ORNIS HUNGARICA

ISSN 1215-1610

JOURNAL OF THE BIRDLIFE HUNGARY

Ornis Hungarica 2020. 28(1): 1–10.
DOI: 10.2478/orhu-2020-0001

Results of national White Stork *(Ciconia ciconia)* census in Hungary in 2019

Péter Lovászi*, Károly Nagy & Zoltán Görögh

Received: May 19, 2020 – Revised: May 27, 2020 – Accepted: May 28, 2020

Lovászi, P., Nagy, K. & Görögh, Z. 2020. Results of national White Stork *(Ciconia ciconia)* census in Hungary in 2019. – Ornis Hungarica 28(1): 1–10. DOI: 10.2478/orhu-2020-0001

Abstract A national White Stork *(Ciconia ciconia)* census was organised in Hungary in 2019. The 14th country-wide nest count was coordinated by MME/BirdLife Hungary, also involving local branches and volunteers of the society and national park directorates.

Altogether 5,018 nests and 2,358 White Stork nest holders without nest material were reported. 89.2% of occupied nests were built on electric poles. Although 80 years ago every third nests were found on trees, in 2019, only 6 were reported at that location. Successful pairs raised 2.62 nestlings on average, breeding success for all breeding pairs was 2.19, which is lower than typical, probably due to chilly and rainy weather during the breeding season. Based on 3,540 reported breeding pairs and former census data, the White Stork population of Hungary is estimated to be 3,860–4,020 pairs in 2019. The size of the population was ca. 15–16 thousand pairs in 1941, which halved by 1958 and decreased to 5 thousand pairs by the late 1960s. For four decades, the population fluctuated between 4,800 and 5,500 pairs but in the last twenty years, the number of breeding pairs slightly decreased in the country. The population decline is stronger in hilly areas of W Hungary, i.e. in Somogy, Vas and Zala counties is about 60%.

Keywords: White Stork, national census, breeding population, decrease

Összefoglalás 2019-ben zajlott le a 14. országos fehér gólya felmérés, amelyet a Magyar Madártani és Természetvédelmi Egyesület (MME) szervezett a helyi csoportjai és egyes nemzetipark-igazgatóságok bevonásával. Összesen 5018 fészekről és 2358 fészekanyag nélküli üres fészektartóról küldtek jelentést a felmérők. A fészkek többsége (89,2%) villanyoszlopon épült. Bár nyolcvan éve még a fészkek harmada fán volt, 2019-ben már csak 6 db lakott fészket találtak ilyen helyen. Az átlagos fiókaszám az összes költőpárra számolva 2,19, a sikeres párokra számolva 2,62 volt. Ez a jellemző értéknél alacsonyabb költési siker valószínűleg a hűvös, esős május-júniusi időjárásnak köszönhető.

A jelentésekben szereplő 3540 fészkelő pár és a korábbi cenzusok adatainak összevetésével a teljes hazai költőállományt 3860–4020 pár közé becsüljük. Az állomány 1941-ben 15–16 000 pár lehetett, ami 1958-ra megfeleződött, az 1960-as évek végére pedig még tovább, 5000 pár körülire csökkent. Négy évtizedig 4800 és 5500 pár között fluktuált a fészkelő párok száma, de az elmúlt két évtizedben ismét csökkenést tapasztalhattunk. Ez a csökkenés Nyugat-Magyarország dombvidékein, Somogy, Vas és Zala megyében a legerősebb, akár 60% is lehet.

Kulcsszavak: fehér gólya, országos felmérés, költőállomány, csökkenés

MME/BirdLife Hungary 1121 Budapest, Költő utca 21., Hungary
**corresponding author, e-mail: lovaszi.peter@mme.hu*

Introduction

The 14th national White Stork *(Ciconia ciconia)* census was organised in Hungary after 1941, 1958, 1963, 1968, 1974, 1979, 1984, 1989, 1994, 1999, 2004, 2009 and 2014. Former national census results were published by Homonnay (1964), Marián (1962, 1968, 1971), Jakab (1978, 1985, 1987, 1991), Lovászi (1998, 2004) and Lovászi *et al.* (2013, 2016). The White Stork population was estimated to be 15–16 thousand pairs in 1941, which halved by 1958. After a further decrease the population stabilized by the late 1960s and fluctuated between 4,800 and 5,500 pairs. At the last census (2014), we found 4,750–4,950 breeding pairs but strong decrease was detected in West Hungary. Results of regional censuses in the intervening years suggest that this decline is a long-term process and not only a fluctuation of the population as in the last decades. A country-wide nest count was able to answer if the population still stable (fluctuating) or decreasing in total.

Materials and methods

The census was organised by MME/BirdLife Hungary involving volunteers and national park directorate workers. Nest count was locally organised by county level coordinators, mainly local MME/BirdLife Hungary Groups.

Participants collected the following data of nests and nesting sites: locality (settlement, address, coordinates), nest features (nest holder base, type of electric pole, thickness of the nest, existence and condition of nest holder), occupancy, breeding success (number of nestlings), other information (dangerous electric poles, mortality cases, remarks).

Data were uploaded to the online stork database of MME Monitoring Centre (www.golya.mme.hu).

Data were summarized for counties and settlements. As we had no data for all settlements, missing values were imputed for each settlement to estimate the whole population, based on former census data of given settlement and regional trends.

Results

The online White Stork database included 12,963 nesting places (nests and metal nest-holders without nest material) at 23rd of February 2020, from which 1,869 was eliminated before 2019, 89 in 2019. The remaining 11,005 locality included 3,907 nesting places (metal nest holder facility) without nest material and 7,098 nests. Data were sent on 2,358 nesting places and 5,018 nests.

Most of the nests were occupied on electric poles (83.7%) or other poles independent from the electric network (8.8%). Buildings held 6.2% of nests, trees only 0.2% and other sites 0.9% *(Figure 1, Table 1)*. Other sites were concrete wall (1), wood pile (1), well-pole (1), loudspeaker pole (1), church (1), castle ruin (1), water tank (1), ventilation chimney (2), aviary (4), grain silo (6), and siren pole (12).

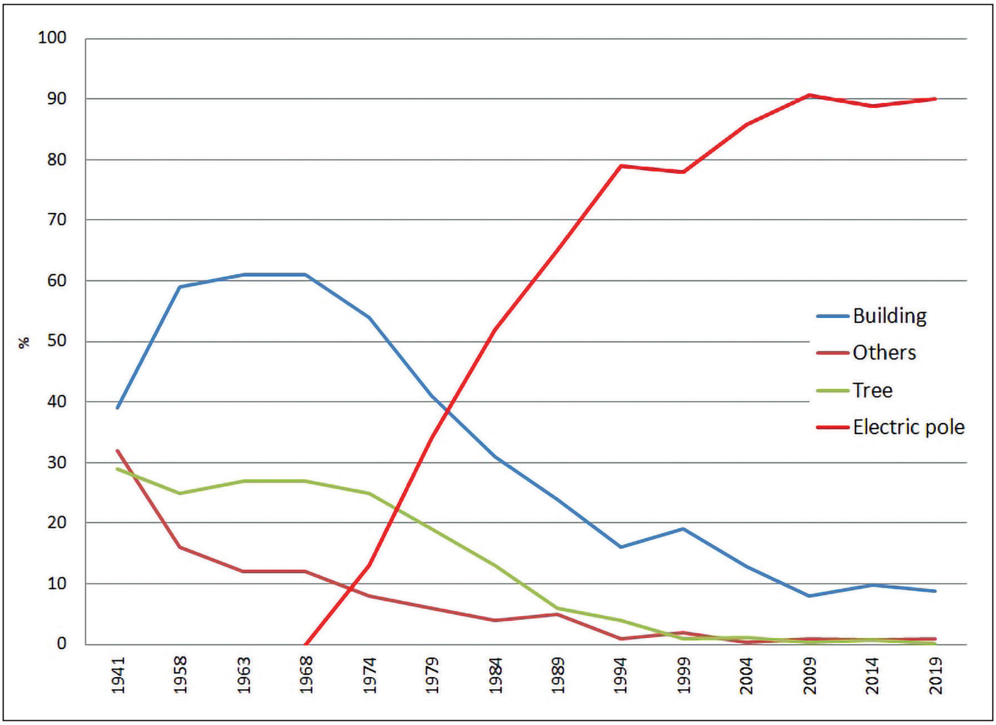


Figure 1. Changes of White Stork nest basements, 1941–2019
1. ábra Fészekaljzatok változása, 1941–2019

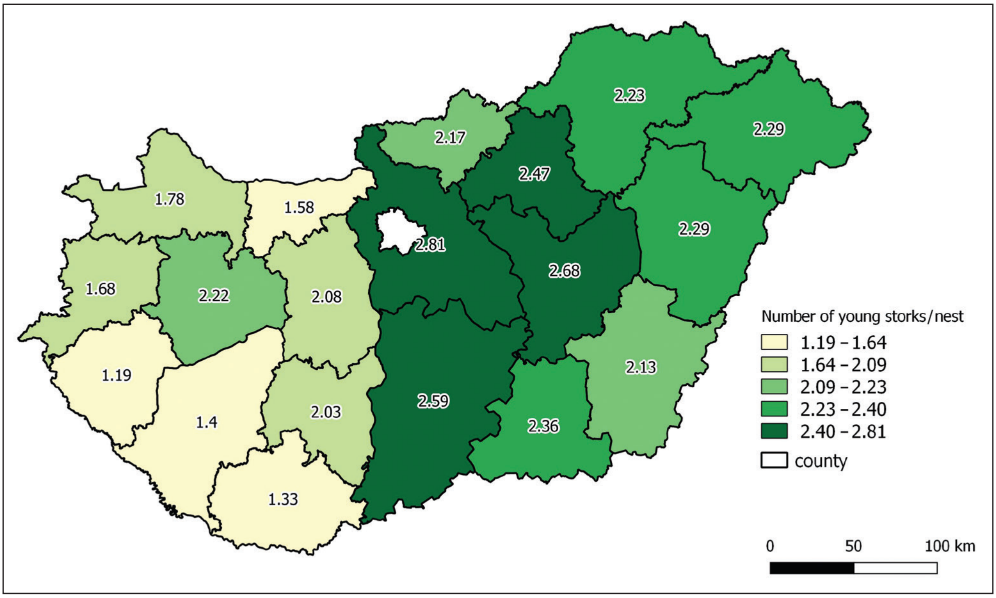


Figure 2. Average number of nestlings/nest (JZa) in counties
2. ábra Átlagos fészkenkénti fiókaszám megyénkénti megoszlása

Table 1. Reported nest basements: occupied nests (unoccupied nests)
1. táblázat Lejelentett fészekaljzatok megoszlása: foglalt fészkek (lakatlan fészkek)

County	Electric pole without holder	El. pole with nest holder	El. pole (nest holder unk.)	Other pole, pylon	Building (roof, chimney, tower)	Factory chimney, boiler house chimney	Water tower	Tree	Others	Total	Total
Bács-Kiskun	51 (11)	215 (44)	6 (1)	22 (8)	13 (6)	9 (1)	2 (1)	2 (-)	2 (-)	322 (72)	394
Baranya	21 (5)	131 (31)	3 (2)	5 (3)	11 (4)	15 (2)	- (-)	- (-)	4 (1)	190 (48)	238
Békés	22 (17)	175 (101)	- (-)	7 (4)	14 (4)	51 (9)	- (1)	- (1)	1 (1)	270 (138)	408
Borsod-Abaúj-Zemplén	43 (38)	343 (219)	3 (-)	16 (9)	10 (7)	15 (12)	- (-)	- (1)	- (-)	430 (286)	716
Csongrád	61 (15)	154 (55)	4 (2)	15 (9)	6 (4)	12 (2)	1 (-)	- (-)	1 (3)	254 (90)	344
Fejér	9 (3)	79 (31)	1 (-)	21 (16)	3 (-)	6 (1)	- (-)	- (-)	1 (1)	120 (52)	172
Győr-Moson-Sopron	22 (5)	85 (22)	3 (-)	10 (0)	12 (-)	10 (1)	- (-)	- (-)	3 (-)	145 (28)	173
Hajdú-Bihar	26 (12)	512 (156)	1 (-)	28 (12)	9 (2)	17 (4)	1 (1)	2 (-)	7 (2)	603 (189)	792
Heves	1 (-)	15 (-)	- (-)	1 (-)	- (-)	- (-)	1 (-)	- (-)	1 (-)	19 (-)	19
Jász-Nagykun-Szolnok	24 (9)	115 (44)	3 (-)	5 (7)	4 (2)	17 (1)	1 (1)	1 (3)	6 (1)	176 (68)	244
Komárom-Esztergom	4 (2)	14 (5)	- (-)	- (5)	1 (-)	1 (1)	- (-)	- (-)	- (-)	20 (13)	33
Nógrád	2 (9)	53 (8)	- (-)	6 (2)	- (-)	10 (2)	- (-)	- (-)	2 (-)	73 (21)	94
Pest	18 (12)	45 (16)	- (1)	4 (4)	4 (4)	2 (-)	3 (-)	- (-)	- (-)	76 (37)	113
Somogy	3 (3)	16 (11)	- (-)	1 (-)	- (-)	1 (-)	- (-)	- (-)	1 (-)	22 (14)	36
Szabolcs-Szatmár-Bereg	62 (14)	358 (86)	1 (1)	30 (18)	9 (5)	2 (1)	1 (-)	1 (-)	3 (-)	467 (125)	592
Tolna	20 (11)	56 (42)	4 (3)	11 (12)	6 (3)	3 (-)	1 (-)	- (-)	1 (1)	102 (72)	174
Vas	12 (4)	78 (41)	- (-)	19 (9)	14 (13)	9 (4)	- (-)	- (-)	- (-)	132 (71)	203
Veszprém	10 (4)	74 (32)	1 (-)	6 (5)	8 (2)	2 (-)	- (-)	- (-)	- (1)	101 (44)	145
Zala	13 (3)	76 (20)	1 (1)	9 (3)	- (-)	1 (-)	- (-)	- (-)	- (1)	100 (28)	128
Total	424 (177)	2594 (964)	31 (11)	216 (126)	124 (56)	183 (41)	11 (4)	6 (5)	33 (12)	3622 (1396)	5018
Total	601	3558	42	342	180	224	15	11	45	5018	

Table 2. Breeding results (HO: unoccupied nest, HE: lonely stork, HPo: unsuccessful pair without fledged nestling, HPm: successful pair, HPa: all breeding pairs)

2. táblázat Költési eredmények (HO: lakatlan fészek, HE: magányos gólya, HPo: sikertelen pár kirepült fióka nélkül, HPm: sikeres pár, HPa: összes költőpár)

County	**Empty nest holder**	**Nest attempt**	**HO**	**HE**	**HPo**	**HPm**	**HPa – reported**	**HPa – total estimated**
Bács-Kiskun	44	3	69	6	39	277	316	346–366
Baranya			48	3	74	113	187	187
Békés	27		138	7	49	214	263	263
Borsod-Abaúj-Zemplén	393	26	260	4	83	343	426	470–500
Csongrád	102	2	88	6	36	212	248	248
Fejér	126		52	1	19	100	119	119
Győr-Moson-Sopron	5		28	4	39	102	141	141
Hajdú-Bihar	611	3	186	22	40	541	581	589–610
Heves					1	18	19	60–90
Jász-Nagykun-Szolnok	146	5	63	2	15	159	174	220–270
Komárom-Esztergom	1		13	1	6	13	19	19
Nógrád	132	17	4	1	12	60	72	72
Pest	37	5	32	1	8	67	75	105–115
Somogy	14	5	9	2	8	12	20	120–200
Szabolcs-Szatmár-Bereg	455	7	118	8	72	387	459	489–494
Tolna	54		72	2	19	81	100	100
Vas	174		71	2	32	98	130	130–135
Veszprém	31		44	6	12	83	95	95
Zala	6		28	4	24	72	96	134–160
Total	**2358**	**73**	**1323**	**82**	**588**	**2952**	**3540**	**3907–4184**

Out of the 5,018 reported nest, there were 73 nest attempt (1.5%), 1,323 unoccupied nests (26.4%), 82 lonely White Stork (1.6%), 588 unsuccessful pairs (11.7%) and 2,952 successful pairs with nestlings (58.8%) *(Table 2)*.

Successful pairs typically raised 3 or 4 nestlings. Breeding success was 2.19, calculated for all pairs, 2.62 for successful pairs *(Table 3)*. Breeding success varied between 1.19 and 2.81 in certain counties *(Figure 2)*.

Most White Storks bred in NE Hungary (Borsod-Abaúj-Zemplén, Hajdú-Bihar and Szabolcs-Szatmár-Bereg counties), 1,550–1,600 pairs, which is about 40% of the country's population. The density is the highest near rivers (especially in the Upper Tisza valley) and around large wet or saline grasslands (like Hortobágy). White Storks do not breed in mountain areas (ca. 500 m above sea level), in the Budapest agglomeration and large monocultural plough lands *(Figure 3)*.

Table 3. Breeding success (JZG: total number of nestlings fledged, JZa:average number of nestlings for all nests, JZm: average number of nestlings for successful nests)

3. táblázat Költési siker (JZG: kirepült fiókák száma, JZa: összes költőpár fészkenkénti fiókaátlaga, JZm: sikeres párok fészkenkénti fiókaátlaga)

County	**Number of nestlings**					**JZG**	**JZa**	**JZm**
	1	**2**	**3**	**4**	**5**			
Bács-Kiskun	15	56	127	69	7	819	2.59	2.96
Baranya	34	34	33	12	-	249	1.33	2.20
Békés	32	63	68	48	1	559	2.13	2.61
Borsod-Abaúj-Zemplén	38	93	125	77	9	952	2.23	2.78
Csongrád	13	42	101	40	5	585	2.36	2.76
Fejér	13	31	44	10	-	247	2.08	2.47
Győr-Moson-Sopron	15	37	38	12	-	251	1.78	2.46
Hajdú-Bihar	22	82	146	154	18	1330	2.29	2.46
Heves	3	4	8	3	-	47	2.47	2.61
Jász-Nagykun-Szolnok	12	33	64	39	8	466	2.68	2.93
Komárom-Esztergom	3	4	5	1	-	30	1.58	2.31
Nógrád	10	18	18	14	-	156	2.17	2.60
Pest	2	10	31	19	4	211	2.81	3.15
Somogy	2	5	4	1	-	28	1.40	2.33
Szabolcs-Szatmár-Bereg	56	95	142	84	9	1053	2.29	2.72
Tolna	15	23	30	13	-	203	2.03	2.51
Vas	19	45	28	4	2	219	1.68	2.23
Veszprém	7	31	36	6	2	211	2.22	2.54
Zala	12	23	16	2	-	114	1.19	1.58
Total Hungary	**323**	**729**	**1064**	**608**	**65**	**7730**	**2.19**	**2.62**

More than 20 pairs occupied nest in Nádudvar (33), Hortobágy (30), Komádi (28), Egyek (27), Görbeháza (27), Berettyóújfalu (25), Sárospatak (25), Akasztó (24), Balmazújváros (24), Mezőcsát (23), Nagyiván (22), Szeghalom (21) settlements *(Figure 4)*.

Unlike Poland, where White Storks breed mainly in settlements with less than 100 thousand inhabitants (Kopij 2017), in Hungary, several cities has considerable population, like Nyíregyháza (12), Szeged (11) and Debrecen (10) cities. However, aggregation of White Storks around landfills reported from several countries (e.g. Bialas *et al.* 2020) was not reported yet from Hungary.

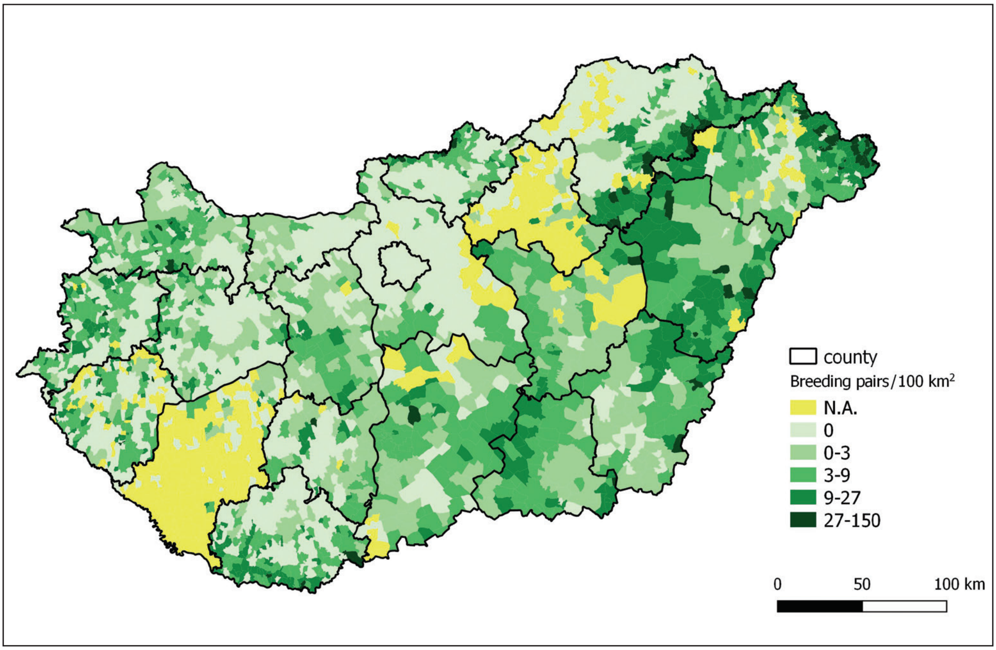


Figure 3. Density of breeding pairs for settlement's administrative boundaries (pair/100 km^2)
3. ábra Költőpárok sűrűsége település közigazgatási határonként (pár/100 km^2)

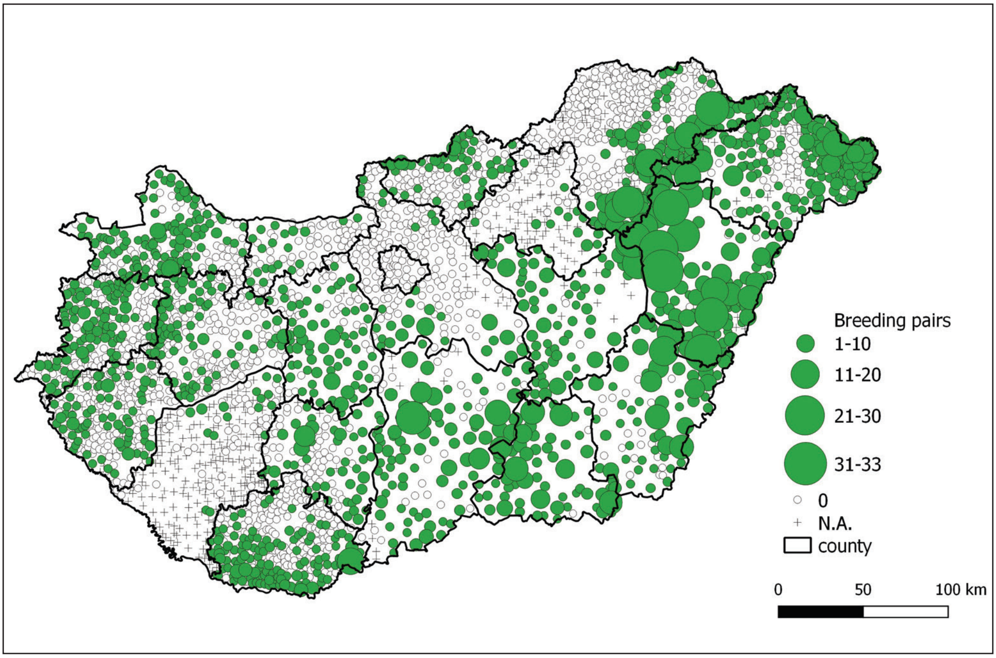


Figure 4. Number of breeding pairs in settlements
4. ábra Költőpárok száma településenként

Discussion

Breeding sites

First White Stork nests placed to electric poles were reported in 1968. Occupation of new nesting basement took place at the same rate in different parts of the country (Gyalus *et al.* 2018). By 1994, altogether 79% of nests were found on electric network or other pylons and it was amounted to a maximum of 90.6% in 2009. Almost the same number of nests were found on buildings and other places in the last 15 years but trees seems disappearing: while every 3rd nest were built on trees in the 1940s (Homonnay 1964), in 2019, only 6 were occupied by White Storks.

