values and sample size (N)) on the timing of migration, stopover duration, the length of wing, third primary and tail, and body mass were created by the `data.table` package (Dowle *et al.* 2013). The annual mean values of timing, body mass, wing-, third primary and tail lengths are plotted against time (year) on scatterplots. Loess smooth lines were fitted to highlight trends (Cleveland *et al.* 1992). The distributions of the same variables were represented with histograms and overlaid smoothed histograms.

Figure 1. Foreign ring recoveries of Thrush Nightingales. The data of birds ringed in Hungary and recovered abroad and the birds ringed abroad and recovered in Hungary are depicted

1. ábra Magyarországon gyűrűzött és külföldön megkerült, illetve külföldön gyűrűzött és Magyarországon visszafogott nagy fülemülék

Boxplots were used to show the body mass distributions by fat score categories. Fat and muscle score frequencies are shown using barplots. We distinguished the age groups throughout the analyses. For more details on the analysis, please visit ocsabirdringing.org. All analyses were carried out in R 3.4.0 (R Core Team 2017).

Results

A total of 14 foreign recaptures were recorded between 1951 and 2017 in relation to Hungary *(Figure 1)*. Annual capture and recapture frequencies at the study site are shown in *Figure 2*. Within-year capture and recapture frequencies, together with cumulative distribution of individual first and last captures are depicted in *Figure 3*, while their respective descriptive statistics are presented in *Table 1–2*. Changes in annual mean arrival dates throughout the study period and the distribution of within-year migration timing according to season and age are presented in *Figure 4*. The trend of annual mean wing lengths and the distribution of wing length measurements according to age are shown in *Figure 5*, while their respective descriptive statistics are presented in *Table 3*.

Third primary length *(Figure 6*, *Table 4)*, tail length *(Figure 7*, *Table 5)* and body mass *(Figure 8*, *Table 6)* are presented in a similar fashion. Body mass in relation to age and fat scores are visualized with boxplots in *Figure 9*. Finally, the distribution of fat and muscle scores grouped by age can be found in *Figure 9 b,d* and *Figure 10*.

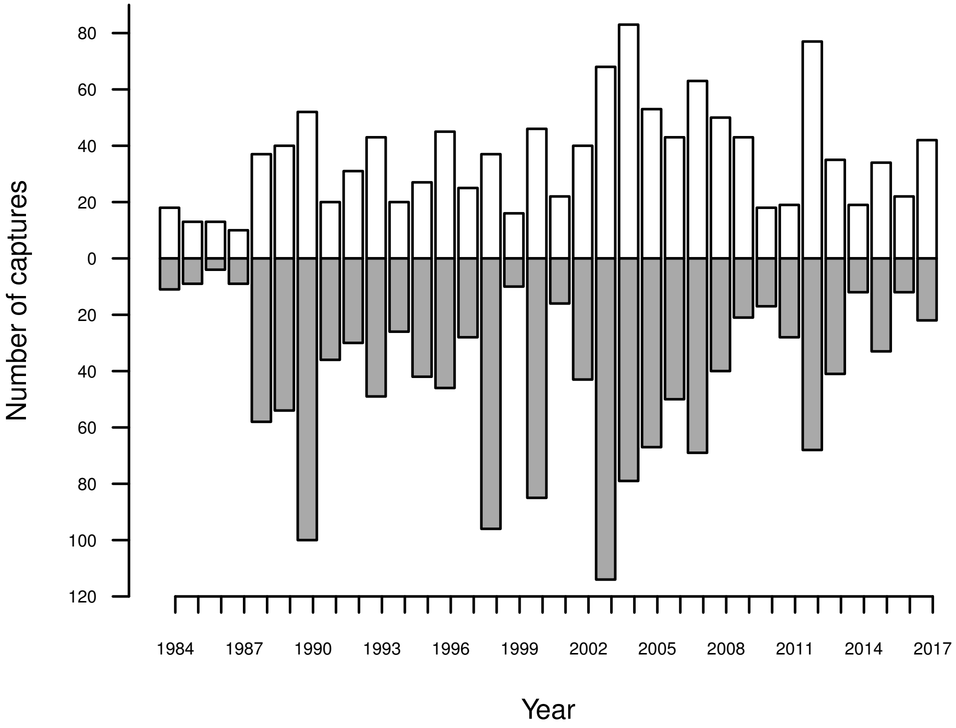

Figure 2. Annual capture (white bars) and recapture (grey bars) frequencies in autumn
2. ábra Éves fogás (fehér oszlopok) és visszafogás (szürke oszlopok) gyakoriságok ősszel

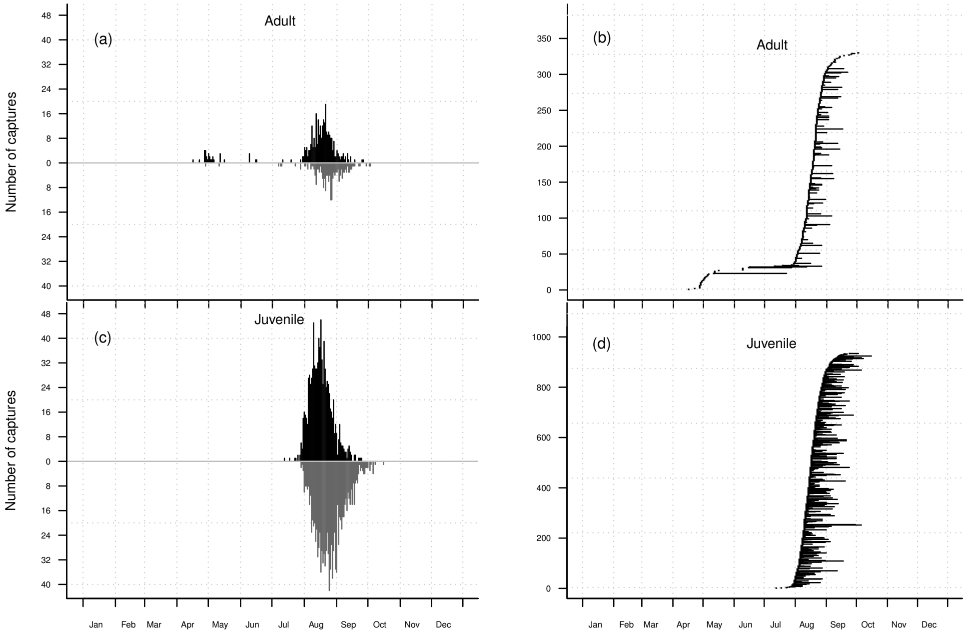

Figure 3. Within-year capture (black bars) and recapture (grey bars) frequencies (a, c) and cumulative distributions of individual first capture dates (b, d) according to age groups (horizontal lines: stopover durations)