Breeding success

Breeding success varied between 1.58 and 3.09 since 1958 on a country-wide level, average was 2.34 nestlings for all breeding pairs. In 2019, only 2.19 young White Stork fledged from a nest on average due to frequent rains and colder temperature in May and June. The number of nestlings were lower in W Hungary (Baranya, Győr-Moson-Sopron, Komárom-Esztergom, Vas, Zala counties), where population loss is the highest. As new breeder, young birds tend to settle in the vicinity of their natal site (Chernetsov *et al.* 2006), further regional shrinking may occur.

Population changes

Although the eastern core populations (Poland, the Baltic States, Belarus, Ukraine) of White Storks counted more than 90 thousand and the southern (Iberian) population was 20 thousand breeding pairs in 2004 (Thomsen 2013), the much smaller Hungarian population is also a considerable part of the population of the species. The national population – similarly to other areas – suffered a significant loss in the 20th century.

The breeding site and habitat selection of the White Stork depends on suitable nest basements and feeding areas. The density is negatively influenced by several factors, like elevation, cover of shrublands and forests, and positively influenced by the presence of wetlands, grasslands, number of grazing animals (Carrascal *et al.* 1993, Wojciechowski & Janiszewski 2006, Tryjanowski *et al.* 2009, Radovic *et al.* 2015). In Hungary due to loss of traditional nest sites (wide chimneys, old trees, traditional hay stacks), loss and degradation of feeding sites (plowing grasslands, drainage, intensification), decrease of the population was caused. The decline of the population stopped when birds started to use electric poles as nesting sites (Lovászi 2013). From the 1970s, nature conservation and electric companies mounted hundreds of metal nest holders onto electric poles. As a result of this controversial help, 90% of White Storks mowed to electric poles. As standards of wiring change nowadays, new networks are built of isolated single cables instead of parallel uninsulated metal wires and older ones are also under change to following new standard, White Storks cannot built (or much more less) new nests to electric poles what can lead to further loss of pairs.

We do not know effect of climate change on breeding success. Weather of the Carpathian basin is influenced by Mediterranean, Atlantic and Continental climate zones, causing very variable temperature and rainfall distribution between years and seasons. Annual rainfall varies between about 400 and 800 mm, decreasing by 10% in the last hundred years (OMSZ 2020). These changes are unfavourable as White Storks primarily use wet or temporary wet grasslands, marshes. The national park directorates made several small and medium scale wetland revitalisations but these habitats hold only a small proportion of the population.

Above mentioned changes may adumbrate further loss of breeding White Stork population of Hungary. Unfortunately, actual population data are not available on international level. Latest reporting under Article 12 of the EU's Birds Directive provides national data from the 2008–2012 period (https://www.eionet.europa.eu/etcs/etc-bd/activities/reporting/article-12/art-12-reporting-2008-2012), also reporting decreasing population in neighbouring Austria and Slovakia.

Acknowledgements

In the last years, several hundreds of professional conservationists and volunteer birdwatchers, organisations uploaded data to MME's White Stork database. It is impossible to mention all of them but we thank for all the help of them. Regional coordinators were or large amount of nests were reported by Péter Balázsi, László Bank, Gellért Bátky, Szabolcs Gál, Zoltán Görögh, Előd Győrig, Béla Habarics, Attila Hankóczi, Péter Homoki, Péter Hunyadvári, Balázs Forgách, Tibor Juhász, András Kóta, Csaba Lendvai, Péter Lovászi, Károly Nagy, Sándor Nagy, Ferenc Papp, Ferenc Polyák, József Serfőző, István Staudinger, Ernő Szelle, Ottó Veszelinov and Hortobágy National Park Directorate and Kiskunsági National Park Directorate.

References

Bialas, J. T., Dylewski, Ł. & Tobolka, M. 2020. Determination of nest occupation and breeding effect of the White Stork by human-mediated landscape in Western Poland. – Environmental Science and Pollution Research 27: 4148–4158. DOI: 10.1007/s11356-019-06639-0

Carrascal, L. M., Bautista, L. M. & Lázaro, E. 1993. Geographical variation in the density of the White Stork *Ciconia ciconia* in Spain: Influence of habitat and climate. – Biological Conservation 65: 83–87. DOI: 10.1016/0006-3207(93)90200-K

Chernetsov, N., Chromik, W., Dolata, P. T., Profus, P. & Tryjanowski, P. 2006. Sex-related natal dispersal of White Storks *(Ciconia ciconia)* in Poland: How far and where to? – The Auk 123(4): 1103–1109. DOI: 10.1093/auk/123.4.1103

Gyalus, A., Végvári, Zs. & Csörgő, T. 2018. Changes in the nest sites of White Stork *(Ciconia ciconia)* in Hungary. – Ornis Hungarica 26(1): 65–88. DOI: 10.1515/orhu-2018-0005

Homonnay, N. 1964. Magyarország és környező területei gólyaállományának mennyiségi felvételezése az 1941. évben [Results of White Stork census in Hungary and surrounding territories in 1941]. – Aquila 69–70: 83–102. (in Hungarian)

Jakab, B. 1978. Magyarország gólyaállományának 1974. évi felmérése [Census of White Stork population of Hungary in 1974.]. – Móra Ferenc Múzeum Évkönyve 1976/77(1): 495–534. (in Hungarian)

Jakab, B. 1985. A gólya populációdinamikájának két évtizede az 1979. évi felmérés eredményeinek tükrében Magyarországon [Population dynamics of two decades of White Storks in the light of census in 1979.]. – Móra Ferenc Múzeum Évkönyve 1982–83(1): 413–451. (in Hungarian)

Jakab, B. 1987. A fehér gólya állománya Magyarországon 1984-ben [Population of the White Stork in Hungary in 1984]. – Móra Ferenc Múzeum Évkönyve 1987(1): 473–512. (in Hungarian)

Jakab, B. 1991. Az 1989. évi gólyaszámlálás értékelése [Evaluation of the White Stork Census in 1989]. – Madártani Tájékoztató 1991(1–2): 3–4. (in Hungarian).

Kopij, G. 2017. Changes in the number of nesting pairs and breeding success of the White Stork *Ciconia ciconia* in a large city and a neighbouring rural area in South-West Poland. – Ornis Hungarica 25(2): 109–115. DOI: 10.1515/orhu-2017-0018

Lovászi, P. 1998. A fehér gólya *Ciconia ciconia* helyzete Magyarországon az 1941–1994 közötti országos állományfelmérések tükrében [Status of the White Stork (*Ciconia ciconia)* in Hungary: results of national censuses between 1941–1994]. – Ornis Hungarica 8(Suppl.1): 1–8. (in Hungarian with English Summary)

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

Lovászi, P., Nagy, K. & Lendvai, Cs. 2013. Results of the White Stork *Ciconia ciconia* census in Hungary in 2004. – In: Thomsen, K-M. & Lachman, L. (eds.) White Stork populations across the world. – Results of the 6th International White Stork census 2004/2005. NABU, Berlin, pp. 25–26.

Lovászi, P., Lendvai, Cs. & Nagy, K. 2016. Results of the 2014 national White Stork *Ciconia ciconia* census in Hungary. – Aquila 122–123: 47–56.

Lovászi, P. 2013. Fehér gólya *Ciconia ciconia* fajmegőrzési terv [White Stork *Ciconia ciconia* Species Action Plan]. – VM Környezetügyért Felelős Államtitkárság, Budapest (in Hungarian)

Marián, M. 1962. Der Weißstorch in Ungarn in dem Jahre 1956–1958. [The White Stork in Hungary between 1956–1958]. – Móra Ferenc Múzeum Évkönyve 1960(2): 231–269. (in German)

Marián, M. 1968. Bestandsveranderung beim Weiss-storch in Ungarn 1958–1963 [Change of population of the White Stork in Hungary 1958–1963]. – Móra Ferenc Múzeum Évkönyve 1968: 283–314. (in German)

Marián, M. 1971. A gólya populáció-dinamikája Magyarországon 1963–1968. [Population dynamics of the White Stork in Hungary 1963–1968]. – Móra Ferenc Múzeum Évkönyve 1971(1): 37–72. (in Hungarian with German Summary)

OMSZ 2020 Magyarország csapadék viszonyai [Precipitation conditions in Hungary]. – https://www.met.hu/eghajlat/magyarorszag_eghajlata/altalanos_eghajlati_jellemzes/csapadek/ (Accessed on 28 April 2020) (in Hungarian)

Radovic, A., Kati, V., Tadic, M. P., Denac, D. & Kotrosan, D. 2015. Modelling the spatial distribution of White Stork *Ciconia ciconia* breeding populations in Southeast Europe. – Bird Study 2014: 1–9. DOI: 10.1080/00063657.2014.981502

Thomsen, M-K. 2013. Results of the 6th International White Stork Census 2004/2005. – In: Thomsen, K-M. & Lachman, L. (eds.) White Stork populations across the world. – Results of the 6th International White Stork Census 2004/2005. NABU, Berlin, pp. 25–26.

Tryjanowski, P., Leszek, J. & Radkiewicz, J. 2009. 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.

Wojciechowski, Z. & Janiszewski, T. 2006. The effect of biotopic conditions on the density of a White Stork population in Central 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

Ornis Hungarica 2020. 28(1): 11–27.
DOI: 10.2478/orhu-2020-0002

A population study of tropical Peregrine Falcons *(Falco peregrinus ernesti)* in West Malaysia

Beng Yean Ooi[1], Marc Kéry[2], Robert Percival[3], Zan Hui Lee[4] & Sein Chiong Chiu[5]

Received: February 29, 2020 – Revised: March 20, 2020 – Accepted: March 21, 2020

Ooi, B. Y., Kéry, M., Percival, R., Lee, Z. H. & Chiu, S. C. 2020. A population study of tropical Peregrine Falcons *(Falco peregrinus ernesti)* in West Malaysia. – Ornis Hungarica 28(1): 11–27. DOI: 10.2478/orhu-2020-0002

Abstract The Peregrine Falcon *(Falco peregrinus)* is the most widely distributed bird species in the world, but very little is known about its tropical populations, where even very basic information (e.g. about population density) is mostly lacking. In January 2017, 2018 and 2019, we conducted three intensive surveys amounting to 27 days and 5,400 km driven by car in West Malaysia at latitudes between 3 and 7 °N, where the *ernesti* subspecies was confirmed to be a resident breeder only as recently as 1996. Here, we summarize our findings and combine them in a synthesis that includes all published and unpublished records of nesting peregrines that we could obtain in that area. In particular, we draw on the foundational work conducted by our late colleague Laurent Molard in 2003–2005. We give information about breeding habitats, local density, behavior and breeding phenology. We also describe and discuss our use of call playback during the surveys. Much more extensive reports for each survey, with plenty of photographs of all sites visited, are available upon request from the authors.

According to current knowledge, Peregrines in West Malaysia nest mainly in cliffs, with some nesters on buildings exceptionally found (in Kuala Lumpur and suspected also elsewhere in cities) and possibly on large towers. Virtually all natural nesting places are limestone mountains with vertical cliffs. Owing to the mostly flat terrain in West Malaysia, with limestone cliffs only occurring very locally, the peregrine breeding distribution is extremely patchy. We found local aggregations in the regions of Ipoh (Perak), Gua Musang (Kelantan) and in the state of Perlis. However, local density is fairly low even in these hotspots, with nearest-neighbor distances in the densest cluster ranging from 3.7–5.6 km (mean 4.7). Overall, by the end of 2019, 36 occupied sites had been found in West Malaysia, of which 10 were known before 2003, 9 were found during the surveys by Molard and his colleagues in 2003–2005, and 17 were new discoveries during our surveys in 2017–2019. In West Malaysia, the start of egg-laying appears to be late January and early February. We found playback of the 'eee-chup' courtship calls to be extremely helpful when locating pairs. Playing a 26-sec sequence twice enticed the majority of birds to become airborne and/or to call, which greatly increased their detection probability and therefore survey success.

In spite of the great increase in the number of known peregrine sites owing to our surveys, the currently known number of pairs is still considerably lower than the estimate by Molard *et al.* (2007) of 70–80 pairs. Although this latter may perhaps be a slight overestimate, we are convinced that many more pairs remain to be discovered in cliffs, where most of the future survey effort should be concentrated. This will then also provide the basic knowledge required to protect limestone outcrop sites, e.g. from quarrying activities, which may destroy entire limestone hills. However, we believe that the major uncertainty about the size of the population of nesting *F. p. ernesti* in Malaysia arguably comes from the population segment of nesters on buildings, which is likely underestimated and hard to survey and even discover in the first place. Moreover, given the rate of increase of nesters on buildings in other parts of the world, it is likely that the proportion of pairs nesting on buildings will increase also in Malaysia. Hence, we believe that new pairs will be discovered in the future also where there were none in earlier years.

Keywords: breeding density, *Falco peregrinus ernesti*, Malaysia, Peregrine Falcon, population density, tropics

Összefoglalás A vándorsólyom *(Falco peregrinus)* a világ legelterjedtebb madárfaja, azonban nagyon keveset tudunk a trópusokon élő populációiról, sokszor még az alapvető információkkal (pl. állománysűrűség) sem rendelkezünk. 2017-ben, 2018-ban és 2019 januárjában három felmérést végeztünk, amelyek során 27 napon át 5400 kilométert tettünk meg Nyugat-Malajziában, az északi szélesség 3° és 7°-a között, ahonnan az *F. p. ernesti* alfaj csak 1996-ban lett leírva, mint állandó fészkelő faj. Jelen cikkben összegezzük az eredményeket, egyúttal bemutatjuk az általunk fellelt, a területen fészkelő vándorsólyom párokról publikált, és eddig még nem közölt adatokat, különös tekintettel néhai munkatársunk, Laurent Molard 2003–2005 között végzett munkájára. Bemutatjuk a fészkelésre használt élőhelyeket, a helyi állománysűrűség, viselkedés és költésfenológia adatokat. Ismertetjük és tárgyaljuk továbbá a felmérésekhez használt hanglejátszási módszert. Kérésre a szerzők jóval részletesebb leírást tudnak adni az egyes években végzett felmérésekről, sok fényképpel kiegészítve.

A jelenleg rendelkezésre álló információk alapján Nyugat-Malajziában a vándorsólymok jellemzően sziklafalakon, kivételes esetben épületeken (Kuala Lumpurban és feltehetően más városokban is) és valószínűleg magas tornyokon fészkelnek. Az összes természetes fészkelőhely mészkőhegységek függőleges sziklafalain található. Mivel Nyugat-Malajzia alapvetően sík, és a mészkőhegyek elszórtan találhatók, a fészkelő vándorsólyom párok elterjedése meglehetősen szigetszerű. Kisebb helyi fészkelőpár-csoportosulásokat találtunk Ipoh (Perak), Gua Musang (Kelantan) régiókban és Perlis államban. A helyi állomány sűrűsége azonban még ezeken a helyeken is alacsony, a legsűrűbb állományokban is, a legközelebbi szomszédtól való távolság 3,7–5,6 km (átlagosan 4,7 km). Összességében 2019 végéig 36 aktív revírt találtunk Nyugat-Malajziában, amelyből 2003 előtt tíz volt ismert, kilencet Molard és kollégái találtak a 2003–2005-ös felmérés során, 17 revírt pedig a mostani 2017–2019-es kutatásaink során fedeztünk fel.

Nyugat-Malajziában a tojásrakás kezdete január vége – február eleje. A vándorsólyom nászrepülési időszakban hallatott „í-csup” hívóhangjának lejátszását különösen hasznosnak találtuk a fészkelő párok keresése közben. Egy 26 másodperces hangfelvétel kétszer ismételt lejátszása a madarak többségét arra késztette, hogy a levegőbe emelkedjen, ezzel jelentősen növelve a felderítés sikerét.

Annak ellenére, hogy kutatásaink eredményeképpen jelentősen nőtt az ismert párok száma, a jelenleg ismert állomány nagysága lényegesen elmarad Molard és munkatársai (2007-es) becslésétől, amely 70–80 párra teszi a párok számát. Bár ez a becslés kissé túlzónak tűnik, meg vagyunk győződve arról, hogy sok fészkelő pár vár felfedezésre a sziklafalakon, amelyekre a jövőbeni kutatásoknak összepontosítaniuk kell. Ez utóbbiak azokat az alapvető információkat is meg fogják adni, amelyekre a mészkő-sziklafalak – például az egész mészkőhegyeket eltüntető mészkő-bányászat elleni – védelméhez szükség van. Úgy véljük azonban, hogy az állománynagyság becslésében a legnagyobb bizonytalanságot az épületeken fészkelő párok okozzák, amelyek száma valószínűleg alulbecsült, és amely párok számát rendkívül nehéz felmérni, vagy egyáltalán felfedezni őket. Emellett, figyelembe véve az épületen fészkelő párok számának növekedési ütemét a világ más részein, valószínű, hogy az épületen fészkelő párok aránya Malajziában is emelkedni fog. Úgy véljük ezért, hogy a jövőben olyan helyeken is meg fognak jelenni új párok, ahol eddig nem voltak jelen.

Kulcsszavak: fészkelő állomány sűrűsége, *Falco peregrinus ernesti*, Malajzia, vándorsólyom, állománysűrűség, trópusok

[1] *182, Jalan Raja Kam, Taman Canning, 31400 Ipoh, Negeri Perak, Malaysia (†)*

[2*] *Swiss Ornithological Institute, 6204 Sempach, Switzerland (marc.kery@vogelwarte.ch)*

[3] *1, Lintasan Taman Tambun, 31400, Ipoh, Perak, Malaysia (robert.pval@gmail.com)*

[4] *School of Environmental and Geographical Sciences, University of Nottingham Malaysia, Semenyih, Malaysia (zanhui96@gmail.com)*

[5] *43, Lorong Gopeng, Taman Golf.31350, Ipoh, Perak, Malaysia (chiusch@gmail.com)*

** corresponding author*

Introduction

Despite a large number of population studies dedicated to the Peregrine Falcon *(Falco peregrinus)*, extremely little is known about this fascinating species in the tropical parts of its worldwide breeding distribution, which comprises parts of tropical South America, Africa and Madagascar, India, Sri Lanka, South-East Asia and Australia (White *et al.* 2013). Only a small handful of studies on tropical peregrines have been published, but even very basic information about distribution, population density and fecundity (i.e. some of the most commonly recorded quantities in raptor population studies) is for the most part lacking for these truly vast areas. Some exceptions include Kéry (2002), who summarized the known distribution for *F. p. cassini* in Peru, and then especially Hermann Döttlinger's studies of *F. p. peregrinator* in Sri Lanka (Döttlinger & Hoffmann 1999, Döttlinger *et al.* 1999, Döttlinger 2002, Döttlinger & Nichols 2005). Laurent Molard and his colleagues (2005, 2007 and 2009) report on their studies in West, i.e. mainland, Malaysia, and describe the known distribution and breeding phenology of *F. p. ernesti*, the darkest peregrine subspecies in the world *(Figure 1)*.

The *F. p. ernesti* subspecies has been known to nest in Malaysia from a single instance of confirmed breeding in 1996 (Chong 2002), although other observations of pairs during the breeding season at two sites in the Kuala Lumpur metropolitan area made breeding likely already during the 1980s. Further confirmed breeding records were then obtained just after the turn of the century (Molard 2005, Chiu *et al.* 2006). The first synthetic overview of the knowledge on breeding peregrines in Malaysia was the unpublished report compiled by Molard (2005). It contained information that was collected by Laurent Molard and was augmented with observations from his colleagues and with information gleaned from the published literature. Molard's 2005 report lists 15 sites in the states of Selangor, Pahang and especially in the Ipoh area of Perak. Based on this information and including later observations, Molard *et al.* (2007) then went on to make an educated guess of the possible number of peregrine breeding pairs in the 135,000 km^2 of West Malaysia and arrived at 70–80 pairs, essentially in the centre and north of the country (see also Molard 2009). Based on the known or suspected 24 territories and that projection, a density of only 0.02–0.06 pairs per 100 km^2 was estimated. This suggests that the peregrine is a fairly widespread, but overall extremely rare breeding bird in Malaysia. During the 10 ensuing years, no other syntheses on resident peregrines in Malaysia have been compiled, but local observers, especially Chiu, Connie Khoo, and some of their colleagues in the Ipoh area, continued to watch peregrines during the breeding season at several sites in that region.

Most parts of West Malaysia are flat and devoid of any rocky outcrops, or they are mountainous, but with old, eroded hills, which also for the most part are devoid of any cliffs. Therefore, the scope for cliff-nesting peregrines is extremely limited in Malaysia. Essentially, the species seems to be restricted to limestone country, where natural cliffs occur and sometimes quarry activities create new, albeit sometimes only ephemeral, cliff faces. The Malaysian economy is growing fast, and hence as in many other countries of SE Asia, there is a huge demand for cement. The latter is produced in quarries that may eventually destroy entire limestone outcrops and the peregrine nesting sites along

Figure 1. Several photographs of *F. p. ernesti* in our study area. Especially in flight, this subspecies can look almost black when viewed from a distance and overall sometimes looks like a species altogether different from *Falco peregrinus*! Photos: Beng Yean Ooi

1. ábra Néhány, a vizsgálati területen készült fotó az *F. p. ernesti* alfajról. Ez az alfaj különösen repülése közben, messziről megfigyelve szinte teljesen feketének tűnik, és összességében néha olyan, mintha egy teljesen másik fajhoz tartozna with them. Therefore, there is a pressing scientific and conservation need to advance our knowledge about this bird in Malaysia. Scientific, since this is one of extremely few tropical regions where knowledge about basic population parameters such as breeding density and productivity has started to accumulate for the peregrine, and conservation, because a good knowledge about distribution and abundance of a species is the obvious, first basic requirement for its conservation.

Between 2017 and 2019, we conducted three surveys in West Malaysia during the courtship period and tried to visit as many of the previously known sites and discover as many new sites as possible (Kéry *et al.* 2017, 2018, Ooi *et al.* 2019). Our goal was to improve our knowledge about breeding distribution, habitat and density of *F. p. ernesti* in this area. In addition, we compiled an Excel database with all known peregrine sites in West Malaysia, drawing on published and unpublished literature as well as on oral communications from friends and colleagues. Based on this, we here give a new synthesis of what is currently known about *F. p. ernesti* as a breeding species in West Malaysia. We build in part on the foundation laid by Laurent Molard (Molard 2005, 2009, Molard *et al.* 2007), but here, we do not attempt to produce a new national population size estimate.

Methods

Field work

We conducted three field surveys on 8 days between 6 and 19 January 2017, on 9 days between 17 and 25 January 2018, and on 10 days from 21–30 January 2019 and covered a total of approx. 5,400 km by car *(Figure 2)*. Before the field work, we studied the locations of all previously known peregrine sites in the covered areas on Google Earth and Google Maps. During the surveys, we used GPS as well as aerial photographs in Google Earth and Google Maps to navigate to the vicinity of some of the cliffs on dirt tracks through oil palm plantations and other habitats that were difficult to overlook from the ground. We used a

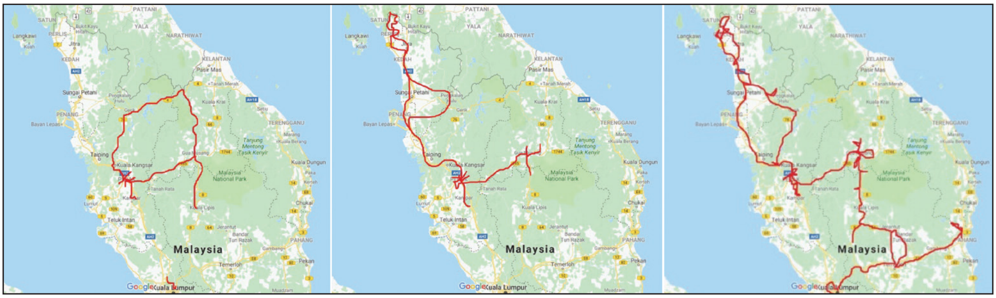


Figure 2. Trajectories of the three Peregrine Falcon Surveys in 2017 (left), 2018 (middle), and 2019 (right), with approx. total lengths of 800, 1,600, and 3,000 kms, and during which we checked 22, 36, and 68 known or potential peregrine sites

2. ábra A három vándorsólyom felmérés útvonala: 2017. év (balra), 2018. év (középen) és 2019. év (jobbra), megközelítőleg 800, 1600 és 3000 megtett kilométer, 22, 36 és 68 ismert vagy feltételezett vándorsólyom előfordulás

Toyota Hilux pickup, which was invaluable to get sufficiently close to many of these sites, so that observations could be made of the birds and playback calls could be broadcasted at an adequate range with any hope of success (see below). That is, closer than about 1 km and ideally also closer than 500 m to the main cliff where peregrine occupancy was known or suspected.

To check a known territory or a likely new site for peregrines, we usually placed ourselves as close to the site as possible, at the base of the cliff, while trying to maximize the view of the sky around the cliff. Observations were made with the naked-eye, with 8–10× binoculars and 20–60× telescopes mounted on a tripod. Key elements of such surveys in the courtship period were the naked-eye scanning for flying birds of the upper edge of the cliff or of the crest of the mountain in which a cliff is located and acoustic attention for the frequent calls. When a cliff was very high and/or steeply above the observation point or when watching birds flying overhead, the best observation position was often found to be flat on one's back (best with a blanket and a pillow, although a nicely browsed pasture could also serve).

In addition, the use of binoculars and telescopes for checking of the cliff for perched birds and for whitewash was also always an important part of the survey at every cliff. Especially during courtship, birds perch actually more often in the first trees just at the top of the cliff, or also in trees within the cliff face, rather than directly on a rock in the cliff itself (MK, pers. obs.). Hence, painstakingly checking all cliff-top trees was particularly important when surveying for peregrines during this stage of the breeding cycle. In West Malaysia, the peregrine appears to be the major moderate to large species which produces whitewash, hence looking for whitewash in a cliff was also an important part of our surveys (but see also Discussion).

Sites were visited between about 8.00 h in the morning and 19.30 h in the evening. Observation periods per site lasted typically about 1 hour, though sometimes they were shorter, e.g. 30 minutes or even less for some of the less-promising-looking cliffs. Sometimes, we spent 2–3 or even more hours at a cliff. The presence of several observers was very beneficial, since it increased the probability of bird detection, especially when they were not calling.

There are several subspecies of the peregrine occurring in Malaysia (White *et al.* 2013): the resident subspecies is usually attributed to *F. p. ernesti*, while in the boreal winter, birds of the *japonensis* or similar subspecies from NE Asia can be found wintering in the country as well. These subspecies can be differentiated quite easily from the locally breeding one, since *F. p. ernesti* is the darkest subspecies in the world (see *Figure 1*), while the peregrines breeding in NE Asia are typically far lighter, with thinner moustaches etc. All birds that we discovered belonged to the locally nesting *F. p. ernesti* subspecies.

Use of playback calls

During the 2019 survey we made frequent use of playback calls to increase the detection probability of the birds at a site (Barnes *et al.* 2012, Ambrose *et al.* 2014). Unless both birds were detected early during a watch, we often used playback of the '*eee-chup'* call (Ratcliffe 1993) from a pair using a FoxPro game call portable amplifier. This mimics the calling of an intruding pair. We used an *eee-chup* recording lasting 26 seconds from *Xeno-canto* (see https://www.xeno-canto.org/357721), which is from a pair recorded on 4 March 2017 in the middle of the Brazilian Amazon where no peregrines are known to nest; therefore, it must be from wintering birds originating from the boreal or arctic parts of North America. We repeated this recording between 1–6 times (though, usually only twice) at a site, that is, for a total of approx. 30 seconds to under 3 minutes. As soon as both birds were detected, we stopped broadcasting the call so as to minimize disturbance.

Collation of other information and literature records

We tried to source as many records as possible of potentially nesting peregrines in West Malaysia, either from the literature, but also from personal communications, either directly or indirectly to one of the authors. We have created an Excel data base which lists (at the time of writing) 94 cliff objects in West Malaysia, drawing on all the information in Molard (2005), Molard *et al.* (2007) and on our three surveys combined and on all other information that we could obtain.

Results

Breeding habitat of *F. p. ernesti* in Malaysia

With the single exception of one breeding pair on a building found by Molard in Kuala Lumpur in 2004 (Molard 2005), all peregrine territories found so far in West Malaysia were in cliffs in limestone hills. While the smallest of these cliffs were exceptionally only 20–30 m tall, the vast majority was much taller and reached about 300 metres and more for the tallest of them. Overall, we got the impression that Malaysian peregrines have an even greater tendency to only nest in the tallest available cliffs than in other places of the world where the second author has observed them, e.g. North and South America, Europe and Australia.

State of knowledge on *F. p. ernesti* in West Malaysia up to 2005

The first confirmed nesting pair in Malaysia was found as late as 1996 (Chong 2002), although Wells (1990) mentioned an observation of a copulating pair in Bukit Takun on the outskirts of Kuala Lumpur in 1984, and pairs had also been recorded in the 1980s at the Batu Cave limestone hill in the Kuala Lumpur metropolitan area. There was also an early record from Bukit Air Jernih in the 1990s (Molard *et al.* 2007). The first breeding pairs in the Ipoh area were found in 2004 (Molard 2005, Chiu *et al.* 2006). Also in 2004, an unsuccessful breeding attempt was recorded on a tall hotel building in downtown Kuala Lumpur (Molard 2005). So far, this appears to remain the only confirmed nesting on a building in the country, in spite of suspicious sightings of *F. p. ernesti* birds in several cities including Penang (Ho Khee An, pers. comm. to Chiu) and also on transmission towers in several places including near Gerik (Lee, pers. obs.) and in the Genting Highlands (Molard 2005). Before Molard's field work during 2003–2005, 10 peregrine territories were known in West Malaysia; he then found 9 new ones, bringing the total to 19 *(Figure 3).*

Major results from our 2017 survey

We visited nine sites that were previously known to hold peregrine territories and 20 additional sites about whose status as a peregrine cliff nothing was previously known. We detected peregrines at 11 sites: a pair at 8 and a single bird at 3 sites. Eight sites were previously known territories and 3 were newly detected ones, bringing the total number of peregrine sites known in West Malaysia to 22 *(Figure 3)*. One of the new territories, in a quarry near the city of Ipoh, was only about 2 km from a previously known neighboring territory. This was much closer than the previously known closest nesting pairs in Malaysia. Although this new pair could not be confirmed again afterwards, this observation emphasized the need to take into account the possible nesting of adjacent pairs at much closer distances than what was previously thought (e.g. at 2–4 km).

Major results from the 2018 survey

We surveyed 36 sites in total. Fourteen sites were in the region of Ipoh (Perak), 11 sites around Gua Musang (Kelantan, including one site in adjacent Pahang), three sites in Kedah and eight sites in Perlis (including one in adjacent Thailand). Nine of the 36 sites were previously known peregrine territories and we found peregrines at 7 (78%) of them, while we did not find any birds at 2 (22%). Five new peregrine sites were discovered, thus bringing the known total in West Malaysia up to 27 *(Figure 3)*.

Major results from the 2019 survey

We surveyed a total of 68 cliffs of which 18 were previously known as peregrine territories. Of these, 17 were confirmed to be occupied by at least a single peregrine, while we did not find any birds at one of these sites. We discovered 9 new sites that had not been known before and re-discovered 2 pairs that had moved to new cliffs, where they had never been seen before. Overall, during our 2019 surveys we found a total of 28 occupied sites: at 25 sites we observed adult pairs, while at 3 sites, only single birds could be detected. At the end of our 2019 survey, the known total sites in West Malaysia stands at 36 *(Figure 3).*

For these 68 checked cliffs with their 28 occupied sites, *Table 1* gives a breakdown by state and shows the percentage of occupied cliffs among the checked ones. The number of checked cliffs broadly provides a crude measure of how common suitable-looking cliffs are in each state, being most common in the surveyed parts of Perak and Kelantan, and also common in Perlis, least common in Selangor and Kedah and intermediate in Pahang. However, the percentage of occupied cliffs (excluding Selangor with its single checked cliff) was greatest in Pahang, where many of the cliffs were isolated from each other and tall, intermediate in Perak and Kedah and lowest in Kelantan and Perlis.

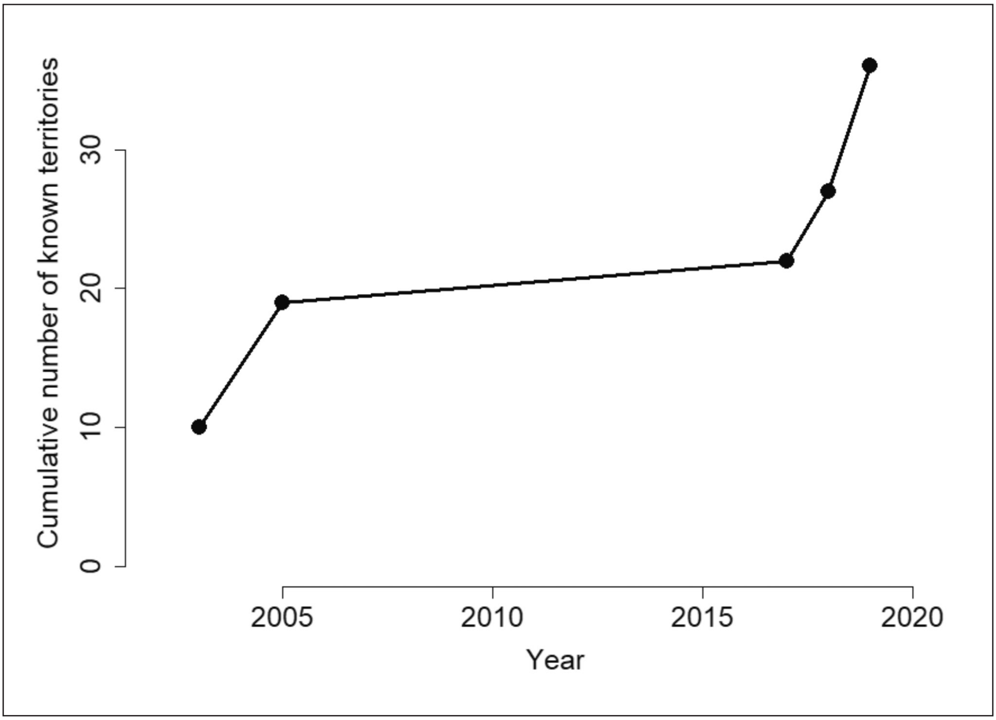


Figure 3. Cumulative number of known peregrine territories in West Malaysia before the surveys of Molard (in 2003), including the surveys of Molard (up to 2005) and at the completion of our surveys in 2017, 2018 and 2019

3. ábra Az ismert vándorsólyom territóriumok összesített száma Nyugat-Malajziában Molard felmérései előtt (2003), beleértve Molard 2005-ig végzett felméréseit és az általunk 2017-ben, 2018-ban és 2019-ben befejezett felméréseket

Table 1. Number of checked and occupied cliffs per state in the 2019 survey

1. táblázat Az ellenőrzött és elfoglalt sziklák száma régiónként a 2019-es felmérés során

State	Number of cliffs checked	Occupied (%)
Selangor	1	1 (100%)
Pahang	11	7 (64%)
Perak	19	9 (47%)
Kelantan	19	5 (26%)
Kedah	4	2 (50%)
Perlis	14	4 (29%)
Total	68	28 (41%)

Distribution of nesting peregrines in West Malaysia

The currently known distribution of 36 peregrine sites in West Malaysia is extremely uneven and reflects the availability of vertical rocky outcrops (see *Figure 4*). As already noted by Molard *et al.* 2007, the three major concentrations of nesting peregrines are the cliff-rich regions around Ipoh/Perak in the centre West, Gua Musang/Kelantan in the centre, and the state of Perlis in the North.

Breeding phenology

All our field observations supported the previous notions (Chiu *et al.* 2006, Molard *et al.* 2007) that the start of egg-laying in our study area is around the end of January and in early February. During our January surveys, we observed plenty of courtship behavior, including many copulations. We never could observe an incubating bird, but this would have been impossible at most sites because the eyries were either too high up or too deep in a karstic pothole. However, during the 2019 surveys we surmised that incubation had started from the behaviour of several pairs.

Population trends

During all our surveys, we re-visited a large proportion of the previously known territories. Typically, we found most of them to be occupied; see above. From this we would tentatively conclude that the population is most likely stable, or possibly even increasing.

Results on our experimentation with call playbacks

We had tremendous success with our short playback sessions of the calls from an *eee-chupping* peregrine pair plaid from a portable playback machine at most of the surveyed sites: even at the tallest cliffs and at distances of up to almost 1000 metres, the pair often became airborne after 36–52 seconds (i.e. during the first two times our recording was played), calling a lot and thus permitting efficient confirmation of an occupied site. Among the 28 sites that were found to be occupied during the 2019 survey, birds were first detected without playback at 10 (36%), while birds were first detected after playback at the remaining 18 (64%).

Discussion

More than a decade after Molard *et al.* (2007), this article provides a new synthesis on what we currently know about resident, nesting peregrines of the subspecies *F. p. ernesti* in West Malaysia. We describe the results of three surveys during the courtship periods 2017–2019 totaling 27 days and 5,400 km driven by car, and we amalgamate our field records with all information that we could obtain on potentially nesting peregrines in this area. Here, we put our

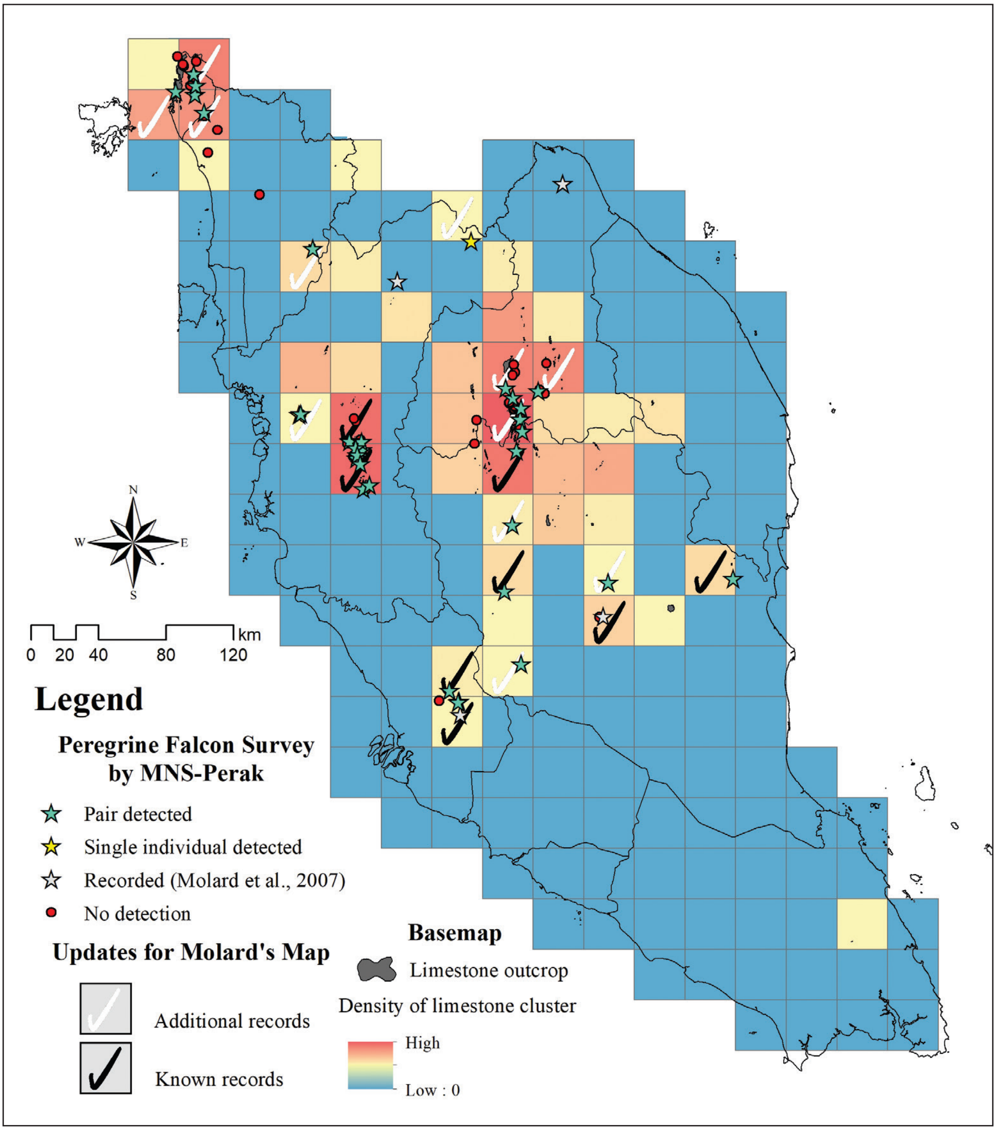


Figure 4. Map showing the currently known breeding distribution of *Falco peregrinus ernesti* in West Malaysia. It shows the combined results of the MNS Perak Peregrine Falcon Survey team during 2017–2019 and compares the progress of our knowledge with one decade earlier, when Laurent Molard conducted intensive surveys in partly the same region. The relative area of limestone outcrops, the major breeding habitat of peregrines here, is shown per 20×20 km square (from Liew *et al.* 2016)

4. ábra A térkép az *F. p. ernesti* alfaj jelenleg ismert költési eloszlását mutatja Nyugat-Malajzia területén. A térképen az MNS Perak Peregrine Falcon Survey kutatócsoport 2017–2019-es felméréseinek összeredménye szerepel az egy évtizeddel azelőtti, Laurent Molard által részben ugyanabban a régióban végzett felmérés eredményeivel összehasonlítva. A mészkőkibúvások relatív területét, ahol a vándorsólymok költőhelyének legnagyobb része található, 20×20 km-es négyzethálón ábrázoltuk (Liew *et al.* 2016 alapján) observations into a context and make some additional comments especially on our most thorough survey, that in January 2019. We also discuss our use of call playback in peregrine surveys, which we have found to be fairly controversial when we discussed it with colleagues.

Our surveys, along with previous work in Malaysia especially by Laurent Molard, represent one of only a small handful of population studies of the peregrine in a tropical country. Thus, we think that we cover uncharted territory even by providing such basic information about the West Malaysia birds as nesting density, population size and timing of breeding.

National population size and density: Currently, the known total of confirmed or suspected peregrine breeding sites in West Malaysia is 36. Molard *et al.* (2007) put forward a population estimate of 70–80 pairs for all limestone cliffs in the 135,000 km^2 area of Peninsular Malaysia, i.e. 0.05–0.06 pairs per 100 km^2. Hence, we currently stand at about half of the projection by Molard *et al.* (2007). Looking at the maps of the known distribution in that publication and at our maps in *Figures 2* and *4*, one may get the impression that perhaps this earlier estimate was a little bit too optimistic? Most areas of Malaysia are flat and devoid of any limestone cliffs or useable (big) quarries and we have now surveyed all major regions of West Malaysia where cliffs occur in any greater number, i.e. the regions around Ipoh and Gua Musang and the state of Perlis. With few exceptions (in part due to lack of accessibility by road), we believe that during our surveys we have checked at least once all major cliffs in the regions visited if they were further apart from known pairs than about 2 kilometres, and hence could have held an additional pair. However, we do not know how many cliffs we have not even seen, mostly because they may have been outside of sight from any reasonable road. As a result, we would not feel comfortable to make an updated population size estimate based on some guesstimate of the proportion of suitable nesting cliffs that we have visited.

However, we plan to conduct future surveys to obtain a (much) more complete picture of the distribution and population density of peregrines in West Malaysia. This will also include in-depth study of aerial maps in Google Earth to try and identify all promising limestone hills in the country. It will also include the study of all available other information, including sightings in eBird for instance.

Compared to many parts of the world, the peregrine seems to be extremely rare in Malaysia. In the best, high-density areas in Europe such as the French Jura mountains, population density is between 1 and 2 pairs per 100 km^2 (Monneret *et al.* 2018), i.e. about 27 times greater than what Molard *et al.* (2007) suggests for West Malaysia. During our survey, the minimum nearest-neighbour distance was just under 4 km (with the exception of one case of two possible pairs at a distance of only 2 km near Ipoh in 2017, see Kéry *et al.* 2017). More often than not, pairs in Malaysia appear to be isolated by many kilometres from the nearest neighbouring site. This is again in stark contrast to high-density populations in temperate and cold latitudes where, for instance in the French Jura, nearest-neighbour distances of 1–2 km are not rare.

In addition, it was remarkable that during the three surveys so far, with many dozen visits to occupied sites, we have observed intruding peregrines only once or twice, and we never observed any immature peregrines during the entire survey. In contrast, in high-density populations, e.g. in the Jura, during the same stage in the breeding cycle (i.e. when courtship is most intense, just before egg-laying), intruding birds can be seen during most full days of surveying, including often immatures (i.e. 2CY birds).