3. ábra Éven belüli fogás (fekete oszlopok) és visszafogás (szürke oszlopok) gyakoriságok (a, c) és az egyedek első megfogási idejének kumulatív eloszlása (b, d) korcsoportonként (vízszintes vonalak: tartózkodási idők)

Table 1. Descriptive statistics of stopover duration (day)

1. táblázat A tartózkodási idő (nap) leíró statisztikái

Season	**Age**	**Mean**	**Median**	**SD**	**Min**	**Max**	**N**
autumn	adult	12.6	11	9.4	1	47	97
autumn	juvenile	12.0	10	9.4	1	57	395

Migration timing

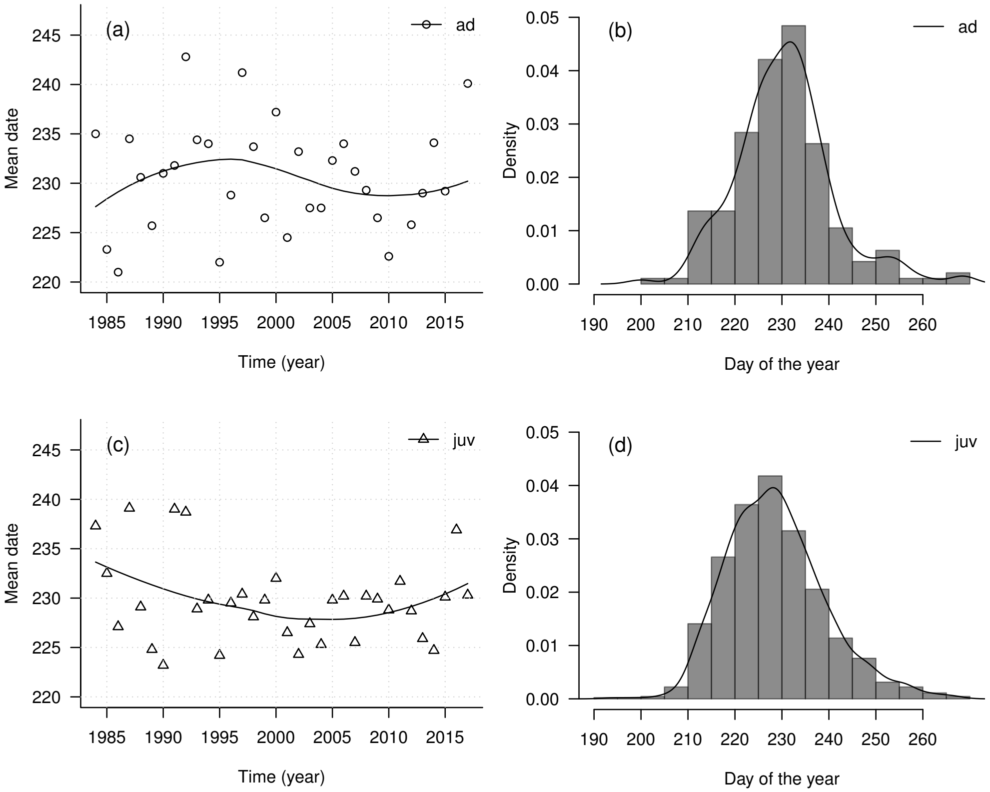

Figure 4. Annual mean migration timing (day of the year) throughout the study period and histograms/smoothed histograms of timing in autumn

4. ábra Az éves átlagos vonulás időzítés (év napja) a vizsgálati időszakban és az időzítés hisztogramja/simított hisztogramja ősszel

Table 2. Descriptive statistics of migration timing (day of the year)

2. táblázat A vonulás időzítés (év napja) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
autumn	adult	230.7	230.5	10.4	200	269	190
autumn	juvenile	228.7	228.0	10.5	194	267	895