In summary, the peregrine seems to be a fairly widespread, but overall extremely rare breeding bird in West Malaysia. It currently appears to be almost completely limited by the occurrence of tall limestone cliffs. It is our impression that the peregrine only inhabits very tall cliffs in Malaysia compared to many other parts of the world where we have observed it (e.g. Europe, South America, Australia, pers. obs. by MK), where the species accepts much smaller cliffs as well. We have seen a great many first-class cliffs (Ratcliffe 1993) in Malaysia that, if they were in some of these other countries, would be bound to have a pair, but they are unoccupied here. We wonder whether this is simply because of the generally much smaller density or for some other reasons?

One possible reason for the apparently much greater selectivity of peregrines for tall and vertical cliffs in Malaysia may be the risk of predation by monkeys. Several species of monkeys occur in the country and they are formidable climbers, either on the cliff-face itself, or especially if there is any vegetation growing in the cliff-face. In this latter case, monkeys may drop from bush to bush to reach many places even in a vertical or overhung crag. For instance, at one of the historically known peregrine cliffs mentioned in Molard (2005), which we visited in 2019 and which was the only known territory where we failed to see any peregrines during that survey, we once saw a large group of monkeys that were virtually "abseiling" vertically down through the tall cliff, dropping from one bush in the cliff to the next one down, over jump distances of 5–10 m. Some parts of the vertical cliff were climbed downwards "nakedly", without the aid of any vegetation. And it has to be said that the very rich texture of many tropical karst cliffs may provide many good grips for climbing monkeys. Hence, we hypothesize that perhaps monkeys represent an important selection pressure for West Malaysia peregrines to nest only in the tallest and most vertical cliffs. There are certainly reports that pairs in smaller nesting cliffs failed and this was attributed to predation by monkeys (Chong 2002, Noack 2002).

Timing of breeding: Our observations confirm what Molard *et al.* (2007) say about the timing of breeding in Malaysia: *"Egg-laying seems to occur from the end of January to the beginning of February"*. During the 2019 survey, we observed at least 8 females spend long times in and at the edge of possible eyrie sites, and in some cases they came out and very soon disappeared again into such sites when we used playback. All this seemed to indicate that they were either about to start laying or already had some eggs. Since the courtship period is the best period in the annual cycle to survey a population for occupancy, and courtship is most intense just before egg-laying, it is clear that peregrine surveys in West Malaysia should not take place after January if the aim is to focus on the number of occupied sites.

Use of whitewash in peregrine surveying: Whitewash (i.e. feces or droppings) in a cliff provides one of the most important hints for occupancy of a site by peregrines (or indeed, most other species of cliff-nesting raptors). Whitewash identification is not an exact science though, and depending on the variety of cliff-nesting species, it may be pretty useless as a pointer to peregrines occupying a site in some regions of the world. However, when large cliff-nesting birds other than peregrines are rare or absent, it may be very important. Malaysia does not have many large bird species that live in cliffs, and hence, whitewash can be very informative in peregrine surveys (if one learns to distinguish the longer and broader streaks produced by a peregrine from the much thinner and shorter streaks produced for instance by cliff-dwelling starlings and mynahs). Nevertheless, our observations during the 2019 survey reminded us that the Barn Owl *(Tyto alba)* is probably a widespread species that also nests in cliffs and it does produce whitewash that can look pretty much like that of a peregrine. Thus, caution is required when trying to predict from white-wash the occupancy of peregrines at a site.

Use of playback in peregrine surveying: Our 2019 survey was the first time that we made large-scale use of playback calls of the *'eee-chup'* courtship call, played from a strong game-call player. This frequently enticed birds to become airborne and to call themselves, typically also giving the 'eee-chup' call. Sometimes, this made detection of a pair very simple even at very large cliffs and with less than optimal visibility (e.g. with strong glare or observing a cliff with the sun in the eyes). About two thirds of all recorded pairs were first detected as a response of the birds' reaction to the playback. And although we drove almost twice as much during the 2019 survey as during the previous survey in 2018 (3,000 vs. 1,600 km), our use of playback was surely in part responsible for us finding more than twice as many occupied sites during the 2019 survey than during the 2018 survey (28 vs. 13). Hence, use of playback can work wonders when conducting peregrine surveys, and we have the impression that this does not seem to have been widely known in the peregrine community worldwide (pers. comm. of several colleagues to MK). This is somewhat surprising, given that the efficacy of playback in peregrine survey work has been described in at least two publications so far (Barnes *et al.* 2012, Ambrose *et al.* 2014).

However, playback may have possible drawbacks and it has been severely criticized by many observers (peregrine or otherwise), because (1) it is sometimes feared to be a serious disturbance of the birds and (2) it may also be very intrusive for a romantic feel of the observer as being in some sort of unity with the environment and the birds. We think that both concerns are valid and must be addressed seriously.

Playback of the *eee-chup* call simulates the soundtrack of an intruding peregrine and hence, the attending birds react in a strongly aggressive manner, by flying off, calling and alighting at exposed places (such as the cliff top or trees there) presumably to better spot the apparent intruders as well as signaling to them the presence of a territory-holder. Interestingly, it is our impression that the females reacted much more predictably to the playback than did the tiercels, even though our recording was of a pair.

During our 2019 survey, we played the *eee-chup* calls at a site for a maximum of 2.6 minutes and stopped as soon as we had detected the pair, in order to minimize disturbance; hence, often we stopped after only 10–20 seconds. At most sites, the observable reaction to the disturbance by the attending birds, i.e. flying and calling, ceased already a few minutes after the playback, flying usually immediately after 1–2 changes of position of the birds and calling a little later.

Our use of playback simulates a natural event (intrusion of another bird into the territory), which will regularly occur during the pre-breeding season, when territories are staked out anew: attending birds will ascertain their claim to their territory and recruits will try to find a new territory, and a mate, to breed. Clearly, peregrines have evolved to deal with this type of disturbance, because it must happen frequently every year in all but the most isolated territories. Even in a very low-density population such as the one in West Malaysia (see above), over the course of a courtship period of between 4 and 6 weeks, we think that it is unlikely that any pair will ever be spared of the experience of an intruder.

Thus, we think that our use of playback in a systematic, large-scale survey will have represented an overall very slight disturbance only and one that is very unlikely to cause any effects on the survival or reproduction of the birds, nor on their decision to stay on the territory or leave it. But it has to be admitted that at the current time, with the current data, this statement has the nature of a mere hypothesis, and it should be tested and confronted with empirical data. That is, it would be valuable to test this hypothesis and corroborate or refute it by quantitative measurements of breeding success and future site occupancy. For instance, it would be important to compare breeding success and local site extinction probability between two groups of sites: one group of sites where there was some playback during the breeding season and another group of sites where there was not. Due to the scarcity of the peregrine in Malaysia, such a controlled experiment would best be conducted in another part of the world where the population densities are much higher.

The second argument that we have heard being made against the use of playback when surveying peregrines is that it destroys some romantic feeling when being in the field, sometimes in very beautiful and almost pristine-looking areas: indeed, it can be a disturbing feeling when suddenly there is that strong “noise” produced in a beautiful area. Actually, we feel the same: i.e. we think that emotionally, for us as observers, use of playback goes against a more romantic approach to peregrine watching where we look for watching the birds in beautiful, natural and quiet environments. However, we are of the opinion that *if* playback does not have any lasting negative effects on the birds, it is up to each individual observer to decide whether s/he does or does not want to make use of this much improved detection method. This decision will also likely depend on the goals of the observations: if observations are made as part of a more systematic survey of some larger region, then we think use of playback can be a great thing to make these surveys much more efficient … and the data collected much more complete and reliable. Otherwise, if observations are made for pleasure only, to rejoice in watching the birds and their behaviour, then we think that use of playback should be avoided. Also, playback should not be used at a site where occupancy has already been ascertained during earlier visits of the same breeding season. We would certainly not endorse use of playback for peregrine photography.

In summary, we have found (as did Barnes *et al.* 2012 and Ambrose *et al.* 2014), that peregrines can react very reliably to the use of playback, mostly of the *eee-chup* call, and clearly, that this can greatly increase the scope and efficiency of a survey. We believe that minimal use of playback (as we did, and not more than 1–2 times per breeding season and site) does not cause any lasting negative effects on the birds, but we caution that there is currently no evidence for or against this hypothesis. This hypothesis should be tested and if serious effects of playback in one season are found (e.g. when birds are more likely to fail a breeding attempt, brood size is reduced or the likelihood that a site is abandoned during the following breeding season), use of playback should be stopped for peregrines.

Outlook

Despite being one of the world's most widespread bird, the peregrine is almost exclusively studied outside of the tropics. Malaysia is one of the very rare tropical countries where some basic information on the population ecology of the peregrine has been collected. In addition, many occupied sites are in danger of being erased by quarry operations that feed the relentless construction boom in Malaysia and other SE Asian countries. Therefore, we argue that there is a considerable scientific and conservation need for further surveys to better know the situation of breeding Peregrine Falcons in Malaysia.

Thus, studies such as ours gain particular value by their relative uniqueness as a population study of the peregrine in the tropics. In the future, we plan to improve our knowledge about distribution and density of the peregrine in West Malaysia by repeating our surveys. This need not happen every year, and a biennial rhythm may be enough detect longer-term trends as well as to further accumulate knowledge about the distribution of the species. In addition, it would be interesting to not only collect information about distribution and density of the population, but also about its productivity, by conducting surveys in April and May to count fledged young.

Currently, peregrines in West Malaysia appear to nest almost exclusively in cliffs and these can sometimes be picked out quite well from aerial photographs in Google Earth. But peregrines have also been found as nesters on buildings (see Molard *et al.* 2007), and the worldwide trend towards increased prevalence of this type of nesting habitat suggests to us to be vigilant for an increase of peregrines nesting on buildings also in Malaysia and perhaps including also tall transmission towers.

Remembrance

This article is meant in part to be a remembrance for the first author, our dear and admired colleague and friend Ooi Beng Yean. Beng passed away barely 1 month after our 2019 peregrine survey, on 2 March 2019 in Sabah, while doing what he perhaps liked to do best: bird-watching in the company of his friends. We plan to continue our surveys, but we know that without Beng, it will never be the same.

Acknowledgements

We warmly thank the Tan Kean Cheong Bird Conservation Memorial Fund (TKCBCMF) of the MNS Perak for a grant to cover our expenses incurred for food, lodging and mileage during the 2018 and 2019 survey. We are also very grateful to Connie Khoo for many helpful and interesting exchanges over the years. Finally, we thank Su Ping Ong, Puan Chong Leong, Henry Goh, and Gerry and Joy Danen who all joined us for some days on the 2017 survey, and Lim Kim Chye and Lim Swee Yian who did the same during our 2019 survey. We also thank the editor and two referees for their valuable suggestions that improved and clarified our paper.

References

Ambrose, S., Ritchie, R. J. & Florian, C. 2014. Use of and responses to audio survey technique by Peregrine Falcons in Alaska. – Northwestern Naturalist 95: 125–128. DOI: 10.1898/NWN13-33.1

Barnes, J. G., Jaeger, J. R. & Thompson, D. B. 2012. Effectiveness of call-broadcast surveys to detect territorial Peregrine Falcons. – Journal of Raptor Research 46(4): 365–377. DOI: 10.3356/JRR-11-61.1

Chiu, S. C., Ooi, B. Y. & Khoo, C. S. Y. 2006. Observations on nesting Peregrine Falcon *Falco peregrinus* in Perak. – Suara Enggang 14(3): 11–15.

Chong, M. H. N. 2002. Peregrine Falcon *Falco peregrinus ernesti* nesting at Temengor Forest Reserve, Perak, in February 1996: a first successful breeding record for Malaysia. – Asian Raptor Bulletin 3: 19–20.

Döttlinger, H. 2002. The Black Shaheen Falcon (*Falco peregrinus peregrinator* Sundevall 1837): its morphology, geographic variation and the history and ecology of the Sri Lanka (Ceylon) population. – PhD Thesis, University of Kent, UK.

Döttlinger, H. & Hoffmann, T. W. 1999. Status of the Black Shaheen or Indian Peregrine Falcon *(Falco peregrinus peregrinator)* in Sri Lanka. – Journal of the Bombay Natural History Society 96(2): 239–243.

Döttlinger, H. & Nicholls, M. 2005. Distribution and population trends of the 'black shaheen' Peregrine Falcon *Falco peregrinus peregrinator* and the eastern Peregrine Falcon *F. p. calidus* in Sri Lanka. – Forktail 21: 133–138.

Döttlinger, H., Nicholls, M. K. & Attapattu, N. 1999. The Black Shaheen *(Falco peregrinus peregrinator)* in Sri Lanka - a report of the 1997 field season. – Falco 13: 15–18.

Kéry, M. 2002. New observations of the Peregrine Falcon *(Falco peregrinus)* in Peru. – Journal of Raptor Research 36: 213–217.

Kéry, M., Chiu, S. C., Ooi, B. Y., Percival, R. C., Ong, S. P. & Puan, L. C. 2017. Malaysian Peregrine Falcon Survey Report 2017. – Report, Swiss Ornithological Institute, Sempach, Switzerland, pp. 1–86.

Kéry, M., Chiu, S. C., Ooi, B.Y. & Percival, R. C. 2018. Malaysian Peregrine Falcon Survey Report 2018. – Report, Swiss Ornithological Institute, Sempach, Switzerland, pp. 1–92.

Liew, T-S., Price, L. & Clements, G. R. 2016. Using Google Earth to improve the management of threatened limestone karst ecosystems in Peninsular Malaysia. – Tropical Conservation Science 9(2): 903–920. DOI: 10.1177/194008291600900219

Molard, L. 2005. Atlas of Peregrine Falcon *Falco peregrinus ernesti* sites in Peninsular Malaysia. – Unpublished report

Molard, L., Kéry, M. & White, C. M. 2007. Estimating the resident population size of Peregrine Falcon *Falco peregrinus* in Peninsular Malaysia. – Forktail 23: 87–91.

Molard, L. 2009. Behaviour and ecology of resident Peninsular Malaysia Peregrine Falcons. – In: Sielicki, J. & Mizera, T. (eds.) Peregrine Falcon Populations – Status and Perspectives in the 21st century. – Turul/Poznan University of Life Sciences Press, Poznan, pp. 479–492.

Monneret, R-J., Ruffinoni, R., Parish, D., Pinaud, D. & Kéry, M. 2018. The Peregrine population study in the French Jura mountains 1964–2016: use of occupancy modeling to estimate population size and analyze site persistence and colonization rates. – Ornis Hungarica 26: 69–90. DOI: 10.1515/orhu-2018-0016

Noack, F. 2002. Breeding Peregrine Falcons in Perlis State Park. – Suara Enggang 2: 18–19.

Ooi, B. Y., Kéry, M., Percival, R. C., Lee, Z. H. & Chiu, S. C. 2019. Malaysian Peregrine Falcon Survey Report 2019. – Report, Swiss Ornithological Institute, Sempach, Switzerland, pp. 1–126.

Ratcliffe, D. A. 1993. The Peregrine Falcon, 2nd edition. – T & AD Poyser, London

White, C. M., Cade, T. J. & Enderson, J. H. 2013. Peregrine Falcons of the world. – Lynx Editions, Barcelona

sciendo

Ornis Hungarica 2020. 28(1): 28–48.
DOI: 10.2478/orhu-2020-0003

The results of spring monitoring on the status of geese populations in 2011–2018 in the North Kazakhstan Region

Ivan Zuban’*, Vladimir Vilkov, Mikhail Kalashnikov,
Konstantin Zhadan & Anar Bisseneva

Received: March 27, 2020 – Revised: May 31, 2020 – Accepted: June 05, 2020

Zuban’, I., Vilkov, V., Kalashnikov, M., Zhadan, K. & Bisseneva, A. 2020. The results of spring monitoring on the status of geese populations in the North Kazakhstan Region during 2011–2018. – Ornis Hungarica 2020(1): 28–48. DOI: 10.2478/orhu-2020-0003

Abstract The article presents the results of monitoring studies on the population dynamics of goose species at one of the largest stopover sites in Northern Kazakhstan during the springs of 2011–2018. Comparative analysis of the phenological phases at the beginning and end of migration over a 50-year period is conducted and changes in timing of migration for the studied groups are established. Data on the number of flocks at various stages of the migration process are presented. Authors revealed characteristics of the distribution of birds in the directions of migration through the region associated with the presence of various migration strategies. Based on the distribution and number of geese in the region for rest and feeding, key zones with characteristics of their natural and anthropogenic state were identified. It has been established that water bodies and large areas have optimal conditions for rest and replenishment of energy reserves for the birds.

Keywords: geese, brants, features of migrations, migration stops, numbers

Összefoglalás A cikk egy Észak-Kazahsztánban végzett monitoring vizsgálat eredményeit mutatja be, amelyben lúdfajok populációdinamikájának alakulását követték nyomon 2011–2018 között, a tavaszi időszakban az egyik legnagyobb kiterjedésű élőhelyen. Összehasonlító elemzést is végeztek egy 50 éves időszakon át, hogy kimutassák a vonulás kezdeti és végső időpontját és az ezekben bekövetkezett változásokat a vizsgált csoportok esetén. A cikk taglalja az állományok számának alakulását is a vonulás különböző fázisaiban. A szerzők feltárták a madarak egyes vonulási irányok közötti megoszlásának sajátosságait a különböző vonulási stratégiákkal összefüggésben. A pihenő- és táplálkozóhelyként is használt vizsgálati régióban a ludak számán és eloszlásán alapulva azonosították a kulcsfontosságú területeket, valamint rögzítették ezek természetességi állapotát, az esetleges antropogén jelleget is beleértve. Megállapították, hogy a víztesteken és a nagy kiterjedésű területeken fennálló környezeti feltételek optimálisak a madarak számára mind a pihenéshez, mind a táplálkozáshoz.

Kulcsszavak: ludak, *Branta*, vonulási jellemzők, pihenőhelyek, egyedszámok

Department of Biology, M. Kozybayev North Kazakhstan State University, 86 Pushkin Str., Petropavlovsk, 150000, Kazakhstan, e-mail: zuban.nksu@list.ru, zuban_ia@mail.ru
**corresponding author*

Introduction

The territory of the forest-steppe zone of Kazakhstan is characterized by the presence of a large number of water bodies in various quality (Filonec 1974), which creates favorable conditions as habitat and migratory stops for birds in the wetland complex (Cresswell *et al.* 1999, Yerokhov 2006, 2013).

A century ago, it was the richest region of Eurasia regarding the number of geese and ducks (Yanushevich & Zolotareva 1947). Every year, hundreds of thousands of eggs of representatives of these groups were harvested here, as well as thousands of molting and migrating birds were hunted (Yanushevich 1940). At the beginning of the 19th century, the economic development of the territory, associated with an increase in the population, plowing of virgin and fallow lands and excessive hunting, caused a significant reduction in the number of breeding and migratory birds. According to Isakov (1969) waterfowl resources decreased by 20 times at the middle of the 20th century in the south of Western Siberia. Studies conducted in the forest-steppe of Kazakhstan in 1986–1988 confirmed the continuation of this process (Vilkov 1989).

Considering that the reduction in the number of waterfowl continues to the present (Rozenfeld *et al.* 2016, Cuthbert *et al.* 2018) and the fact that the North Kazakhstan region is an area through which significant flocks of geese migrate to the north in spring (Lorentsen *et al.* 1998, Vilkov 2011, Cranswick *et al.* 2012, Zuban' & Vilkov 2015, R. Cuthbert *et al.* 2017, Vilkov *et al.* 2017), the study of their distribution in the region including dynamics of abundance in the long-term will allow us to answer many questions.

The hypothesis, that the authors adhered to when conducting the research, was that the species composition, abundance, phenology and distribution of geese over the territory depend on the conditions of a particular year, but the main stopping places remain constant, that is favorable for carrying out protective measures. During the monitoring work carried out by us in the period 2011–2018, a number of new key migration sites were identified that are important for geese. In this paper we discuss the current condition of such sites, as well as their role in preserving biological diversity.

Methods

This section summarizes the materials obtained by the authors during many years of field research on the migration of geese in the North Kazakhstan region (hereafter NKR). During the field works, authors researched almost the entire forest-steppe part of the NKR: the total length of the routes was more than 10 thousand km, more than 320 lakes, swamps and temporary water bodies on grain fields (meltwater) were examined *(Figure 1)*.

Determination of species composition and population assessment
Water bodies were examined using direct observations, where all birds were identified to a species level and counted. In order to estimate the number and determine the species composition of migrating flocks of geese in the spring, authors used the method set out in the "Instructions for field monitoring of the Lesser White-fronted Goose" (Tolvanen *et al.* 1999, Cuthbert & Aarvak 2017). In general, the methodology included determining the total number of geese departing from the lakes in the early morning and evening hours at the places of feeding, by counting them directly. The following optical instruments were used for counting: binoculars Bushnell (magnification 10×50) and telescopes Viking (magnification 200×80).

Figure 1. Map of the main surveyed lakes
1. ábra A vizsgált fő tavak térképe

The species composition of birds, in case of insufficient visibility in the morning, was clarified by identifying birds in flocks returning to the lakes from their feeding places in the middle of the day. In addition to the determination of the species, authors widely used photographing of flying flocks, with further detailed analysis of photographs, which made it possible to avoid errors in the identification of birds (Rozenfeld *et al.* 2016). Since photographing can only be done during daylight hours, samples were taken throughout the day from different parts of the cluster, both on the feeding fields and on daytime rest areas, trying to get as many photos of birds as possible. The series of photographs were taken of different parts of the flocks, since especially the large ones have a complex structure, due to the fact that small species (Lesser White-fronted Goose *Anser erythropus* (Linnaeus, 1758) – hereafter LWfG – or Red-breasted Goose *Branta ruficollis* (Pallas, 1769) – hereafter RBG) often fly either in the center or along the periphery, forming their own flock inside the main one.

Study of the migration path

To determine the boundaries of key stops and migration terms, as well as the timing of work, authors used information on the movement of RBG marked with GSM trackers based on Gydan (2012), Taimyr (2013) and Yamal (2014) (Vangeluwe *et al.* 2012, Rozenfeld *et al.* 2016). In addition, we used data on the movements of 9 LWfG, marked with ARGOS satellite transmitters in the east of the Bolshezemelskaya tundra in 2012–2014 (Rozenfeld, personal comment), as well as available information in Internet sources on the results of satellite tracking of the White-fronted Goose *Anser albifrons* (Scopoli, 1769) – hereafter WfG – (www.blessgans.de) and LWfG (www.piskulka.net). To determine the timing of the start of monitoring work, we compared polling data and satellite tracking data. When analyzing the dynamics of migration, in order to avoid obtaining a biased trend, we used counting data for a 5-day period of time.

Statistical analysis
Statistical data processing was carried out using the computer program Microsoft Excel 2010. Statistical analysis was carried out using Student's t-test.

Results

Phenology of migration

In the course of observations, we found that the spring migration of Greylag Goose *Anser anser* (Linnaeus, 1758) – hereafter GlG – in the territory of NKR began between the third week of March and the first week of April. Analysis of the first GlG arrival during 2009–2018 showed an average date of March 27. The earliest date for the appearance of single individuals in this territory was March 20–21.