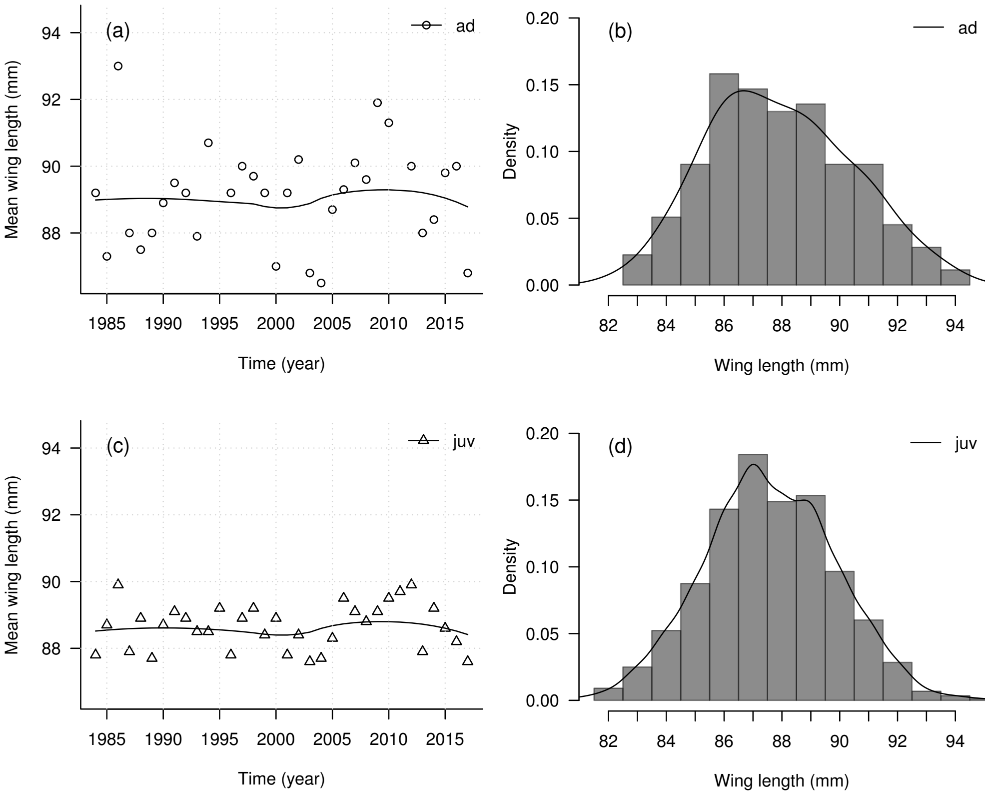

Figure 5. Annual mean wing length (mm) throughout the study period and histograms/smoothed histograms of wing length in autumn

5. ábra Az éves átlagos szárnyhossz (mm) a vizsgálati időszakban és a szárnyhossz hisztogramja/simított hisztogramja ősszel

Table 3. Descriptive statistics of wing length (mm)

3. táblázat A szárnyhossz (mm) leíró statisztikái

Season	**Age**	**Mean**	**Median**	**SD**	**Min**	**Max**	**N**
autumn	adult	88.9	89.0	2.5	83	95	177
autumn	juvenile	88.6	88.0	2.3	82	96	880

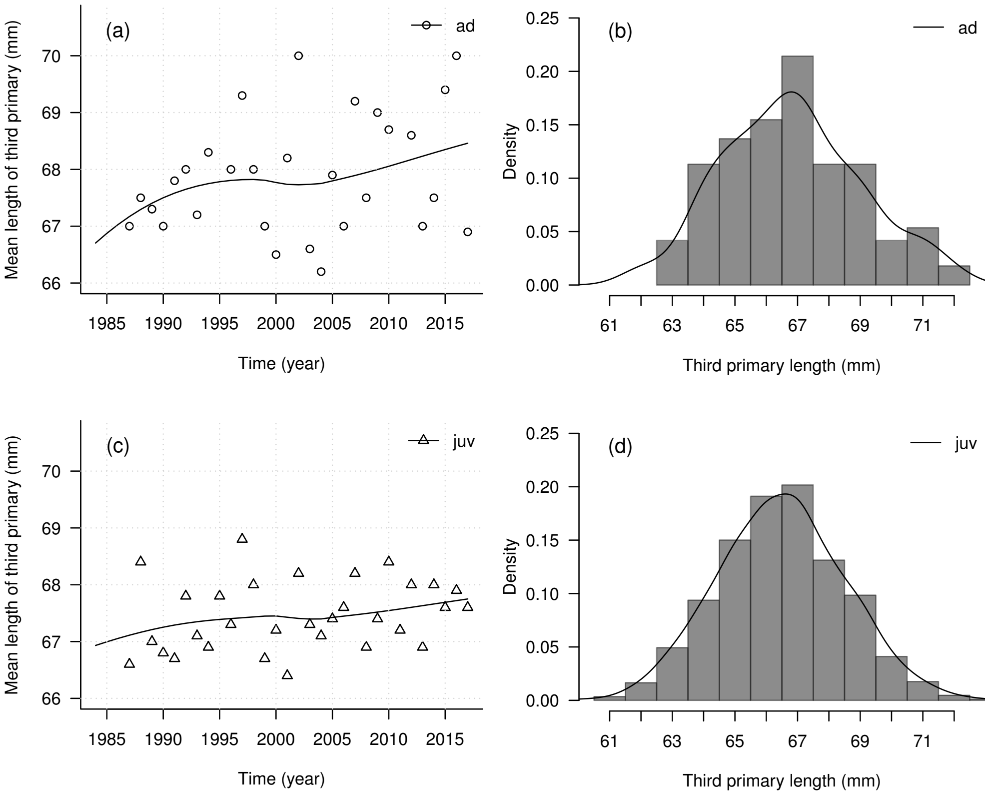

Figure 6. Annual mean third primary length (mm) throughout the study period and histograms/smoothed histograms of third primary length in autumn

6. ábra Az éves átlagos harmadik evező hossz (mm) a vizsgálati időszakban és a harmadik evező hosszának hisztogramja/simított hisztogramja ősszel

Table 4. Descriptive statistics of third primary length (mm)

4. táblázat A harmadik evező hosszának (mm) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
autumn	adult	67.8	68.0	2.2	63	73	168
autumn	juvenile	67.5	67.0	2.0	61	74	853