During this period of the year, almost all water bodies are still covered with ice, and there is still quite a lot of snow around them, with thawed patches beginning to appear on natural elevations of the relief. Considering the timing of the arrival of the first birds in relation to the transition of daily average temperatures through 0 °C to positive, it was found that this dependence is negative (–0.67), since in 2014 and 2016 the birds arrived at the studied region later than the optimal conditions were formed, and in the remaining 8 years – earlier *(Figure 2)*.

Early arrival for Northern Kazakhstan also includes Bean Goose *Anser fabalis* (Latham, 1787) – hereafter BN – which appears during the spring migration at about the same time as

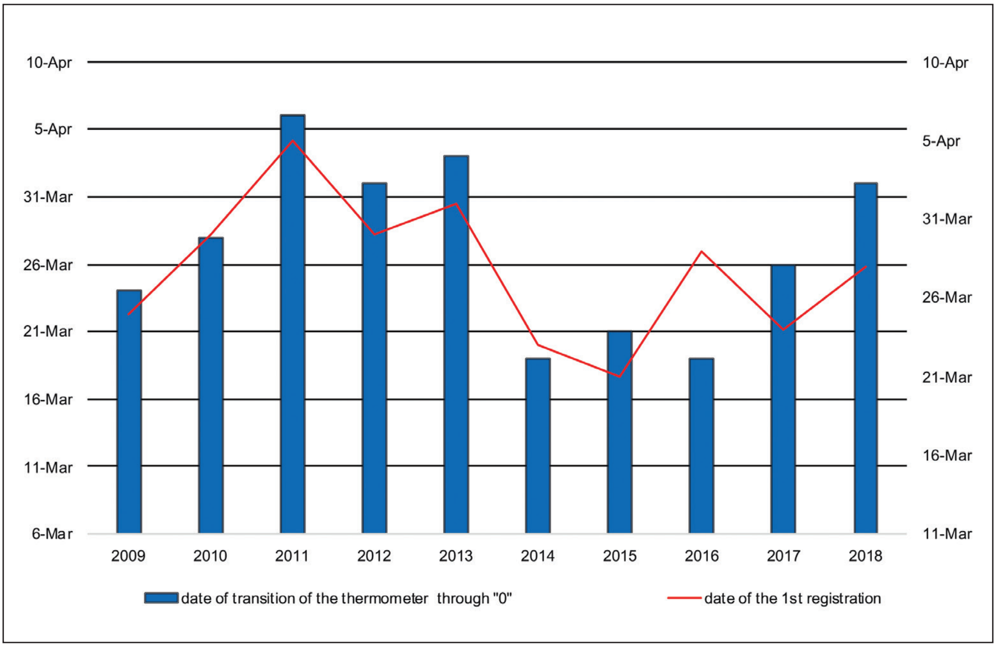


Figure 2. Dynamics of spring arrival of GlG to the NKR in 2009–2018
2. ábra A nyári lúd tavaszi érkezésének alakulása az észak-kazahsztáni régióban 2009 és 2018 között

the GlG. 3 subspecies of *Anser fabalis* are reliably found in the region: *A. f. fabalis, A. f. rossicus* and *A. f. middendorffii.* The migration of the species is practically not pronounced and irregular on the territory of the North Kazakhstan region.

The first registrations of WfG in the region are timed to the beginning of the second week of April. Their arrival coincides with the period of transition of average daily temperatures through the mark of + 5–8 °C. These temperature indicators determine the partial melting of snow from the ground, the formation of temporary water bodies, the beginning of the growth of coastal vegetation, thereby ensuring unhindered access of birds to feed. Simultaneously with the appearance of WfG on the span, the mass migration of GlG begins. And from late April, an increase in the flow of migratory WfG has been observed. By May 5–10, its intensity reaches its peak, after which the numbers decline and by the 20th of May the migration almost completely ends. Individuals or small flocks (3–30 specimens) of this species are recorded until the end of May *(Table 1)*.

Migration of LWfG and RBG begins at approximately the same time, starting from the end of the second decade of April. At the beginning of migration, RBG fly in small flocks of 5–15 individuals, often in joint flocks with the WfG. From the end of the third decade of April, the migration rate of the RBG increases, reaching its maximum by the second decade of May. At this time, single-species flocks, forming separate clusters from 200 to 1000 birds on the periphery of flocks of WfG, are more often registered. Often migrating RBG stay on the territory of the region until the end of May, and in some years, they can be found until the first decade of June. At the same time, in the 60s–70s of the 20th century, the RBG were not registered for the territory during the spring migration. At that time, only isolated observations of this species were known in various parts of the region in the autumn period (Drobovtsev 1976).

The analysis of the data available in the literature on the migration dates of the WfG and GlG for 1966 and our data indicates a shift in the dates of the first registration compared to earlier periods *(Table 2)*. So, for example, according to data of Drobovtsev (1972), the average date of arrival of the first individuals of GlG in 1966–1969 accounted for 13 days earlier. A similar situation is observed for the WfG – the average dates of the first registration shifted by 9 days *(Table 3)*. Accordingly, there was a shift in the timing of the end of the migration of the GlG, which now ends 6 days earlier. WfG migration also ends 5 days earlier.

Table 1. Phenology of the main phases of the spring migration of geese in the NKR according to observations in 2009–2018

1. táblázat A ludak főbb tavaszi vonulási fázisainak fenológiája az észak-kazahsztáni régióban tett megfigyelések szerint 2009 és 2018 között

Species	**Terms of migration**								
	March			**April**			**May**		
	I	**II**	**III**	**I**	**II**	**III**	**I**	**II**	**III**
Anser anser			▨	▨	■	■	▨		
Anser fabalis			▨	▨	▨	▨	▨	▨	
Anser albifrons				▨	▨	▨■	■	■▨	
Anser erythropus					▨	▨■	■	■▨	
Branta ruficollis					▨	▨■	■	■	▨

Table 2. Dates of spring migration of GlG on the territory of the NKR in 1966–2018
2. táblázat A nyári ludak tavaszi vonulásának időpontjai az észak-kazahsztáni régióban 1966 és 2018 között

Research period	1966–1969 (Sokolov, 2005)	2009–2018 (Our data)
first registration	09.04±2.65	28.03±4.9
last registration	03.05±2.8	27.04±3.5

Table 3. Dates of spring migration of WfG on the territory of the NKR in 1966–2018
3. táblázat A nagy lilikek tavaszi vonulásának időpontjai az észak-kazahsztáni régióban 1966 és 2018 között

Research period	1966–1969 (Sokolov, 2005)	2009–2018 (Our data)
first registration	20.04±6.4	11.04±4.6
last registration	31.05±6.7	26.05±5.9

Direction of migration

The main stream of arctic geese follows the valley of the river Ishim. A significant part of it, up to the city of Petropavlovsk, deviates in the northeast direction (96.8% of the total number of flocks). Then, broad fronts (about 100 km) of birds fly along the floodplain of the dry river Kamyshlovka to the borders with the Omsk and Tyumen regions of the Russian Federation. The dominance of the general direction is most likely determined by clearly defined landmarks along the Kamyshlovka river bed, as well as by the location of the end points of the route, i.e. – the tundra zone in the area of the peninsulas Gydan, Taimyr and others. The total width of the migration route of geese in the spring within the region is about 470 km. For GlG during the spring migration period, the northern direction of the migration is more characteristic *(Figure 3)*.

The cases of emigration of geese (in the south-western direction) during the period of our observations were noted only once on May 1, 2014, and were associated with increased winds of the northern points, with gusts of up to 25 m/s and heavy precipitation in the form of snow.

Seasonal dynamics of migration

According to the results of visual observations conducted in the spring seasons of 2011–2016, 1,710,125 individuals of geese were counted. Considering the seasonal dynamics of their migration, it was possible to detect numerous waves *(Figure 4)* which, by their specificity, can be combined into two groups: 1. having two main peaks of the migration and 2. having one peak of the migration or with a not clearly pronounced peak.

So, in 2011 and 2012 the migration took place according to the first variant, when during the spring two peaks were recorded: in the beginning and in the middle of May. In the remaining years, only one upturn was clearly visible, preceded by a mild flow of migrants. In 2014, a sharp increase in the number of migratory birds began from the end of April, and,

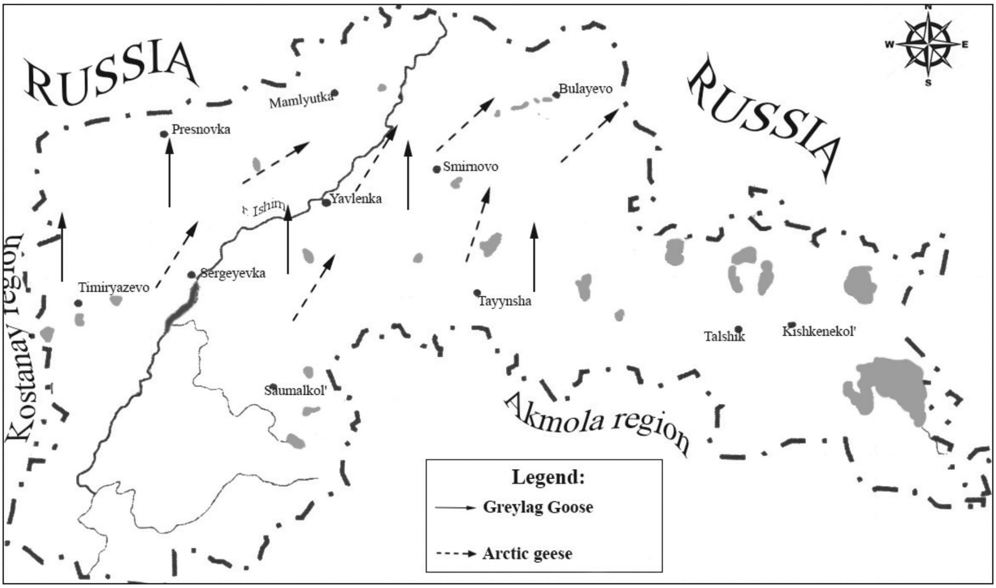


Figure 3. The main directions of spring migration of geese on the territory of NKR
3. ábra A ludak főbb tavaszi vonulási irányai az észak-kazahsztáni régióban

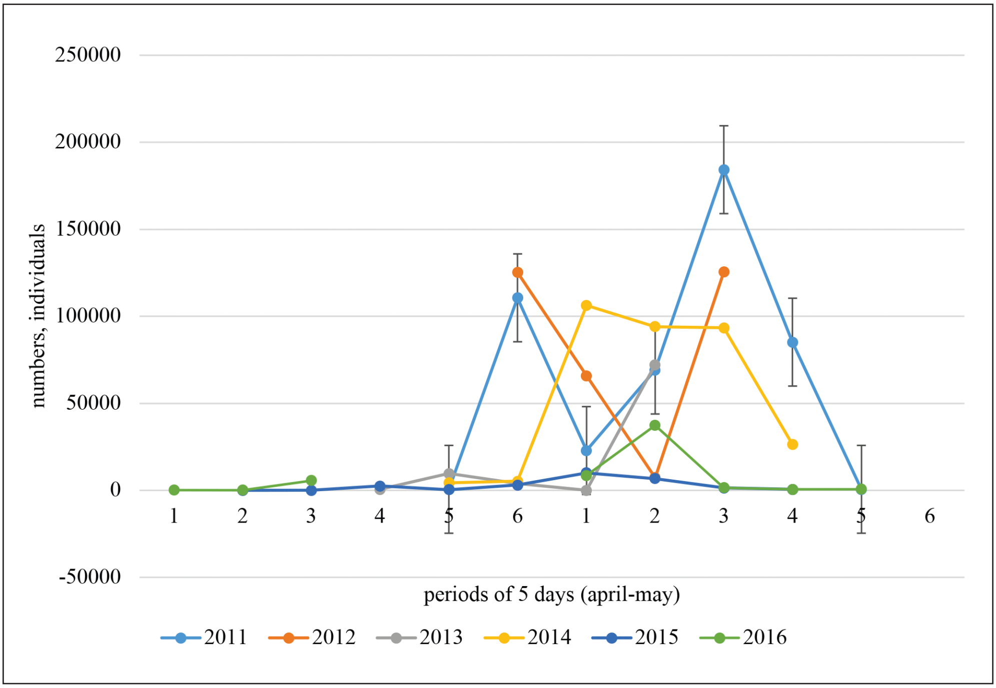


Figure 4. Seasonal dynamics of spring migration of geese in the NKR in 2011–2016
4. ábra A ludak tavaszi vonulásának dinamikája az észak-kazahsztáni régióban 2011 és 2016 között

by the end of the first week of May, reached its maximum for the entire spring. The number of migrants decreased gradually until the third week of May, only after which the completion of migration occurred.

The number of migrating birds

Over 8 years of monitoring studies at temporary and fixed points of observation, authors counted about 2 million individuals of five species of geese *(Table 4)*.

The most common species during the spring migration in all the years was the WfG, whose share was 94.03% of the total number of recorded geese. The second most abundant species was the RBG (5.7%). The share of other species of geese is not large and ranges from 0.17 to 0.0004%.

Analysis of the data in *Table 4* shows that the maximum abundance of the studied species was observed in the water bodies of the region in the period from 2011 to 2014. The main reason for this, in our opinion, is the drought that began in 2008. Starting from 2015, the number of geese decreased 4.7 times, and in the spring of 2017 a record low number was recorded.

For the Red Book species, unstable indicators are also recorded. For example, for the RBG, the maximum number was recorded in 2011, 2014 and 2018. In the remaining years

Table 4. The number of migrating geese in the spring of 2011–2018 in NKR
4. táblázat A vonuló ludak száma a tavaszi időszakokban 2011 és 2018 között az észak-kazahsztáni régióban

Species	**Numbers, individual**							
	2011	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**
Anser albifrons	536,073	395,733	226,677	330,544	60,819	67,294	30,593	159,108
Anser erythropus	755	385	69	100	8	7	3	120
Anser anser	180	100	195	147	218	586	48	1,729
Anser fabalis	1	1	–	–	6	–	1	–
Branta ruficollis	40,951	26,081	39,57	12,984	1,764	4,490	1,153	18,612
Total	**577,960**	**422,300**	**230,898**	**343,775**	**62,815**	**72,377**	**31,798**	**179,659**

Table 5. Aggregative behavior of geese during the spring migration on the territory of the NKR in 2011–2017
5. táblázat A ludak csapatalkotó magatartása a tavaszi vonulás során az észak-kazahsztáni régióban 2011 és 2017 között

Numbers (individuals)	**from 1 to 10**	**from 11 to 50**	**from 51 to 100**	**more than 100**
Number of flocks	342 (2.7%)	4265 (33.8%)	6542 (51.8%)	1476 (11.7%)
Percentage (%)	1.5	14.8	56.5	27.1
Number of individuals	12,580	122,405	467,099	224,352
Average number of birds in a flock	7.2±2.1	28.7±11.3	71.4±14.1	151.6±46.6

there was a sharp decline in numbers. The maximum number of LWfG during the spring migrations was noted in 2011, 2012 and 2018. From 2015 to 2017 its number remained stably low, i.e. 3 to 8 individuals per season.

When studying the aggregation behavior of birds *(Table 5)*, it was found that flocks of 50 to 100 individuals accounted for 56.5% of the registered. Flocks of 11 to 50 individuals accounted for 34% of registrations (14.8% of the population). The proportion of flocks with more than 100 individuals was 11.7% (27.1% of the total number of migrating birds). Most of the large clusters (73.2%) were observed in 2011–2012.

Migratory stops

The spread of representatives in the spring period by region and specific areas of large flocks are subject to annual changes depending on the nature and extent of use of agricultural land, as well as the hydrological regime and meteorological conditions of a particular season. Using the obtained observation results, we managed to identify 9 their main localizations *(Figure 5)*.

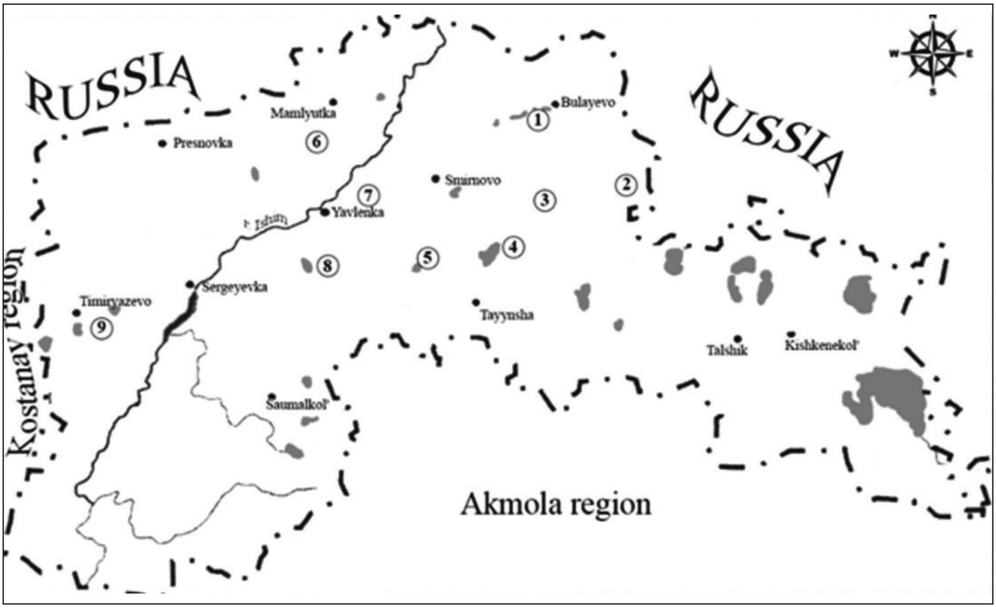


Figure 5. The main stops of geese of the genus *Anser* and *Branta* during spring migration in the territory of NKR (1 – Kamyshlovskiy migration zone; 2 – Vozvyshenskiy migration zone; 3 – Sovetskiy migration zone; 4 – Shaglytenizskiy migration zone; 5 – Balykty-Karasorskiy migration zone; 6 – Mengiserskiy migration zone; 7 – Karatau tract; 8 – Tarangul-Sarykolskiy migration zone; 9 – Timiryazevskiy migration zone)

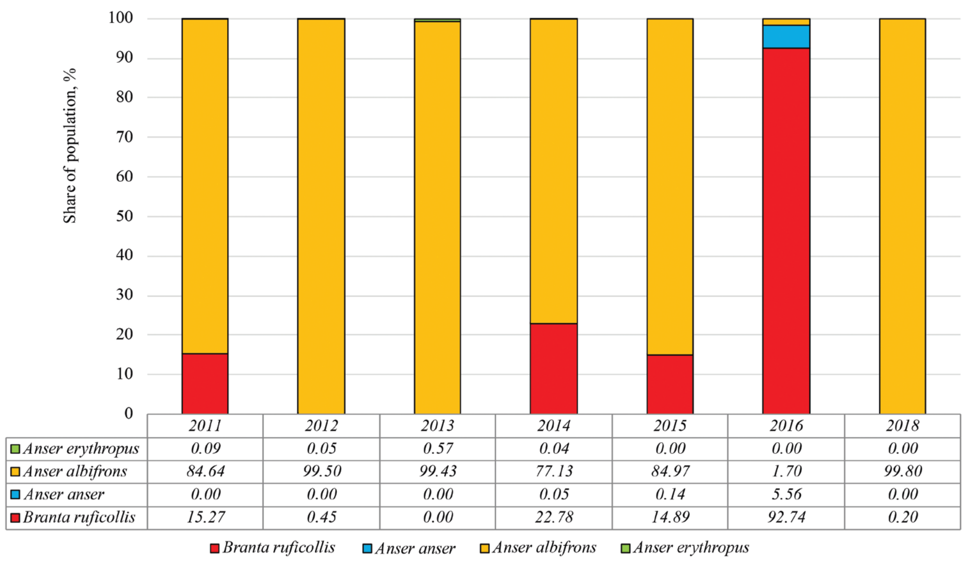
5. ábra Az *Anser* és a *Branta* nemzetségbe tartozó lúdfajok főbb pihenőhelyei a tavaszi vonulás során az észak-kazahsztáni régióban (1 – Kamyshlovskiy vonulási zóna; 2 – Vozvyshenskiy vonulási zóna; 3 – Sovetskiy vonulási zóna; 4 – Shaglytenizskiy vonulási zóna; 5 – Balykty-Karasorskiy vonulási zóna; 6 – Mengiserskiy vonulási zóna; 7 – Karatau terület; 8 – Tarangul-Sarykolskiy vonulási zóna; 9 – Timiryazevskiy vonulási zóna)

Kamyshlovskiy migration zone

The zone is located in the administrative boundaries of the district named after M. Zhumabayev, in the floodplain of the former Kamyshlovka river. Its area, used by birds in different years, is about 13.5 thousand ha. The most important water bodies include a number of freshwater (Pitnoe, Polovinoye, Sukhoe swamp) and brackish (Kamyshlovo, Bolshoye Solenoye). The water area of most of them has dense vegetation (up to 70% of the area), which creates good protective conditions for birds. A significant part of the arable land is occupied by crops, which determines favorable feeding conditions for stopping birds. Among the negative factors, grazing by domestic animals along the coastline and active fishing were noted.

The intensity of use of the considered zone by birds changes throughout the entire observation period. The main limiting factor in the formation of stopover is the hydrological regime, which directly depends on the amount of precipitation during the year. So, in the spring of 2014–2016, the area of the most water bodies of the Kamyshlovskiy migration zone increased significantly due to the large amount of melting water coming from the catchment area. The typology of water bodies has changed and they have lost their significance as a migration stop. In the following years after the filling of water bodies, birds were not recorded in most areas.

The average share of Red Book species was 20.9±30% for RBG and 0.11±0.20% for LWfG *(Figure 6)*. The average annual density of migrating geese in the main water bodies of the zone during the spring migrations is 46.01±87.4 individuals per 100 ha.