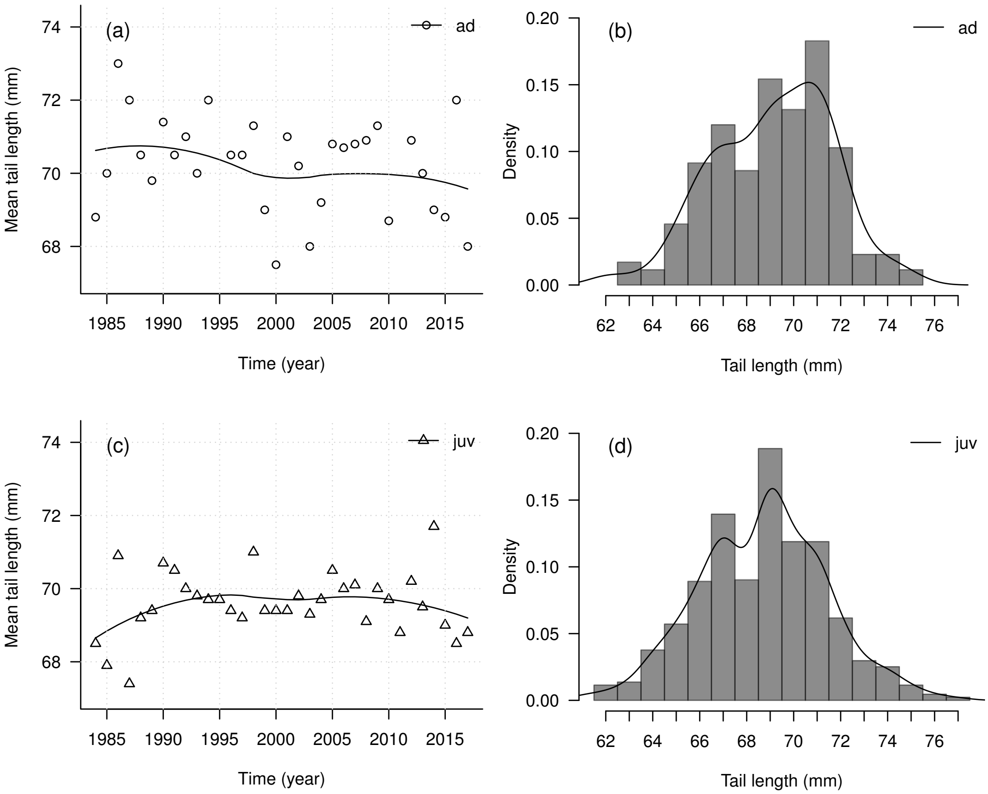

Figure 7. Annual mean tail length (mm) throughout the study period and histograms/smoothed histograms of third primary length in autumn

7. ábra Az éves átlagos farokhossz (mm) a vizsgálati időszakban és a farokhossz hisztogramja/simított hisztogramja tavasszal ősszel

Table 5. Descriptive statistics of tail length (mm)
5. táblázat A farokhossz (mm) leíró statisztikái

Season	**Age**	**Mean**	**Median**	**SD**	**Min**	**Max**	**N**
autumn	adult	70.1	70.0	2.5	63	76	175
autumn	juvenile	69.7	70.0	2.7	62	78	875

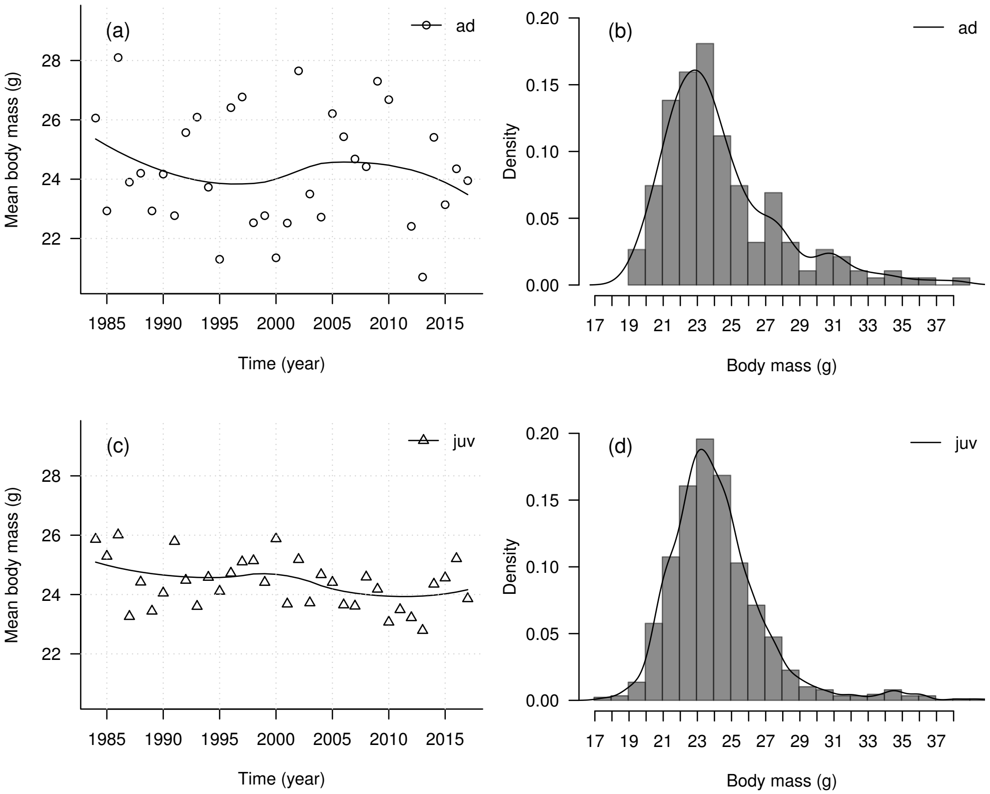

Figure 8. Annual mean body mass (g) throughout the study period and histograms/smoothed histograms of body mass in autumn

8. ábra Az éves átlagos testtömeg (g) a vizsgálati időszakban és a testtömeg hisztogramja/simított hisztogramja ősszel

Table 6. Descriptive statistics of body mass (g)

6. táblázat A testtömeg (g) leíró statisztikái

Season	**Age**	**Mean**	**Median**	**SD**	**Min**	**Max**	**N**
autumn	adult	24.5	23.6	3.4	19.4	38.3	188
autumn	juvenile	24.2	23.8	2.8	17.5	39.4	884

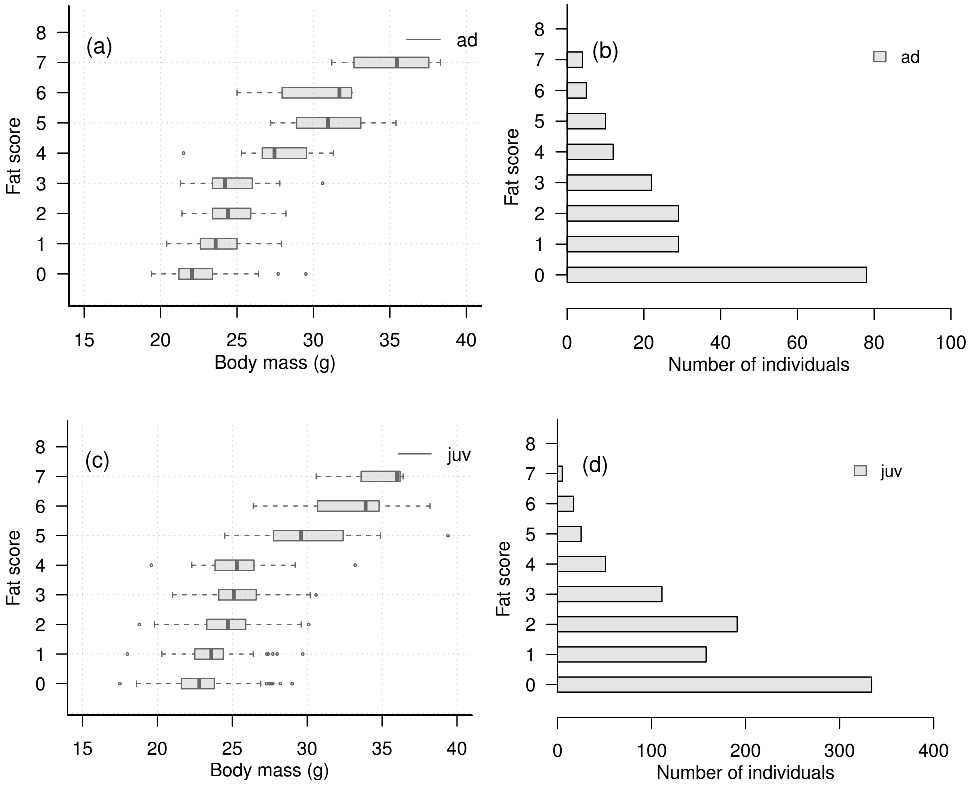

Figure 9. Boxplots of body mass according to fat score, and fat score frequencies in autumn
9. ábra A testtömeg boxplot-ja zsírkategóriánként és a zsírkategóriák gyakoriságai ősszel

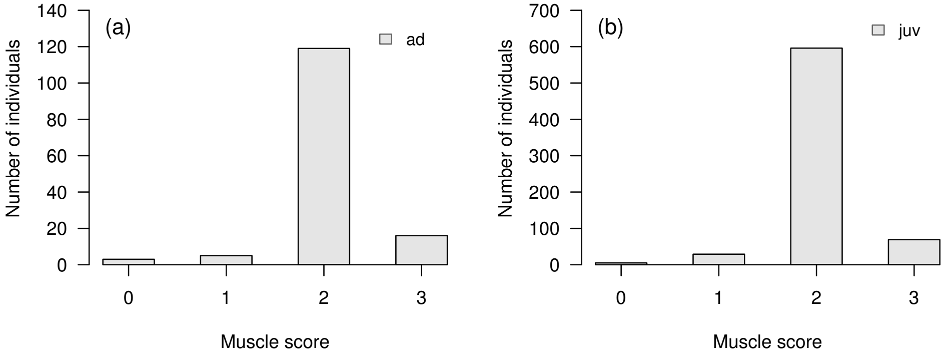

Figure 10. Muscle score frequencies in autumn
10. ábra Izom kategória gyakoriságok ősszel

Discussion

The exploratory analyses of timing and morphometrics of the Thrush Nightingale revealed several patterns of interest. Apparently, there is considerable variation (the maximum is cca. four times the minimum) annual capture and recapture frequencies in autumn *(Figure 2)*. During the last two decades of the previous century, when the number of birds was lower in Sweden, the numbers were also lower at the study site. Only 27 birds were captured in spring suggesting loop migration. The stopover durations are similar in all age groups *(Figure 3 b,d, Table 1)*.

The amount of juveniles greatly exceeds the amount of the adults *(Figure 3 a,c)*.

The autumn migration timing advanced in the first half and then delayed in the second half of the study period in case of the juveniles *(Figure 4 c)*. Timing of the adults is a bit delayed compared to that of the juveniles *(Figure 4 a,c, Table 2)*. The distribution of arrival timings are similar in the two age groups *(Figure 4 b,d)*. While there is no apparent trend over the years in wing length, there is a slight increasing trend in the third primary length *(Figures 5–6 a,c,e)*.

Tail length seems to be decreasing in case of adults although with a considerable inter-annual variation *(Figure 7 a)*, which can be caused by the low number of birds annually. This trend cannot be observed in case of juveniles *(Figure 7 c)*. The mean body mass seems to be constant over the years *(Figure 8 a)*, however a slight decreasing trend can be observed during the autumn season in case of the juvenile birds *(Figure 8 c)*.

The wing and tail distributions are slightly bimodal indicating some dimorphism between the sexes *(Figure 5–8 a,c,e)*.

The fat score distributions suggest that the birds can accumulate fat reserves *(Figure 9)*. Muscle score distributions suggest that the birds also build their muscles *(Figure 10)*.

Our results show that comprehensive exploratory analyses may reveal intriguing patterns, which may be investigated in more detail in the future. However, we emphasize that although the temporal extent of the data reported here is considerably large, all information presented here derives from a single location and thus has to be interpreted accordingly. Nonetheless, we hope that our results will help researchers conducting comparative or meta-analyses with baseline data and may also encourage others to report their data in a similar fashion. We also seek cooperation with interested parties and are willing to share all data reported here. Please contact the corresponding author for details.

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References

Ács, Z. & Kováts, D. 2013. Phylogenetic patterns of a Nightingale population in a contact zone of *Luscinia megarhynchos* and *L. luscinia* in Hungary. – North-Western Journal of Zoology 9(2): 365–373.

Alerstam, T. 2006. Conflicting evidence about long-distance animal navigation. – Science 313(5788): 791–794. DOI: 10.1126/science.1129048

Bairlein, F., Dierschke, J., Dierschke, V., Salewski, V., Geiter, O., Hüppop, K., Köppen, U. & Fiedler, W. 2014. Atlas des Vogelzugs [Bird Migration Atlas]. – AULA-Verlag, p. 471. (in German with English Summary)

Becker, J. 1995. Sympatric occurrence and hybridization of the Thrush Nightingale *(Luscinia luscinia)* and the Nightingale *(Luscinia megarhynchos)* at Frankfurt (Oder), Brandenburg. – Vogelwelt 116(10): 109–118.