	2011	2012	2013	2014	2015	2016	2018
🟩 *Anser erythropus*	0.09	0.05	0.57	0.04	0.00	0.00	0.00
🟨 *Anser albifrons*	84.64	99.50	99.43	77.13	84.97	1.70	99.80
🟦 *Anser anser*	0.00	0.00	0.00	0.05	0.14	5.56	0.00
🟥 *Branta ruficollis*	15.27	0.45	0.00	22.78	14.89	92.74	0.20

Figure 6. The ratio of the number of geese of the genus *Anser* and *Branta* on the Kamyshlovskiy migratory zone in 2011–2018

6. ábra Az *Anser* és a *Branta* nemzetségbe tartozó lúdfajok számának aránya a Kamyshlovskiy vonulási zónában 2011 és 2018 között

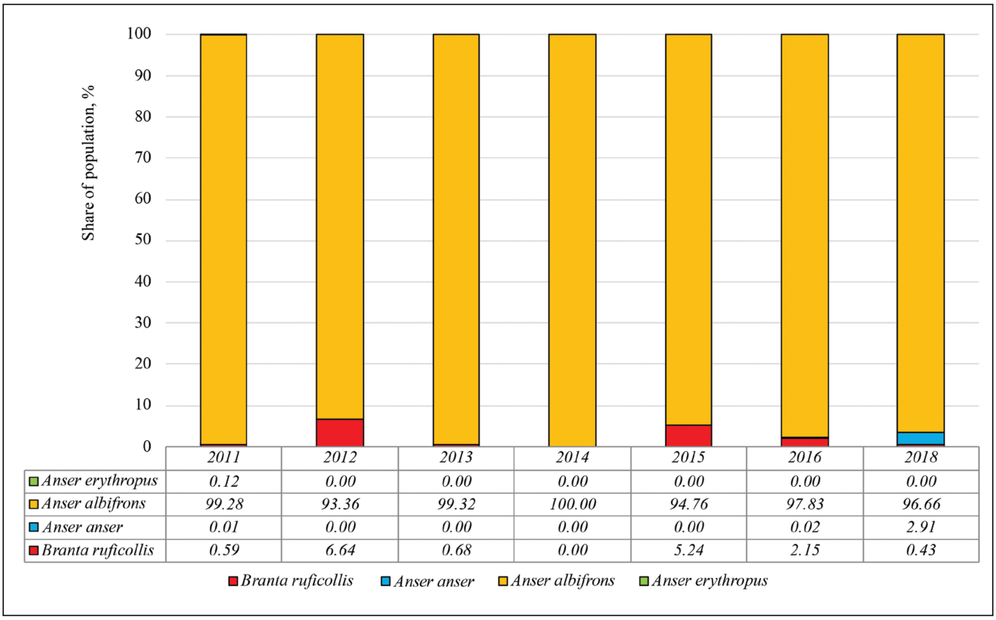
Vozvyshenskiy migration zone

The territory is located in the eastern part of the region, along the border with the Russian Federation (Omsk region). In general, the migration zone covers an area of about 10.5 thousand hectares and has an unexpressed relief, with a large number of lowlands, in which temporary water bodies form in spring. Large reservoirs are represented by lakes Alva and Keltesor. The water area of the lakes has vegetation along the edges, which creates good protective conditions for the birds that stop here. Most of the land is occupied by agricultural (up to 60%) crops (mainly wheat), which creates favorable food conditions for migratory birds. Intensive fishing plays a negative role for birds.

The intensity of the use of the zone as a stopping place for birds is unstable throughout the entire period. The main limiting factor is its hydrological regime. During the migration period, this area represents good conditions for recreation and feeding of geese. Low disturbance factor and many temporary water bodies near the feeding fields result in concentration of birds. Since 2011, 212,913 individuals of geese have been counted in this area, and the share of species from the Red Book is on average 2.3±2.66% *(Figure 7)*.

Sovetskiy migration zone

The territory is located in the central part of the region, within two administrative districts: Akkainskiy and M. Zhumabaev. Within the zone, several independent plots can be



	2011	2012	2013	2014	2015	2016	2018
🟩 *Anser erythropus*	0.12	0.00	0.00	0.00	0.00	0.00	0.00
🟨 *Anser albifrons*	99.28	93.36	99.32	100.00	94.76	97.83	96.66
🟦 *Anser anser*	0.01	0.00	0.00	0.00	0.00	0.02	2.91
🟥 *Branta ruficollis*	0.59	6.64	0.68	0.00	5.24	2.15	0.43

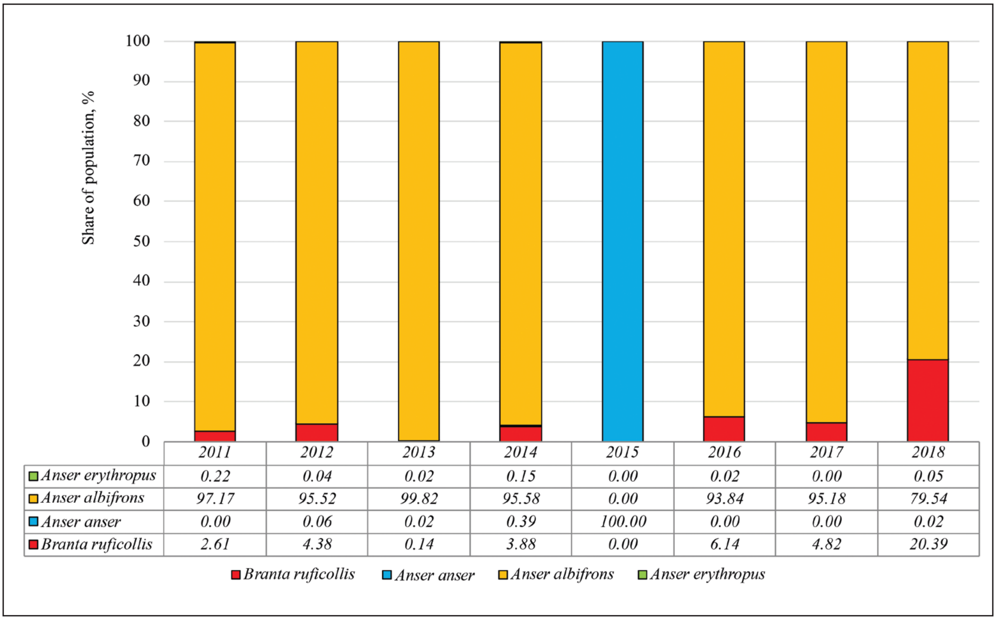
Figure 7. The ratio of the number of geese of the genus *Anser* and *Branta* on the Vozvyshenskiy migration zone in 2011–2018

7. ábra Az *Anser* és a *Branta* nemzetségbe tartozó lúdfajok számának aránya a Vozvyshenskiy vonulási zónában 2011 és 2018 között distinguished, in which the bulk of the birds are concentrated: 1) Letovka (former sovkhoz “Maybalykskiy”); 2) lake Karabul; 3) Kotovsko-Sovetskiy zone, discovered and investigated in the spring of 2018. Most likely, the last site was used by birds for more than a year, but due to the high waterlogging of the territory in spring and the lack of roads, it was not possible to visit it in previous years. In general, the migration zone covers an area of about 120 thousand hectares and has an unexpressed relief, with a large number of lowlands filled with water. In wet years, the territory is difficult for road transport, which increases its importance as a key stop. In addition to lowlands and marshes, there are more than 20 small and large lakes, mostly freshwater ones, which are used by birds for overnight stay. The territory is used in agricultural production (about 70%), and is sown with grain crops. Livestock is underdeveloped. Settlements are small; therefore, the degree of influence of the human population on birds during the spring migration is minimal.

In total, 159,834 individuals of geese, including 17,336 individuals (10.8%) of the Red Book species, were counted in this area. The total average annual density was 58.8±81.3 individuals per 100 ha *(Figure 8)*.

Shaglytenizskiy migration zone

The zone is located in the central part of the region, within 2 administrative districts: Akkayinsky and Tayinshinsky. The total area is about 120 thousand hectares. The zone is located between 2 waterbodies: in the West – lake Shaglyteniz, and in the East – lake Tayinsha. The



	2011	2012	2013	2014	2015	2016	2017	2018
🟩 *Anser erythropus*	0.22	0.04	0.02	0.15	0.00	0.02	0.00	0.05
🟨 *Anser albifrons*	97.17	95.52	99.82	95.58	0.00	93.84	95.18	79.54
🟦 *Anser anser*	0.00	0.06	0.02	0.39	100.00	0.00	0.00	0.02
🟥 *Branta ruficollis*	2.61	4.38	0.14	3.88	0.00	6.14	4.82	20.39

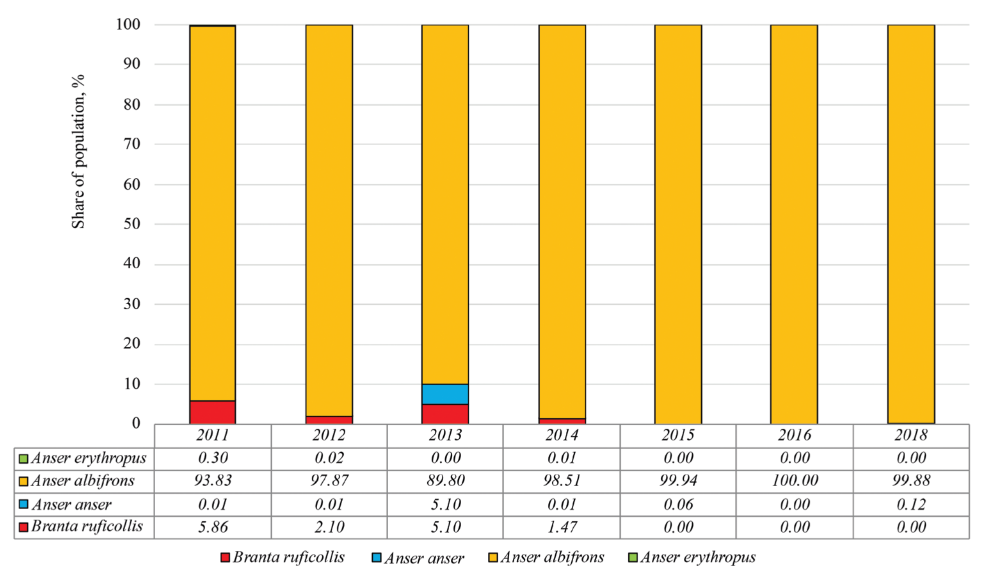
Figure 8. The ratio of the number of geese of the genus *Anser* and *Branta* on the Sovetskiy migration zone in 2011–2018

8. ábra Az *Anser* és a *Branta* nemzetségbe tartozó lúdfajok számának aránya a Sovetskiy vonulási zónában 2011 és 2018 között lakes are freshwater; along the perimeter are thickets that create a natural protective barrier for birds. The rest of the territory has an unexpressed relief surface with lowlands, which in spring form a network of shallow temporary water bodies. A significant part of the territory (55–60%) is used for agricultural purposes and is occupied by grain crops, which determines favorable feeding conditions for stopping birds.

The intensity of using the migratory zone as a stopover is unstable throughout the entire observation period. In years with little snowfall, there are no spring temporary water bodies in the fields, which determine the concentration of migratory birds on key lakes. This is also favored by an increase in surface vegetation up to 60–80%. As the lakes fill, their depth increases, thickets disappear, and accordingly, a decrease in the number of stopping birds is noted. During the years of low water level (2011–2012), 16387 and 71304 individuals of 4 species of geese, respectively, were counted here. Density was 9,583 individuals per 100 ha in 2011 and very high – 41,698 individuals per 100 ha in 2012 *(Figure 9)*. As the lake is filled, thickets of surface vegetation disappear almost completely, the water depth increases almost 2 times, reaching 3 m. For this reason, the water body ceases to play the role of a key stopping area.

Balykty-Karasorskiy migration zone

This zone is located in the central part of the region, in the administrative boundaries of two districts – Akkayinskiy and Tayinshinskiy, covering about 132 thousand hectares. The main landscapes are represented by steppe areas, most of which are plowed up and used for



	2011	*2012*	*2013*	*2014*	*2015*	*2016*	*2018*
🟩 *Anser erythropus*	*0.30*	*0.02*	*0.00*	*0.01*	*0.00*	*0.00*	*0.00*
🟨 *Anser albifrons*	*93.83*	*97.87*	*89.80*	*98.51*	*99.94*	*100.00*	*99.88*
🟦 *Anser anser*	*0.01*	*0.01*	*5.10*	*0.01*	*0.06*	*0.00*	*0.12*
🟥 *Branta ruficollis*	*5.86*	*2.10*	*5.10*	*1.47*	*0.00*	*0.00*	*0.00*

Figure 9. The ratio of the number of geese of the genus *Anser* and *Branta* on the Shaglytenizskiy migration zone in 2011–2018

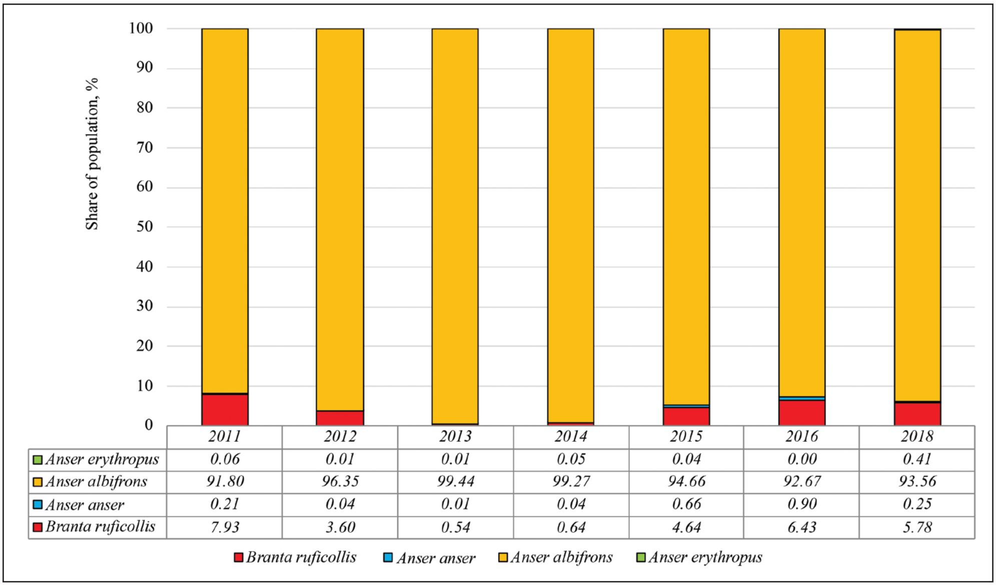
9. ábra Az *Anser* és a *Branta* nemzetségbe tartozó lúdfajok számának aránya a Shaglytenizskiy vonulási zónában 2011 és 2018 között the cultivation of crops. Large water bodies are presented by freshwater (Uzynkol, Balykty, Zhylandy) and brackish (Kumdykol, Malye Balykty, Karasor) lakes. All the main water bodies of the zone have a strip of shallow water, and overgrown vegetation (20–70%) in the water area. The main part of the migration zone is represented by agricultural land used for growing crops, which are a feed resource for migratory birds.

All this in a complex creates favorable conditions for stopping migratory geese in the spring, especially during the period of a general decrease in water level. In total, since the beginning of 2011, 288,500 individuals of 4 species of geese have been registered in this territory. In all the years, the WFG was the leader in numbers and its average annual share in the total aggregations of geese was 95.4±3.1%, the RBG share was 4.2±2.7%. The share of other species is not significant *(Figure 10)*.

Mengiserskiy migration zone

This zone includes water bodies and the territories surrounding them, located in the northern part of the region, on the left coast of the river Ishim, within two administrative districts – Mamlyutskiy and Kyzylzharskiy. In the southern part, the boundary of the zone is Lake Mengiser, in the eastern part – the village Andreyevka, and in the northern part – the village Simaki. The area is about 430 thousand hectares.

The territory is characterized by a slightly undulating relief, the presence of small lakes and swamps. Lowlands during the spring flood are difficult to transport, which reduces the disturbance factor for birds. The key body of water is a shallow bitter-salty lake Mengiser



	2011	2012	2013	2014	2015	2016	2018
🟩 *Anser erythropus*	0.06	0.01	0.01	0.05	0.04	0.00	0.41
🟨 *Anser albifrons*	91.80	96.35	99.44	99.27	94.66	92.67	93.56
🟦 *Anser anser*	0.21	0.04	0.01	0.04	0.66	0.90	0.25
🟥 *Branta ruficollis*	7.93	3.60	0.54	0.64	4.64	6.43	5.78

Figure 10. The ratio of the number of geese of the genus *Anser* and *Branta* on the Balykty-Karasorskiy migration zone in 2011–2018

10. ábra Az *Anser* és a *Branta* nemzetségbe tartozó lúdfajok számának aránya a Balykty-Karasorskiy vonulási zónában 2011 és 2018 között

(4 thousand ha), with extensive shallows in the eastern part and sparse thickets of surface vegetation along the western shore. For smaller water bodies (lake Egora Andreevicha, swamp Krasnaya Shapka) the presence of sites with floating islands and humps that attract geese for overnight is characteristic. A significant part of the migration zone is used for agricultural purposes and is sown (50–55%) with crops, which determines favorable forage conditions for stopping birds.

Totally, 20,767 individuals of 4 species of geese have been counted in the zone since 2013. In almost all the years, the WfG was the leader in numbers. Its average annual share in the total concentrations of geese was 92.7±11.7%. RBG on the second place with share 7.2±11.67%. Share of other species was not significant. The average annual population density of geese in the water bodies of the considered area was 58.8±81.3 individuals per 100 ha.

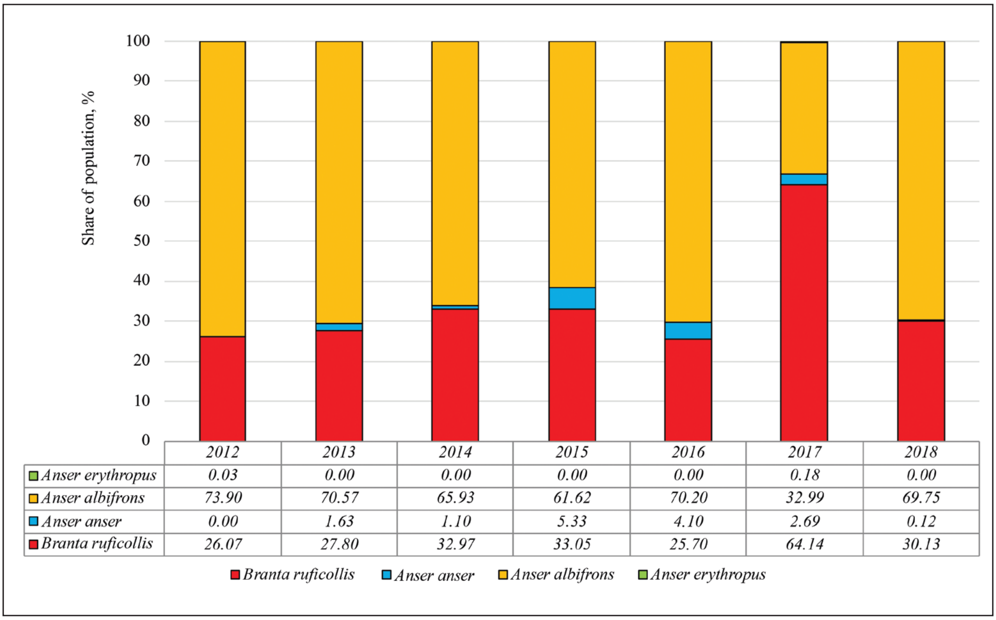
Karatau tract

Tract Karatau is located 400 m east of village Chirikovka of Esilskiy district and 3 km from the main waterway of the region, the Ishim river. The total area of land used by birds in different years, with varying degrees of intensity, is about 670 hectares. It is a network of various-sized relief depressions, filled with water, alternating with hills and islands. During years of high humidity, most of the hills and islands are flooded with water, forming a single shallow water area with areas covered by surface vegetation. A significant part of the territory (40–50%) is used for agricultural purposes and is occupied by crops, which determines favorable feeding conditions for stopping birds. Of the negative factors, it is worth noting the close location of roads (including community significance), which creates a noisy background that causes concern in birds.

The intensity of use of the considered territory as a stopping site for birds is relatively stable throughout the entire observation period. Since 2012, the tract is a place of regular stops for geese during the spring migration. In total, for the period of studies in the spring period, 21,390 individuals of 5 species of geese were counted in this area. The average share of the Red Book species was 34.26±13.5% for RBG and 0.03±0.06% for LWfG *(Figure 11)*. The average annual density of migratory geese in this area in spring is 416.3±332.1 individuals per 100 ha, and the for the Red Book species is 132±93.6 individuals per 100 ha.

Tarangul-Sarykolskiy migration zone

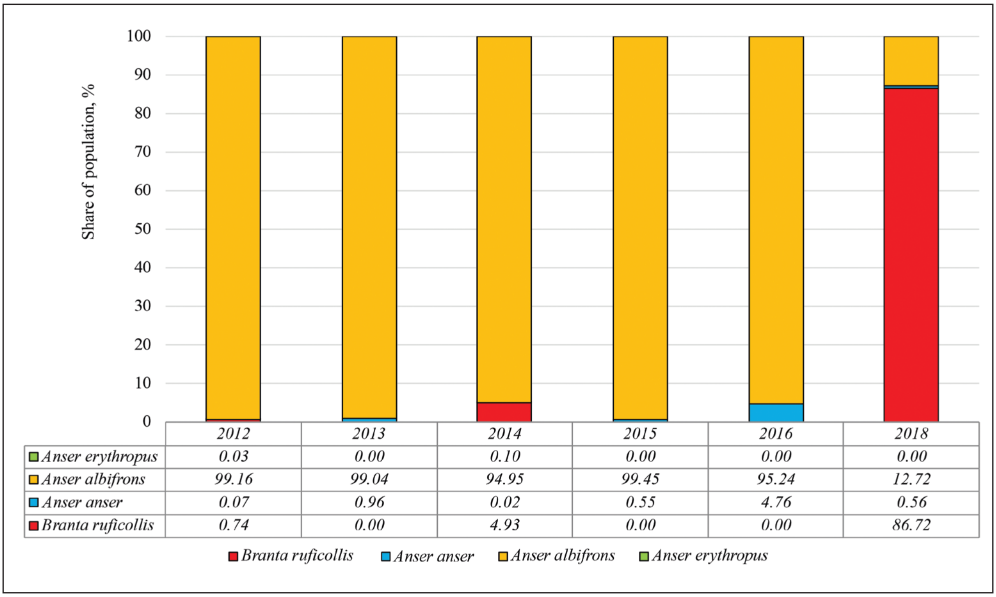
This zone is located in the central part of the region, within the Esilskiy district. The total area is about 5 thousand hectares. The territory is characterized by an unexpressed low relief, partially occupied by swamps, which are filled with water in spring, creating favorable conditions for stopping migratory birds. In the southern border of the zone is the lake Bolshoy Tarangul, and in the north-east the Lake Sarykol and Batpakol swamp. Extensive vegetation bands (up to 250–300 m) are located along the shallow coasts of water bodies. Agricultural activity within the zone is intense, but in the early spring, due to the erosion of roads, it decreases. A significant part of the adjacent territory (55–65%) is sown with crops, which provides the necessary food for migratory birds.