Becker, J. 2007. Nachtigallen *Luscinia megarhynchos*, Sprosser *L. luscinia* und ihre Hybriden im Raum Frankfurt (Oder) – weitere Ergebnisse einer langjährigen Beringungsstudie [About Nightingales *Luscinia megarhynchos*, Thrush Nightingales *L. luscinia* and their hybrids in the area of Frankfurt (Oder) – further results of long-term investigations using bird ringing]. – Vogelwarte 45: 15–26. (in German with English Summary)

BirdLife Hungary 2018. Magyarország madarai: nagy fülemüle [Birds of Hungary: Thrush Nightingale]– Magyar Madártani és Természetvédelmi Egyesület [BirdLife Hungary]. URL: http://www.mme.hu/magyarorszagmadarai/madaradatbazis-luslus, downloaded on 12 May 2018. (in Hungarian)

BirdLife International 2018. Species factsheet: *Luscinia luscinia*. Downloaded from http://www.birdlife.org on 16/05/2018.

BirdLife International 2004. Birds in Europe: population estimates, trends and conservation status. – BirdLife International, BirdLife Conservation Series No.12., Cambridge, U.K., pp. 269–271.

Bogucki, Z. & Sorjonen, J. 1997. *Luscinia luscinia*, Thrush Nightingale. – In: Hagemeijer, W. J. & Blair, M. J. (eds.) The EBCC atlas of European breeding birds: Their distribution and abundance. – T & AD Poyser, London, pp. 514–515.

Bønløkke, J., Madsen, J. J., Thorup, K., Pedersen, K. T., Bjerrum, M. & Rahbek, C. 2006. Dansk trækfugleatlas [Danish Bird Migration Atlas]. – Rhodos, Humlebæk, p. 602. (in Danish with English Summary)

Cleveland, W. S., Grosse, E. & Shyu, W. M. 1992. Local regression models. – In: Chambers, J. & Hastie, T. (eds.) Statistical Models in S. – Pacific Grove, California, pp. 309–376.

Collar, N. 2018. Handbook of the birds of the world alive. – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. & de Juana, E. (eds.) Handbook of the Birds of the World Alive – Lynx Edicions, Barcelona (https://www.hbw.com/node/58454 on 15 May 2018)

Cooper, C. B., Shirk, J. & Zuckerberg, B. 2014. The invisible prevalence of citizen science in global research: Migratory birds and climate change. – PLoS ONE 9(9): e106508. DOI: 10.1371/journal.pone.0106508

Cramp, S. 1988. Handbook of the Birds of the Western Palearctic, Vol. 5. – Oxford University Press, Oxford, pp. 616–626.

Csörgő, T., Fehérvári, P., Karcza, Zs. & Harnos, A. 2017. Exploratory analyses of migration timing and morphometrics of the Common Nightingale *(Luscinia megarhynchos)*. – Ornis Hungarica 25(2): 116–140. DOI: 10.1515/orhu-2017-0019

Csörgő, T. & Harnos, A. 2018. Az Ócsai Madárvárta működése és fontosabb kutatási eredményei – Természetvédelem és kutatás a Turjánvidék északi részén [The operation and selected research results of the Ócsa Bird Ringing Station – Conservation and research at the northern part of "Turjánvidék"]. – Rosalia 10: 929–960. (in Hungarian)

Csörgő, T., Harnos, A., Rózsa, L., Karcza, Zs. & Fehérvári, P. 2016. Detailed description of the Ócsa Bird Ringing Station, Hungary. – Ornis Hungarica 24(2): 91–108. DOI: 10.1515/orhu-2016-0018

Csörgő, T. & Kováts, L. 2009. Nagy fülemüle [Thrush Nightingale]. – 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. 444–445. (in Hungarian with English Summary)

Csörgő, T. & Lövei, G. L. 1986. Nagy fülemüle *(Luscinia luscinia)* testtömeg gyarapodása őszi vonulás előtt [Premigratioy fattening of the Thrush Nightingale *(Luscinia luscinia)*]. – Magyar Madártani Egyesület II. Tudományos Ülése, Szeged. pp: 143–148. (in Hungarian with English Summary)

Csörgő, T. & Lövei, G. L. 1995. Migration and recurrence of the Thrush Nightingale *Luscinia luscinia* at a stopover site in Central Hungary. – Ardeola 42: 57–68.

Demongin, L. 2016. Identification guide to birds in the hand. – Beauregard-Vernon, p. 246.

Dittberner, H. & Dittberner, W. 1989. Alters-und Geschlechtskennzeichen beim Sprosser [Age and sex characteristics of the Thrush Nightingale]. – Falke 36: 255–259. (in German)

Dowle, M., Short, T. & Lianoglou, S. 2013. data.table: Extension of data.frame for fast indexing, fast ordered joins, fast assignment, fast grouping and list columns. – R package version 1.8.10; with contributions from Srinivasan, S., Lianoglou, A. & Saporta, R. URL: http://CRAN.R-project.org/package=data.table

Eason, P., Rabia, B. & Attum, O. 2016. Hunting of migratory birds in North Sinai, Egypt. – Bird Conservation International 26(1): 39–51. DOI: 10.1017/S0959270915000180

EURING 2015. The EURING Exchange Code 2000 Plus. – The European Union for Bird Ringing, Thetford, UK. URL: http://www.euring.org/data_and_codes/euring_code_list/index.html

Farkas, T. 1954. Der Sprosser (*Luscinia luscinia* L.) als Brutvogel in Ungarn: nebst einige Bemerkungen zu seiner Systematik [The Thrush Nightingale (*Luscinia luscinia* L.) as a breeding bird in Hungary: notes on its sistematics]. – Annales Biologicae Universitatum Hungariae (2): 57–81. (in German)

Finch, T., Butler, S. J., Franco, A. M. A. & Cresswell, W. 2017. Low migratory connectivity is common in long-distance migrant birds. – Journal of Animal Ecology 86(3): 662–673. DOI: 10.1111/1365-2656.12635

Fransson, T. & Hall-Karlsson, S. 2008. Thrush Nightingale *(Luscinia luscinia)*. – In: Svensk Ringmärkningsatlas, Vol. 3. [Swedish Bird Ringing Atlas, Vol. 3.]. – Stockholm, Naturhisto ed., pp. 62–78. (in Swedish with English Summary)

Fransson, T., Jakobsson, S. & Kullberg, C. 2005. Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover areas. – Journal of Avian Biology 36(1): 6–11. DOI: 10.1111/j.0908-8857.2005.03471.x

Gienapp, P., Leimu, R. & Merilä, J. 2007. Responses to climate change in avian migration time microevolution versus phenotypic plasticity. – Climate Research 35: 25–35. DOI: 10.3354/cr00712

Ginn, H. & Melville, D. 1983. Moult in birds. BTO Guide 19. – British Trust for Ornithology, Tring

Hadarics, T. & Zalai, T. 2008. Nomenclator avium Hungariae – Magyarország madarainak névjegyzéke [An annotated list of the birds of Hungary]. – Magyar Madártani és Természetvédelmi Egyesület, Budapest, p. 175. (in Hungarian)

Hahn, S., Korner-Nievergelt, F., Emmenegger, T., Amrhein, V., Csörgő, T., Gursoy, A., Ilieva, M., Kverek, P., Pérez-Tris, J., Pirrello, S., Roselaar, C. S., Zehtindjiev, P. & Salewski, V. 2016. Longer wings for faster springs – wing length relates to spring phenology in a long-distance migrant across its range. – Ecology and Evolution 6(1): 68–77. DOI: 10.1002/ece3.1862

Harnos, A., Csörgő, T. & Fehérvári, P. 2016. Hitchhikers' guide to analysing bird ringing data. Part 2. – Ornis Hungarica 24(1): 172–181. DOI: 10.1515/orhu-2016-0010

Harnos, A., Csörgő, T. & Fehérvári, P. 2017. Hitchhikers' guide to analysing bird ringing data. Part 3. – Ornis Hungarica 25(2): 141–156. DOI: 10.1515/orhu-2017-0020

Harnos, A., Fehérvári, P. & Csörgő, T. 2015. Hitchhikers' guide to analysing bird ringing data. Part 1. – Ornis Hungarica 23(2): 163–188. DOI: 10.1515/orhu-2015-0018

Heldbjerg, H. & Fox, T. 2008. Long-term population declines in Danish trans-Saharan migrant birds. – Bird study 55(3): 267–279. DOI: 10.1080/00063650809461532

Hildén, O. & Koskimies, P. 1984. Pesimdlinnuston kannanmuutokset Suomessa 1973–82 kyselytutkimuksen valossa [Summary: Population changes of Finnish breeding birds in 1973–82]. – Lintumies 19: 15–25. (in Finnish with English Summary)

Hogg, P., Dare, P. & Rintoul, J. 1984. Palaearctic migrants in the central Sudan. – Ibis 126(3): 307–331.

Jenni, L. & Winkler, R. 1994. Moulting and ageing of European passerines. – Academic Press, New York, p. 94.

Karlsson, L., Ehnbom, S. & Walinder, G. 2005. A comparison between ringing totals at Falsterbo, SW Sweden, ringing totals at Ottenby, SE Sweden, and point counts from the Swedish breeding bird census during 20 years (1980–1999). – Ornis Svecica 15: 183–205.

Klaassen, M., Lindström, Å. & Zijlstra, R. 1997. Composition of fuel stores and digestive limitations to fuel deposition rate in the long-distance migratory Thrush Nightingale, *Luscinia luscinia*. – Physiological Zoology 70(1): 125–133. DOI: 10.1086/639556

Klvaňa, P., Cepák, J., Munclinger, P., Michálková, R., Tomášek, O. & Albrecht, T. 2018. Around the Mediterranean: an extreme example of loop migration in a long-distance migratory passerine. – Journal of Avian Biology 49(2): jav–01595. DOI: 10.1111/jav.01595

Kováts, D. 2012. Autumn migration of the Thrush Nightingale *(Luscinia luscinia)* in northern Hungary. – Ring 34(1): 23–36. DOI: 10.2478/v10050-012-0001-4

Kováts, D. & Harnos, A. 2015. Morphological classification of conspecific birds from closely situated breeding areas – A case study of the Common Nightingale. – Ornis Hungarica 23(2): 20–30. DOI: 10.1515/orhu-2015-0011

Kováts, D., Végvári, Z. & Varga, Z. 2013. Morphological patterns of a nightingale population in a contact zone of *Luscinia megarhynchos* and *L. luscinia*. – Acta Zoologica Academiae Scientiarum Hungaricae 59(2): 157–170.

Kverek, P., Storchová, R., Reif, J. & Nachman, M. 2008. Occurrence of a hybrid between the Common Nightingale *(Luscinia megarhynchos)* and the Thrush Nightingale *(Luscinia luscinia)* in the Czech Republic confirmed by genetic analysis. – Sylvia 44: 17–26.

Marra, P. P., Francis, C. M., Mulvihill, R. S. & Moore, F. R. 2004. The influence of climate on the timing and rate of spring bird migration. – Oecologia 142(2): 307–315. DOI: 10.1007/s00442-004-1725-x

Merikallio, E. 1958. Finnish birds: their distribution and numbers. – Fauna Fennica 5: 1–181.

Miller-Rushing, A. J., Primack, R. B. & Stymeist, R. 2008. Interpreting variation in bird migration times as observed by volunteers. – The Auk 125(3): 565–573. DOI: 10.1525/auk.2008.07005

Moreau, R. E. & Dolp, R. M. 1970. Fat, water, weights and wing-lengths of autumn migrants in transit on the northwest coast of Egypt. – Ibis 112(2): 209–228. DOI: 10.1111/j.1474-919X.1970.tb00094.x

Newton, I. 2008. The ecology of bird migration. – Academic Press, London

Pearson, D. & Backhurst, G. 1976. The southward migration of Palaearctic birds over Ngulia, Kenya. – Ibis 118(1): 78–105. DOI: 10.1111/j.1474-919X.1976.tb02012.x

Pearson, D. J. & Lack, P. C. 1992. Migration patterns and habitat use by passerine and near-passerine migrant birds in eastern Africa. – Ibis 134(s1): 89–98.