	2012	2013	2014	2015	2016	2017	2018
🟩 *Anser erythropus*	0.03	0.00	0.00	0.00	0.00	0.18	0.00
🟨 *Anser albifrons*	73.90	70.57	65.93	61.62	70.20	32.99	69.75
🟦 *Anser anser*	0.00	1.63	1.10	5.33	4.10	2.69	0.12
🟥 *Branta ruficollis*	26.07	27.80	32.97	33.05	25.70	64.14	30.13

Figure 11. The ratio of the number of geese of the genus *Anser* and *Branta* on the Karatau tract in 2012–2018

11. ábra Az *Anser* és a *Branta* nemzetségbe tartozó lúdfajok számának aránya a Karatau vonulási zónában 2012 és 2018 között



	2012	2013	2014	2015	2016	2018
🟩 *Anser erythropus*	0.03	0.00	0.10	0.00	0.00	0.00
🟨 *Anser albifrons*	99.16	99.04	94.95	99.45	95.24	12.72
🟦 *Anser anser*	0.07	0.96	0.02	0.55	4.76	0.56
🟥 *Branta ruficollis*	0.74	0.00	4.93	0.00	0.00	86.72

Figure 12. The ratio of the number of geese of the genus *Anser* and *Branta* on theTarangul-Sarykolskiy migration zone in 2012–2018

12. ábra Az *Anser* és a *Branta* nemzetségbe tartozó lúdfajok számának aránya a Tarangul-Sarykolskiy vonulási zónában 2012 és 2018 között

The role of this zone as a stopping site for migrating geese in the spring is unstable and is of key importance only in dry years. In total, for the period of research in the spring period, 26,780 individuals of 4 species of geese were counted in this area. The average share of species from the Red Book was 3.2% *(Figure 12)*. The average annual density of migrating geese in the main water bodies of the territory during the spring migrations was 90.7±172.9 individuals per 100 ha.

Timiryazevskiy migration zone

It is located on the southwestern outskirts of the region and borders the Kostanai region. The main terrestrial landscapes are represented by the steppe, 80–85% of which is plowed and is mainly used for sowing grain crops. In this zone, there are three large water bodies: freshwater lake Aksuat and two salt lakes Bolshoy Kak and Maliy Kak. The first lake is up to 79% overgrown with depths of up to 2 m, the next two are shallow lakes (up to 0.7–1 m) with thickets along the coastline and a wide strip of shallow water. During years of lowering the level of the water surface, the area of water areas decreases by 20–40%, also the depth decreases to 0.3–0.5 m. The main part of the territory (40–50%) is used for agricultural purposes and is occupied by grain crops.

The role of this migratory stopping place in the life of migrating geese during the spring period is insignificant. This zone is used by birds not annually and only for a short period of time. During our work, migratory aggregations of geese were noted only in 2014 and 2018. In 2014, 17,670 individuals of 4 species of geese were recorded in this area. Species from the Red Book are registered only on 1 of 3 water bodies: lake Aksuat with about 2000 individuals of the RBG and 7 individuals of the LWfG and their share in the total aggregation was 11.8%. The maximum density is noted for the WfG: 60.6 individuals per 100 ha. In 2018, 11,310 individuals of 3 species were counted in the territory. The WfG was in the first place in terms of numbers (10,939 individuals), and the proportion of Red Book species, compared to 2014, decreased to 3.3%, i.e. 371 individuals.

Discussion

Analysis of the obtained and published data shows that at the local level, interannual fluctuations in the dates of the beginning of spring migration are determined by the presence of a number of meteorological conditions. Compared with the 60s and 70s of the 20th century, the timing of the appearance of the representatives of the group in transit, as well as its end, began to fall on earlier periods. A similar trend was noted in other regions (Fouquet *et al.* 2009). Apparently, the main reason for the general shift in the timing of migration is climate warming in the northern regions of Eurasia, forcing geese to leave their wintering places much earlier (Sokolov 2005, Pistorius *et al.* 2006, Bridge *et al.* 2010, Fox & Walsh 2012, Fox *et al.* 2012, Gashev *et al.* 2017). According to our observations, the average arrival time of GlG correlates with the onset of daytime spring temperatures of 0 °C. Many ornithologists (Gordienko & Drobovtsev 1979, Belyankin & Ilyashenko 1986, Postavnoy 1986) also drew attention to the regularity of the arrival of the first birds during the onset of daytime positive temperatures, although in more northern latitudes migration can begin at lower temperatures (Vengerov 1978). Along with this, there are other opinions about the reasons for the appearance of the first birds. So, according to V. Styanavichus (1983), appearance of the first birds, which include GlG, coincides with the timing of snow melt by 20–40%. Obviously, this fact is due to trophic and morpho-physiological characteristics of birds (Ataev 1978). Herbivorous birds, in particular GlG, use the seeds of various plants as food resources in open areas of land.

The first registration of the remaining studied species (WfG, LWfG and RBG) in the region are timed to the beginning of the second week of April and last until the end of May. The reason for such a long migration period of WfG is the possible difference in the time of departure of birds from different wintering sites, since birds most likely first fly from Caspian wintering areas, and then from European ones, since the second migration routes are much longer (Drobovtsev 1976).

Local influences of various meteorological factors affecting the intensity of migration on different days do not determine the general course of its dynamics, since they are characterized by a one-way progressive change in any considered spring season. The dominance of the general direction is most likely determined by clearly defined landmarks and the location of the end points of the route. The main migration wave follows the Ishim River valley, deviating in a northeasterly direction. A significant change in direction was noted in a single case, which was associated with a sharp deterioration in weather conditions, increased winds of the northern points with gusts of up to 25 m/s and heavy snowfall.

Fluctuations in the number of birds during spring migration in the region are undulating, which is most likely due to regional changes in weather conditions at stopping sites, as well as the important need for birds to combine transit flights with delays to replenish their energy reserves (Dolnik 1976). According to the results of 8-year observations, there was a significant reduction in the number of migrants from 2011 to 2017. The maximum abundance of species and large clusters (73.2%) were observed on the lakes of the region in 2011–2014. In our opinion, the main reason for this was the drought that began in 2008. Geese, deprived of the opportunity to use temporary water bodies and small lakes on migration routes, are forced to concentrate on larger and deeper water bodies that cover a significant part of the area. Usually, geese leave from such sites at the same time, forming large flocks (Dolnik 1976). Starting in 2015, as the water bodies filled with water, the number of birds began to decrease.

Studies have shown that the permanent migration stops of geese in the region in the spring occupy quite large areas. They include 1) grain-sown feeding sites; 2) resting sites represented by temporary water bodies on grain fields; 3) overnight stays located a few kilometers from the feeding places. Over the past decade, permanent stops have formed in the places where the most powerful migration flows have passed. Depending on the hydrological state of a particular territory, the ratio and number of geese inside them may vary over the years.

The instability of the use of various water bodies by birds as sites is due to the hydrological situation of the spring period in different years, the degree of anthropogenic load and disturbing factors on birds. During a period of general decline in water level, part of the coasts is represented by extensive shallows alternating with open areas with vegetation, which provide shelter and the water body is intensively used by birds during spring migrations. Furthermore, on the contrary, during periods of rising water levels, a change in the typology of water bodies occurs, which, in this regard, lose their importance as a place of migration stopping sites due to the redistribution of birds to more favorable places, with less concern.

The observed climate changes, while maintaining this trend in the future, can lead to both negative and positive consequences. Among the first are the instability of temperature conditions in the early spring period, which can lead (in case of snowstorms and frosts) to the migrations of birds that appeared early to the south, which are accompanied by unforeseen expenses of energy resources. At the same time, there are positive aspects for populations. In particular, since spring field work and sowing of grain and other crops in the region begin from May 5–10, the time increases during which the geese will not experience the disturbance factor in the food fields.

In the long run, the importance of the region and its individual sections for migratory birds may change, because in a market economy, more agricultural producers increase the share of cultivated areas sown by industrial crops. If this process continues, the feed value of the region will decrease, and this will lead to the redistribution of some birds outside the study area and reduce the importance of the region for geese staying here.

Conclusions

The results of a study of spring migrations of geese on the territory of Kazakhstan made it possible to clarify a number of features. Over the past 50–60 years, the timing of the appearance of representatives of the group in transit, as well as its end, began to be recorded in earlier periods. The probable cause is climate warming, the result of which are positive temperatures and melting snow observed since mid-March, and by mid-April, the snow cover has completely disappeared and a significant number of temporary water bodies have formed.

The increase in the number of birds in the region is undulating. This is most likely due to regional changes in weather conditions at the places of migration stops, as well as the important need of migrating geese to combine transit flights over areas of scarce feed resources, with delays in places rich in feed during the worst weather conditions to replenish their energy reserves.

Highlighted key migration zones are characterized by a complex of favorable factors providing optimal conditions for migratory birds, hence the highest concentration of geese beings recorded in them. One of the most important factors in the formation of temporary stopover sites for migratory birds is the presence of forage fields with grain crops. Depending on the annual state of a particular territory, the ratio and number of representatives of the considered groups within them may vary. At the local level, interannual fluctuations in the number and density of birds in individual migration zones are determined by the presence of a number of conditions: the amount of spring melt water, the area of spring temporary water bodies on grain fields, as well as the beginning of intensive agricultural work at feeding sites for geese, which determines the perturbation coefficient of migrants.

References

Ataev, K. 1978. Migration of birds in the East Karakum. – Alma-Ata

Belyankin, A. F. & Ilyashenko, V. V. 1986. Migratsii ptits v doline srednego techeniya r. Tomi (Zapadnaya Sibir') osen'yu 1978 goda [Migrations of birds in the valley of the middle stream of the Tom River (Western Siberia) in the autumn of 1978]. – Migrations of Birds in Asia. – Novosibirsk (in Russian)

Bridge, E. S., Kelly, J. F., Bjornen, P. E., Curry, C. M., Crawford, P. H. C. & Paritte, J. M. 2010. Effects of nutritional condition on spring migration: Do migrants use resource availability to keep pace with a changing world? – Journal of Experimental Biology 213(14): 2424–2429. DOI: 10.1242/jeb.041277

Cranswick, P. A., Raducescu, L., Hilton, G. M. & Petkov, N. 2012. International Single Species Action Plan for the conservation of the Red-breasted Goose *(Branta ruficollis)*. – Bonn, AEWA

Cresswell, W., Yerokhov, S., Berezovikov, N., Mellanby, R., Bright, S., Chaves, C. J. & McLaughlin, D. 1999. Important wetlands in northern and eastern Kazakhstan. – Wildfowl 50: 181–194.

Cuthbert, R. & Aarvak, T. (eds.) 2017. Population estimates and survey methods for migratory goose species in Northern Kazakhstan (2016). – Bonn, UNEP/AEWA

Cuthbert, R. J., Aarvak, T., Boros, E., Eskelin, T., Fedorenko, V., Karvonen, R., Kovalenko, A., Lehikoinen, S., Petkov, N., Szilágyi, A., Tar, J., Timonen, S., Timoshenko, A., Zhadan, K. & Zuban, I. 2018. Estimating the autumn staging abundance of migratory goose species in northern Kazakhstan. – Wildfowl 68: 44–69.

Dolnik, V. R. 1976. Theories explaining the discontinuity of migration of birds. Methods for studying the migration of birds. – Moscow, pp. 16–17.

Drobovtsev, V. I. 1972. Dinamika chislennosti i razmeshcheniya serogo gusya v Severo-Kazakhstanskoy oblasti [The dynamics of the number and stationing of Greylag Geese in the North Kazakhstan region]. – Geese in USSR, Tartu, pp. 70–78. (in Russian)

Drobovtsev, V. I. 1976. O yuzhnom puti proleta belolobykh gusey s gollandskikh zimovok [On the southern route of the migration of the White-fronted Geese from the Dutch wintering]. – Proceedings of the Meeting on Commercial Ornithology, Moscow, pp. 87–89. (in Russian)

Filonec, P. P. 1974. Ozera Severnogo, Zapadnogo i Vostochnogo Kazakhstana [Lakes of Northern, Western and Eastern Kazakhstan]. – Moscow: Gidrometeoizdat (in Russian)

Fouquet, M., Schricke, V. & Fouque, C. 2009. Greylag Geese *Anser anser* depart earlier in spring: An analysis of goose migration from western France over the years 1980–2005. – Wildfowl 59: 143–151.

Fox, A. D., Boyd, H., Walsh, A. J., Stroud, D. A., Nyeland, J. & Cromie, R. L. 2012. Earlier spring staging in Iceland amongst Greenland White-fronted Geese *Anser albifrons flavirostris* achieved without cost to refuelling rates. – Hydrobiologia 697(1): 103–110. DOI: 10.1007/s10750-012-1174-1

Fox, A. D. & Walsh, A. 2012. Warming winter effects, fat store accumulation and timing of spring departure of Greenland White-fronted Geese *Anser albifrons flavirostris* from their winter quarters. – Hydrobiologia 697(1): 95–102. DOI: 10.1007/s10750-012-1173-2

Gashev, S. N., Aleshina, A. O., Zuban, I. A., Lupinos, M. Y., Mardonova, L. B., Mitropolskiy, M. G., Selyukov, A. G., Sorokina, N. V., Stolbov, V. A. & Shapovalov, S. I. 2017. Holocene faunal trends in West Siberia and their causes. – Izvestiya, Atmospheric and Oceanic Physics 53(8): 791–803. DOI: 10.1134/S0001433817080059

Gordienko, N. S. & Drobovtsev, V. I. 1979. O vesennem pereselenii i gnezdovanii Podicipedidae v severnoy chasti Kazakhstana [On the spring migration and nesting of Podicipedidae in northern Kazakhstan]. – The Pan-Soviet Conference of Young Scientists "Ecology of Bird Nesting and Methods for Studying It": 51–52. Samarkand (in Russian)

Isakov, Yu. A. 1969. O sostoyanii resursov vodoplavayushchikh ptits SSSR [On the state of the resources of waterfowl of the USSR]. – Waterfowl resources in the USSR, their reproduction and use 3: 70–78. Moscow (in Russian)

Lorentsen, S-H., Øien, I. J. & Aarvak, T. 1998. Migration of Fennoscandian Lesser White-fronted Geese *Anser erythropus* mapped by satellite telemetry. – Biological Conservation 84(1): 47–52. DOI: 10.1016/S0006-3207(97)00088-8

Pistorius, P., Follestad, A. & Taylor, F. 2006. Temporal changes in spring migration phenology in the Norwegian Greylag Goose *Anser anser*, 1971–2004. – Wildfowl 56: 23–36.

Postavnoy, G. V. 1986. Sroki sezonnykh migratsiy v Ara-Karagay [Timing of seasonal migrations in Ara-Karagai]. – Migrations of Birds in Asia, Novosibirsk, pp. 76–82. (in Russian)

Rozenfeld, S. B., Timoshenko, A. Y. & Zuban, I. A. 2016. Monitoring sostoyaniya populyatsiy gusey I kazarok Severo-Kazakhstanskoy migratsionnoy ostanovki kak osnova dlya razrabotki mer po ikh sokhraneniyu

[Monitoring of the state of geese and *Branta* populations of North Kazakhstan migration stop as a basis for the development of measures for their conservation]. – Casarca 19(1): 94–128. (in Russian)

Sokolov, L. V. 2005. Vliyaniye izmeneniya klimata na fenologiyu ptits [Impact of climate change on phenology of birds]. – Anseriformes of Northern Eurasia, St. Petersburg, pp. 238–240. (in Russian)

Styanavichyus, V. 1983. Izucheniye vliyaniya gidrometeorologicheskikh faktorov na sroki prileta ptits v rayon zapovednika Zhuvintas [Study of the influence of hydrometeorological factors on the time of arrival of birds in the area of the reserve Juvintez]. – The Second Baltic Ornithological Conference, Tallinn, pp. 202–204. (in Russian)

Tolvanen, P., Litvin, K. E. & Lampila, P. 1999. Monitoring the autumn staging of Lesser White-fronted Geese in north-western Kazakhstan. – In: Tolvanen, P., Øien, I. J. & Ruokolainen, K. (eds.) Fennoscandian Lesser White-fronted Goose conservation project. – Annual Report 1998, Helsinki: WWF, pp. 42–46.

Vangeluwe, D., Rozenfeld, S. B., Dmitriev, A. E. & Bulteau, V. 2012. Preliminary results from GPS remote tracking of Red-breasted Geese *(Branta ruficollis)* from Gydan Peninsula (Russia) breeding grounds. – Casarca 15(2): 80–90.

Vengerov, M. P. 1978. O vesennem pereselenii lebedya-klikuna na Nizhnyuyu Ob' [On the spring migration of the Whooper Swan on the Nizhnyaya Ob']. – The Second Pan-Soviet Bird Migration Conference 2: 24–25. Alma-Ata (in Russian)

Vilkov, V. S. 1989. Biologiya vodoplavayushchikh ptits lesostepi Severnogo Kazakhstana [Biology of waterfowl of forest-steppe of North Kazakhstan]. – PhD Thesis, Moscow (in Russian)

Vilkov, V. S. 2011. Migratsii krasnozoboy kazarki *Branta ruficollis* v Severo-Kazakhstanskoy oblasti [Migration of *Branta ruficollis* in North Kazakhstan region]. – Russian Ornithological Journal 20(647): 716–725. (in Russian)

Vilkov, V. S. & Zuban', I. A. 2017. Perspektivnyye klyuchevyye ornitologicheskiye territorii Severo-Kazakhstanskoy oblasti [Perspective key ornithological territories of North Kazakhstan region]. – Collection of Reports of the XIX. International Scientific and Practical Conference "Problems of River Basin Management during the Development of Siberia and the Arctic in the Context of Global Climate Change in the XXI. Century", Tyumen: TIU., pp. 41–45. (in Russian)

Yanushevich, A. I. 1940. Materialy po biologii vodoplavayushchey dichi Baraby [Materials on the biology of waterfowl of Baraba]. – Biological Institute of Tomsk State University (in Russian)

Yanushevich, A. I. & Zolotareva, O. S. 1947. Vodoplavaiushchie ptitsy Baraby [Waterfowl of Baraba]. – Novosibirsk (in Russian)

Yerokhov, S. N. 2006. Past and current status of Anatidae populations in Kazakhstan. – In: Boere, G. C., Galbraith, C. A. & Stroud, D. A. (eds.) Waterbirds Around the World. – Edinburgh, UK: The Stationery Office, pp. 269–274.

Yerokhov, S. N. 2013. The current status of the Lesser White-fronted Goose *Anser erythropus* in Kazakhstan: Monitoring, threats and conservation measures. – Ornis Norvegica 36: 47–51. DOI: 10.15845/on.v36i0.440

Zuban', I. A. & Vilkov, V. S. 2015. Monitoring gusya-piskul'ki na vodoyemakh severo-kazakhstanskoy oblasti v 2014 godu [Monitoring of Lesser White-fronted Goose in the waters of North Kazakhstan region in 2014]. – Bulletin of Tyumen state University. Ecology and Nature Management 1(2): 143–151. (in Russian)

sciendo

Ornis Hungarica 2020. 28(1): 49–64.
DOI: 10.2478/orhu-2020-0004

Avian assemblage along an urban gradient: diversity, abundance and richness

Ghulam Mustafa Rashid[1], Abida Butt[1*], Abdul Qadir[2] & Mirza Habib Ali[3]

Received: March 23, 2020 – Revised: June 11, 2020 – Accepted: June 13, 2020

Rashid, G. M., Butt, A., Qadir, A. & Ali, M. H. 2020. Avian assemblage along an urban gradient: diversity, abundance and richness. – Ornis Hungarica 28(1): 49–64. DOI: 10.2478/orhu-2020-0004

Abstract Diversity in avian assemblages of urban (UR), peri-urban (PE) and rural (RU) areas was studied to explore variations in the avian community dynamics in rural – urban gradient. For this purpose, sampling was done from September 2013 to August 2015. A total of 35 sites, each covering an area of 300 m^2 were sampled by using point count method. At each site, randomly three points (minimally 5 m apart from each other) were selected to study the birds. According to data, species richness ($F_{2, 32}$=47.18, P<0.001) varied significantly along a rural-urban gradient. A significant difference in avian density per sampling site ($F_{2, 32}$=105.41, P<0.001) was also observed along urbanization gradient. In PE and RU areas, avian assemblages were more diverse than UR areas. Among avian guilds, omnivores were the most abundant in UR while insectivores in PE areas. Frugivores and carnivores were abundant in RU areas. Granivores were recorded in all habitats with similar diversity. A close association was recorded in bird density of RU and PE areas than UR areas. Bird species richness and diversity showed negative correlation with built area and positive correlation with vegetation cover in an area.

Keywords: avian guilds, species richness, abundance, avian diversity, habitat structure, urban (UR), peri-urban (PE), rural (RU)

Összefoglalás Három madárközösség, városi (UR), városhoz közeli (PE) és vidéki (RU) diverzitását és a dinamikáját tanulmányoztuk 2013. szeptember és 2015. augusztus között. Összesen 35, egyenként 300 m^2 területen számoltuk össze a madarakat és madárfajokat. Minden mintavételi terület további 50 m^2-es részekre lett felosztva. A fajgazdagság ($F_{2, 32}$= 47,18, P<0,001) jelentős változatosságot mutatott a vidéki-városi gradiens mentén. A mintaterületenkénti madársűrűség szignifikáns különbséget mutatott ($F_{2, 32}$= 105,41, P<0,01) a városiasodás mértéke mentén. A városhoz közeli és vidéki területek madárközössége változatosabb, mint a városi. Öt különböző madár-guildet azonosítottunk. A mindenevők voltak a leggyakoribbak a városban, míg a rovarevők nagy abundanciát mutattak a városhoz közeli területeken. A gyümölcsevők és a ragadozók a vidéki területeken voltak a leggyakoribbak. Szignifikáns összefüggés adódott a madársűrűség és az élőhely szerkezete között a vidéki és a városhoz közeli területek esetében, mind a klaszter analízis, mind a Sorensen hasonlósági koefficiens alapján. A fajgazdagság és diverzitás negatív összefüggést mutatott az épített területek arányával, de pozitívat a növényborítottsággal.

Kulcsszavak: madár guildek, fajgazdagság, faj abundancia, madár diverzitás, élőhelyszerkezet, városi, városhoz közeli, vidéki

[1] *Department of Zoology, University of Punjab, Quaid-e Azam Campus, Lahore, Pakistan*
[2] *College of Earth and Environmental Sciences, University of the Punjab, Lahore, Pakistan*
[3] *Pakistan Science Foundation, Islamabad, Pakistan*
**corresponding author: abidajawed.zool@pu.edu.pk*

Introduction

Urbanization is considered as the leading force behind habitat fragmentation and degradation (Seress & Liker 2015, Leveau & Leveau 2016, Hensley 2018) but its consequences on avian biodiversity are studied only sparingly in Pakistan (Joshua & Ali 2011, Ali *et al.* 2013, Khan *et al.* 2014, Abbasi *et al.* 2015, Ali *et al.* 2016, Altaf *et al.* 2018). Urban expansion has impacted local avian species dynamics worldwide (Rottenborn 1999, Melles *et al.* 2003, White *et al.* 2005, Chace & Walsh 2006, Aronson *et al.* 2014, Peck *et al.* 2014).

Avian communities respond differently to urban development (Hostetler 2001, Lim & Sodhi 2004, Ortega-Álvarez & MacGregor-Fors 2009, Trammell & Bassett 2012). Their density increases and richness decrease as they approach the urban core. Omnivore fauna is almost similar in urban core throughout the world (McKinney 2008, Garaffa *et al.* 2009, Dallimer *et al.* 2012) and holds a few, very abundant species (Bellanthudawa *et al.* 2019). Urbanization also leads to a numerical increase in exotic species and decrease in native species (McKinney 2006, van Rensburg *et al.* 2009, Luck & Smallbone 2010, Sol *et al.* 2017). Relative contribution of introduced and native species influences the response patterns of the total avian fauna (Hansen & Urban 1992, Lim & Sodhi 2004, Villegas & Garitano-Zavala 2010).