R Core Team 2017. R: A Language and Environment for Statistical Computing. – R Foundation for Statistical Computing, Vienna, Austria, URL: https://www.R-project.org/

Ranoszek, E. 2001. Occurrence and habitat preferences in breeding season of the Thrush Nightingale *Luscinia luscinia* and the Nightingale *Luscinia megarhynchos* in the Barycz river valley. – Ptaki Slaska 13: 19–30. (in Polish with English Summary)

Reifová, R., Kverek, P. & Reif, J. 2011a The first record of a female hybrid between the Common Nightingale *(Luscinia megarhynchos)* and the Thrush Nightingale *(Luscinia luscinia)* in nature. – Journal of Ornithology 152(4): 1063–1068. DOI: 10.1007/s10336-011-0700-7

Reifová, R., Reif, J., Antczak, M. & Nachman, M. W. 2011b Ecological character displacement in the face of gene flow: Evidence from two species of Nightingales. – BMC Evolutionary Biology 11(1): 138. DOI: 10.1186/1471-2148-11-138

Robinson, R. A., Julliard, R. & Saracco, J. F. 2009. Constant effort: Studying avian population processes using standardised ringing. – Ringing & Migration 24(3): 199–204. DOI: 10.1080/03078698.2009.9674392

Schaub, M. & Jenni, L. 2000. Fuel deposition of three passerine bird species along the migration route. – Oecologia 122(3): 306–317. DOI: 10.1007/s004420050036

Schaub, M., Jenni, L. & Bairlein, F. 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. – Behavioral Ecology 19(3): 657–666. DOI: 10.1093/beheco/arn023

Schmidt, E. 1973. Zur Okologie des Sprossers (*Luscinia luscinia* L.) in der Theissauen bei Tiszatelek, nach seiner Ankunft im Frühling [On the ecology of the Sposser (*Luscinia luscinia* L.) in the Tisza at Tiszatelek, after spring arrival]. – Tiscia 8: 79–81.

Sorjonen, J. 1986. Mixed singing and interspecific territoriality – consequences of secondary contact of two ecologically and morphologically similar Nightingale species in Europe. – Ornis Scandinavica 17(1): 53–67. DOI: 10.2307/3676753

Spina, F. & Volponi, S. 2009. Atlante della migrazione degli uccelli in Italia, Vol. 2.: Passeriformi [Italian Bird Migration Atlas, Vol. 2.: Passeriformes]. – Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Roma (Italy) ISPRA, pp. 156–157. (in Italian with English Summary)

Stach, R., Jakobsson, S., Kullberg, C. & Fransson, T. 2012. Geolocators reveal three consecutive wintering areas in the Thrush Nightingale. – Animal Migration 1: 1–7. DOI: 10.2478/ami-2012-0001

Storchová, R., Reif, J. & Nachman, M. W. 2010. Female heterogamety and speciation: Reduced introgression of the z chromosome between two species of Nightingales. – Evolution 64(2): 456–471. DOI: 10.1111/j.1558-5646.2009.00841.x

Svensson, L. 1992. Identification Guide to European Passerines. – Ugga, Stockholm, 4th ed., pp. 110–111.

Szentendrey, G., Lövei, G. & Kállay, Gy. 1979. Az Actio Hungarica madárgyűrűző tábor mérési módszerei [Measuring methods in the bird ringing camps of Actio Hungarica]. – Állattani Közlemények 66: 161–166. (in Hungarian)

Thorup, K., Tøttrup, A. P., Willemoes, M., Klaassen, R. H., Strandberg, R., Vega, M. L., Dasari, H. P., Araújo, M. B., Wikelski, M. & Rahbek, C. 2017. Resource tracking within and across continents in long-distance bird migrants. – Science Advances 3(1): e1601360. DOI: 10.1126/sciadv.1601360

Tøttrup, A., Klaassen, R., Willemoes, M., Strandberg, R., Vardanis, Y., Lindström, Å., Rahbek, C., Alerstam, T. & Thorup, K. 2012. Drought in Africa caused delayed arrival of European songbirds. – Science 338(6112): 1307–1307. DOI: 10.1126/science.1227548

Tøttrup, A. P., Rainio, K., Coppack, T., Lehikoinen, E., Rahbek, C. & Thorup, K. 2010. Local temperature fine-tunes the timing of spring migration in birds. – Integrative and Comparative Biology 50(3): 293–304. DOI: 10.1093/icb/icq028

Tøttrup, A. P., Thorup, K. & Rahbek, C. 2006. Patterns of change in timing of spring migration in North European songbird populations. – Journal of Avian Biology 37(1): 84–92. DOI: 10.1111/j.0908-8857.2006.03391.x

Tucker, G. M. & Heath, M. F. 1994. Birds in Europe: their conservation status. – Cambridge, U.K.: BirdLife International (BirdLife Conservation Series no. 3., p. 450.

Valkama, J., Saurola, P., Lehikoinen, A., Lehikoinen, E., Piha, M., Sola, P. & Velmala, W. 2014. Suomen Rengastusatlas. Osa II. [The Finnish Bird Ringing Atlas Vol. II.]. – Finnish Museum of Natural History and Ministry of Environment, Helsinki, pp. 404–407. (in Finnish with English Summary)

Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Škorpilová, J. & Gregory, R. D. 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. – Ibis 156(1): 1–22. DOI: 10.1111/ibi.12118

Yohannes, E., Biebach, H., Nikolaus, G. & Pearson, D. J. 2009a Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa. – Journal of Avian Biology 40(2): 126–134. DOI: 10.1111/j.1600-048X.2008.04403.x

Yohannes, E., Biebach, H., Nikolaus, G. & Pearson, D. J. 2009b Passerine migration strategies and body mass variation along geographic sectors across East Africa, the Middle East and the Arabian Peninsula. – Journal of Ornithology 150(2): 369. DOI: 10.1007/s10336-008-0357-z

Zalakevicius, M., Bartkeviciene, G., Raudonikis, L. & Janulaitis, J. 2006. Spring arrival response to climate change in birds: a case study from eastern Europe. – Journal of Ornithology 147(2): 326–343.