Many studies reported that urbanization is decreasing the diversity of bird species due to loss of habitat. Fernandez-Juricic and Jokimäki (2001) reported that wooded trees in urban areas can increase landscape connectivity by increasing alternative foraging and nesting sites for birds in breeding season. Increased size of parks may enhance diversity and density of birds in urban habitats. The abundance of resident breeding birds is negatively affected by urban sprawl (van Rensburg *et al.* 2009). The work of van Rensburg *et al.* (2009) reported that the process of biotic homogenization increase in alien bird species in urban habitat. Parsons *et al.* (2006) documented that native vegetation in gardens of urban habitats positively influence the density of small birds. In Southeast Asia, heavy losses of native habitat resulted in 13-85% of decline in biodiversity in the region, including birds (Yap & Sodhi 2004, Peh 2010). However, in Pakistan a very little work has been done so far. Altaf *et al.* (2018) recorded avian diversity around river Chanab, Pakistan. They documented decrease in avian diversity from forest habitats to urban habitats. The study showed that bird diversity in urban habitat is related with anthropogenic activities and vegetation cover in the area. Joshua and Ali (2011) reported an increase in abundance of granivorous birds in densely populated areas of Lahore city that have pockets of vegetation Ali *et al.* (2013) reported that old residential areas of Islamabad city as main nesting and roosting sites of Feral Pigeons *(Columba livia domestica)*. The density of pigeons change with rooting and nesting sites and available food and water sources.

The aim of the study is to analyze the structure of residing and breeding bird community along urbanization gradient with an emphasis to explore effect of urbanization on avian assemblage. The following hypotheses were tested through this study.

1. How much species diversity and relative abundance of avifauna is similar in UR, PE and RU areas?
2. On what landscape components (viz., built area, small vegetation, bushes, woody structure and water bodies/watered soil) avian diversity depends along rural-urban gradient?

Material and methods

Study area

The present study was conducted in Gujranwala district (32.1877°N, 74.1945°E, 226 m asl) which is the 7th most populous district of Pakistan with a current human population exceeding over two million (Hussain *et al.* 2012, Minallah *et al.* 2016, Basit *et al.* 2018). Climatic conditions highly varied and temperatures above 45 °C was recorded in summer and close to or below freezing point during winter nights (Mehmood *et al.* 2017). It is located in the alluvial plains of Indus with the Chenab in north and the Ravi in the south covering an area of 3198 km^2. The study area (approximately 226 km^2) represents a mosaic of urban (49 km^2), peri-urban (30 km^2) and rural (147 km^2) areas.

Sampling strategy

Based on proportion of built area, the study area was divided into three zones i.e. urban (UR), peri-urban (PE) and rural (RU) following Marzluff and Ewing (2001), Clergeau *et al.* (2006) and McKinney (2002) using geographic information system (GIS) *(Figure 1)*. In

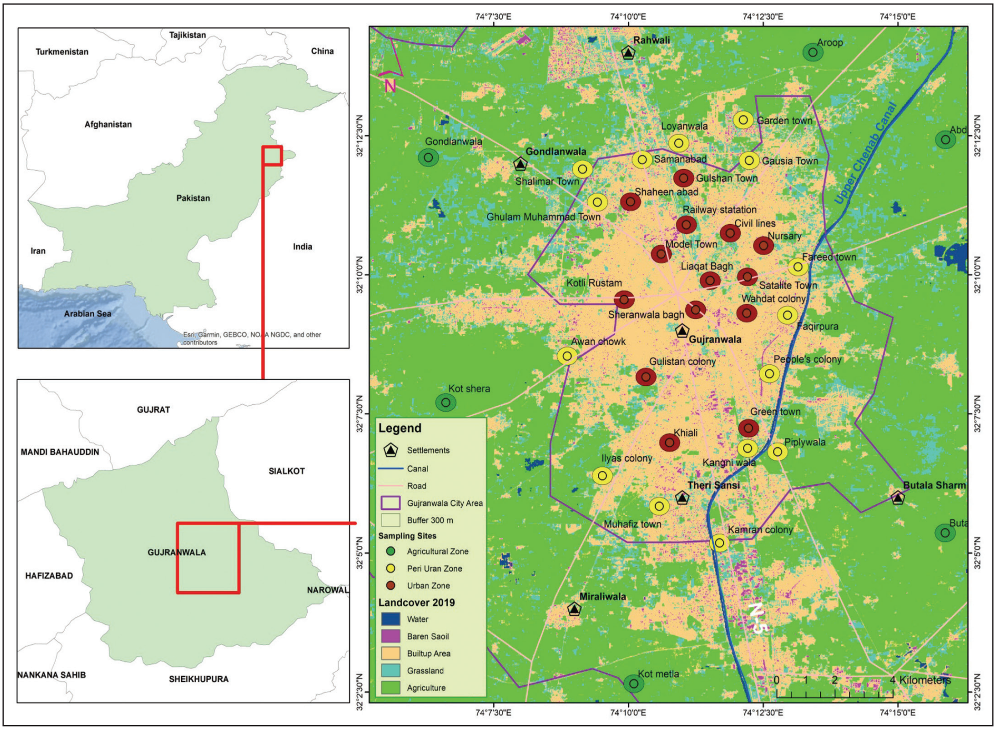


Figure 1. Location of sampling sites with land cover classes in different ecological zones along rural-urban gradient

1. ábra A mintavételi területek elhelyezkedése és felszínborítottságuk a különböző ökológiai zónákban each zone, different site each of 300 m^2, was selected to study the density and diversity of birds. At each site, the data of residential area, vegetation cover, and water bodies or watered soil was recorded using GIS (Anjum *et al.* 2016).

Avian diversity and density was recorded from all (UR, PE and RU) sites each month for a period of two years extending from September 2013 to August 2015. A total of 35 study sites were sampled once every month for 10 min. At each site, three points approximately 5 m apart from each other, were randomly selected for the survey of birds. Surveys were conducted in clear skies avoiding windy or rainy weather in evening (3–4 p.m., until sunset) to collect data of resident bird only. At each study point, birds present within 5 m radius on the grounds and on plantation were recorded. For this purpose, Olympus (10×50) binocular was also used to see birds present on the tree. High flying individuals were not recorded in the data. For identification Ali and Ripley (1983), Grimmett *et al.* (2016) and (Davidar *et al.* 1997) were used as ready reference.

Guild diversity

All avian species encountered during this study were classified into five guilds viz., granivores, frugivores, carnivores, insectivores and omnivores. Percentage share in the abundance of these guilds was calculated for each ecological zone (Jongman *et al.* 1995, Fraterrigo & Wiens 2005).

Data analysis

Relative abundance of bird species was used to determine basic ordinal scales of abundance (abundant > 7.0, common 5.1–7.0, frequent 2.1–5.0, uncommon 0.6–2.0 and rare 0.0–0.5) (Aynalem & Bekele 2008). Rarefaction curve was used to compare species diversity across habitat along the rural-urban gradient. The species richness and species abundance in three zones viz., UR, PE, and RU was plotted. The steeper curves indicated greater diversity in bird communities. The total number of species recorded for each site was considered as species richness due to equal effort of sampling at each site. For diversity, Shannon-Wiener index and for evenness, Pielou J index was calculated for each sampling site (Magurran 1988). Sorensen similarity index was applied to compare habitats on the bases of abundance data. One way ANOVA with Tukey post-hoc test was used to compare the abundance of birds in each area.

Cluster Analysis (UPGMA) was used to reveal the similarity in bird composition between different areas (Kent & Coker 1992). Canonical Correspondence analysis (CCA) revealed the association of bird species with different landscape classes along the rural urban gradient (Melles *et al.* 2003). For UPGMA and CCA, bird species that have relative abundance < 2.00 in overall abundance data per sampling site were not included in the analysis and considered as rare species.

Results

Diversity abundance and richness of the avian fauna of the three zones

To study avian diversity, 35 sites (14 UR, 15 PE and 6 RU) were sampled for two years *(Table 1, Figure 1)*. A total of 7891 birds belonging to 30 species were observed along the rural-urban gradient. Avian density was highest in RU than UR and PE areas ($F_{2, 32}$=21.41, P=0.001) *(Table 2)*. However, no difference was recorded in the bird density of UR and PE areas. Four abundant species viz., *Pycnonotus cafer*, *Corvus splendens*, *Acridotheres tristis*, and *Passer domesticus* accounted for 52.08% of total density *(Figure 2)*. The highest species richness was recorded in RU areas (30 species) followed by PE (24) and UR (14) areas. Out of thirty species, 14 were present in all three areas viz., UR, PE and RU but differ in their densities. Rarefaction accumulation cure of overall bird species showed sufficient sampling in all studied areas and significantly low richness in UR areas than PE and RU areas ($F_{2, 32}$=47.18, P=0.001) *(Figure 3)*. According to Sorensen coefficient UR and PE areas show 74%, PE and RU areas 85% and UR and RU areas 64% similarity in bird species. The avian diversity was highest in RU and lowest in UR areas ($F_{2, 32}$=32.57, P=0.001). Species evenness in UR and PE was significantly higher than RU areas ($F_{2, 32}$=10.15, P=0.001).

Avian community structure (guild)

A total of five feeding guilds of avian species were recorded in the data i.e., granivores, frugivores, insectivores, carnivores and omnivores. Among avian guilds, omnivores were the most abundant in UR while insectivores in PE areas. Frugivores and carnivores were abundant in RU areas. Granivores were recorded in all habitats with similar diversity. The highest percentage of carnivorous birds in RU areas indicated their association with the availability of a variety of insect prey items in croplands *(Figure 4)*.

Impact of landscape

The average composition of all the areas is given in *Table 3*. Results showed the highest percentage of the residential area in UR, low vegetation in RU and woody plants in PE. A slight difference in the percentage of shrub cover was observed in PE and RU. The highest percentage of water bodies was observed in RU.

A negative correlation of bird diversity and residential area (km^2) (R^2=0.38, $F_{1, 34}$=20.34, P<0.001) and positive correlation in bird diversity and small vegetation (R^2=0.44, $F_{1, 34}$=26.03, P<0.001) was recorded along rural urban gradient. However, species richness and diversity did not show any relationship with woody tree cover (km^2), bush cover and water bodies *(Figure 5)*.

Cluster analysis depicted that on the basis of species abundance, RU and PE areas showed a close relationship with each other than UR areas *(Figure 6)*. The canonical correspondence analysis (CCA) explained the association of dominant bird species with different components of landscape viz., residential area, Low vegetation cover, woody plants, shrubs

Table 1. Bird species richness (S) and abundance (N) for various study sites
1. táblázat Fajgazdagság (S) és abundancia (N) a különböző vizsgálati területeken

Site No.	Sites	Location of site	S	N
1	Civil lines	Urban Zone	14	204
2	Gulshan Town	Urban Zone	13	208
3	Model Town	Urban Zone	14	315
4	Nursary	Urban Zone	13	182
5	Railway station	Urban Zone	13	272
6	Satalite Town	Urban Zone	12	328
7	Sheranwala Bagh	Urban Zone	13	213
8	Liaqat Bagh	Urban Zone	11	140
9	Green town	Urban Zone	12	97
10	Kotli Rustam	Urban Zone	9	111
11	Khiali	Urban Zone	13	92
12	Shaheen abad	Urban Zone	14	136
13	Gulistan colony	Urban Zone	13	128
14	Wahdat colony	Urban Zone	12	262
15	Awan chowk	Peri-urban Zone	13	82
16	Loyanwala	Peri-urban Zone	16	102
17	Ghulam Muhammad Town	Peri-urban Zone	16	67
18	Gausia Town	Peri-urban Zone	10	52
19	Kangni wala	Peri-urban Zone	15	122
20	Piplywala	Peri-urban Zone	15	121
21	Ilyas colony	Peri-urban Zone	11	63
22	Kamran colony	Peri-urban Zone	12	75
23	Garden town	Peri-urban Zone	22	341
24	People's colony	Peri-urban Zone	18	352
25	Shalimar Town	Peri-urban Zone	20	251
26	Muhafiz Town	Peri-urban Zone	22	331
27	Fareed town	Peri-urban Zone	20	132
28	Faqirpura	Peri-urban Zone	15	139
29	Samanabad	Peri-urban Zone	14	129
30	Gondla wala	Agriculture Zone	24	325
31	Aroop	Agriculture Zone	26	443
32	Kot shera	Agriculture Zone	28	539
33	Butala sharm Singh	Agriculture Zone	28	669
34	Abdal	Agriculture Zone	23	382
35	Kotmetla	Agriculture Zone	26	425

Table 2. Ordinal scale of avian relative abundance per sampling site of study
2. táblázat A madarak relatív abundanciájának rangskálája az egyes mintavételi területeken UR – városi, PE – városhoz közeli, RU – vidéki

Bird species	**UR/site**	**PE/site**	**RU/site**	**N**	**RA**	**Ordinal scale**
Vanellus indicus	0	1	10	11	1.35	Uncommon
Columba livia	19	6	5	30	3.67	Frequent
Psittacula krameri	2	5	16	23	2.83	Frequent
Athene brama	0	0	2	2	0.28	Rare
Apus apus	0	2	3	5	0.64	Uncommon
Hylcyon smymensis	0	0	9	9	1.06	Uncommon
Upupa epops	0	1	0	1	0.18	Rare
Motacilla alba	6	7	28	41	5.01	Common
Coracina melaschistos	0	2	2	4	0.49	Rare
Pycnonotus cafer	12	12	43	67	8.25	Abundant
Dicrurus macrocercus	5	6	14	25	3.11	Frequent
Corvus splendens	48	17	30	95	11.66	Abundant
Acridotheres ginginianus	16	5	5	26	3.18	Frequent
Acridotheres tristis	15	20	86	121	14.83	Abundant
Passer domesticus	19	28	95	142	17.34	Abundant
Spilopelia senegalensis	6	11	15	32	3.88	Frequent
Milvus migrans	32	7	12	51	6.27	Common
Centropus sinensis	0	0	3	3	0.37	Rare
Cinnyris asiaticus	0	0	5	5	0.61	Uncommon
Bubulcus ibis	0	6	22	28	3.41	Frequent
Ardeola grayii	0	1	4	5	0.56	Uncommon
Streptopelia orientalis	0	1	4	5	0.64	Uncommon
Riparia riparia	4	7	6	17	2.07	Frequent
Cercomela fusca	0	1	10	11	1.33	Uncommon
Turdus merula	0	2	1	3	0.31	Rare
Turdoides striata	3	3	16	22	2.75	Frequent
Dinopium benghalense	0	0	2	2	0.27	Rare
Egretta garzetta	0	0	3	3	0.37	Rare
Merops orientalis	6	6	11	23	2.84	Uncommon
Gracupica contra	0	1	2	4	0.44	Rare
	192	**157**	**463**	**817**		

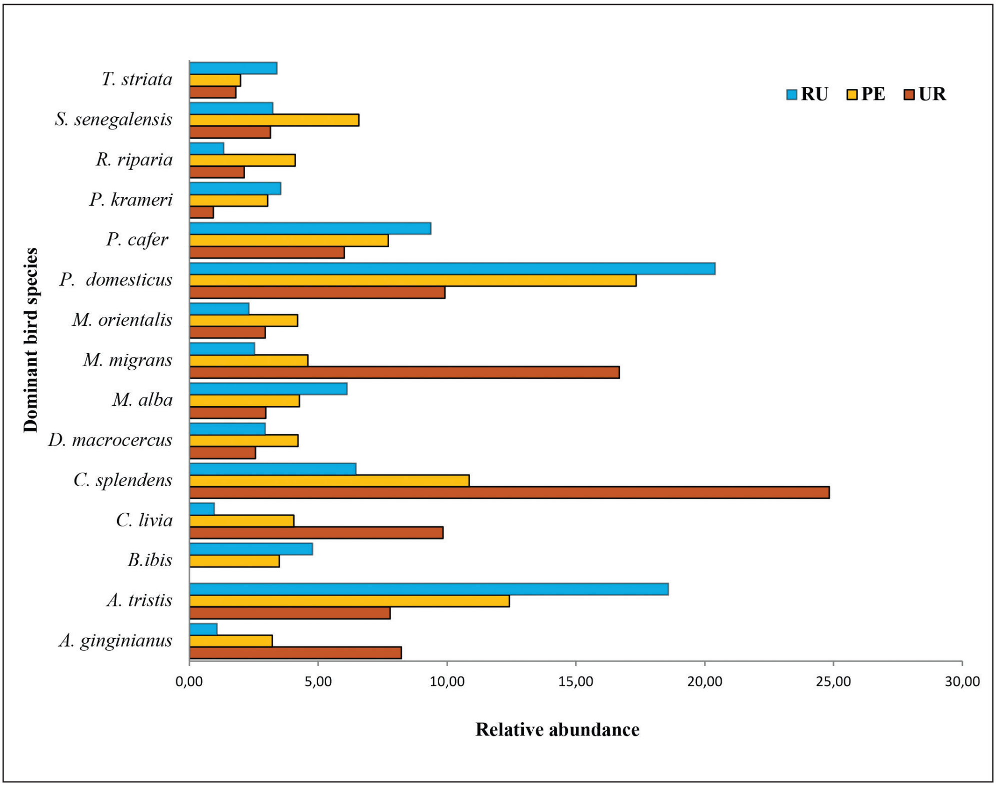


Figure 2. Variations in relative abundance per sampling site of bird species (excluding <2.00 of relative abundance) in different habitats along urban gradient

2. ábra A madárfajok relatív abundanciájának változatossága mintaterületenként a különböző élőhelyeken (a 2-nél kisebb relatív abundanciájú fajok kivételével). UR – városi, PE – városhoz közeli, RU – vidéki

Table 3. Landscape classification in 300 m^2 of circle area at each sampling site along rural-urban gradient

3. táblázat A területborítottság osztályozása a 300 m^2-es mintaterületeken. UR – városi, PE – városhoz közeli, RU – vidéki

Landscape classes	UR (n=14)			PE (n=15)			RU (n=6)		
	Av. Area (Km^2)	SD	Area %age (Km^2)	Av. Area (Km^2)	SD	Area %age (Km^2)	Av. Area Km^2)	SD	Area %age (Km^2)
Residential area	207.48	36.27	73.42	109.28	8.23	38.67	20.67	3.42	7.31
Low vegetation	45.59	24.42	16.13	85.82	14.94	30.37	217.43	6.07	76.94
Woody plants	5.94	4.79	2.10	19.03	14.63	6.73	4.45	1.20	1.57
Shrubs	22.25	17.10	7.87	59.56	20.10	21.08	34.50	4.39	12.21
Water body or Watered Soil	1.33	1.66	0.47	8.91	7.60	3.15	5.55	0.66	1.96

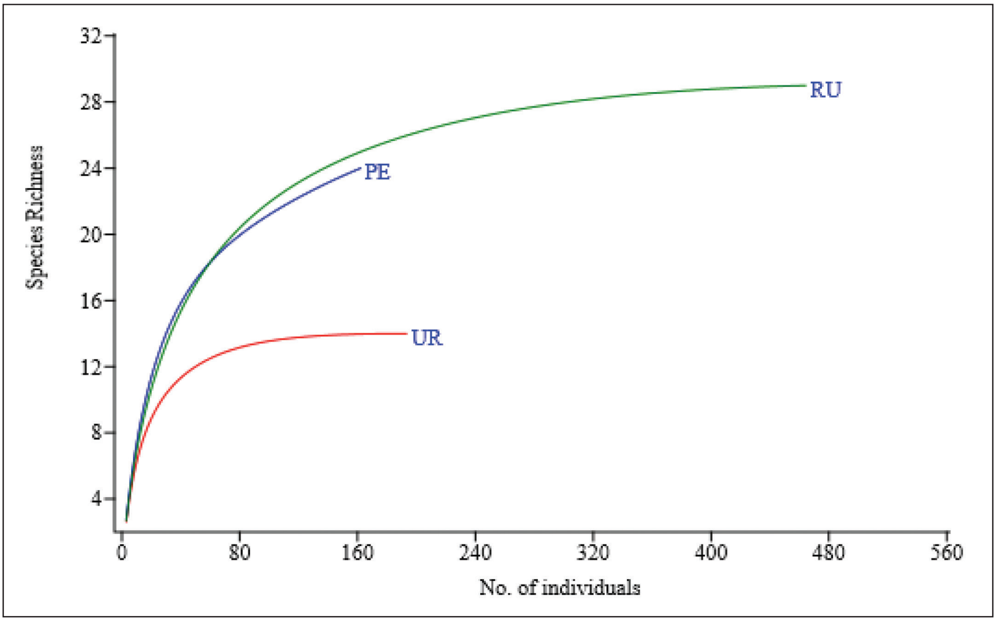


Figure 3. Rarefaction curve showing bird species richness along urban gradient on the basis of the number of individuals / sampling site

3. ábra A fajgazdagság ritkulási görbéje a mintavételi területek egyedszáma alapján. UR – városi, PE – városhoz közeli, RU – vidéki

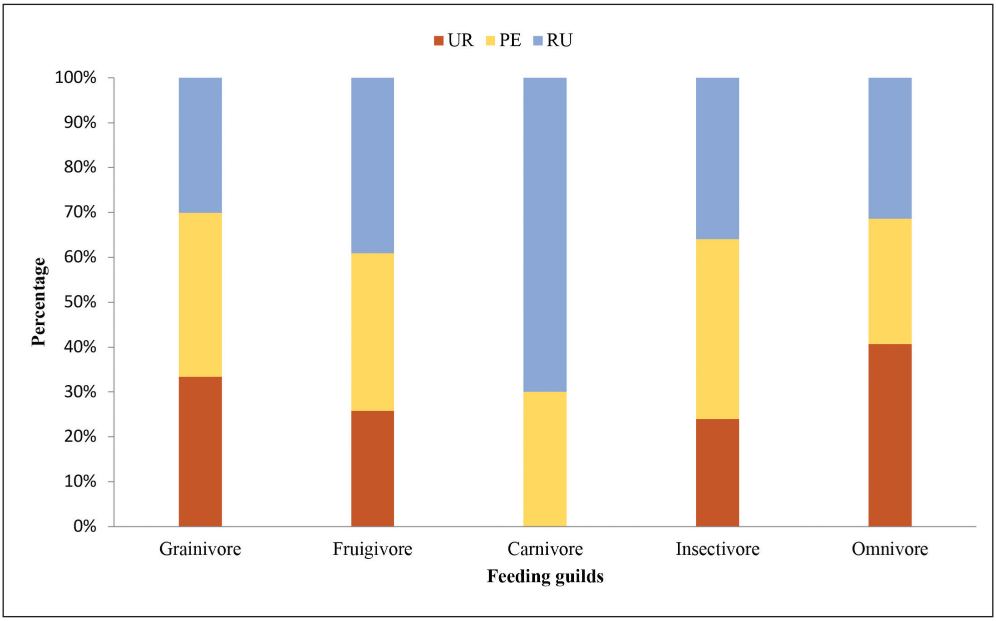


Figure 4. Percentage share of different feeding guilds of birds along urban gradient on overall data

4. ábra A különböző táplálkozási guildek százalékos megoszlása a teljes adatsor alapján. UR – városi, PE – városhoz közeli, RU – vidéki

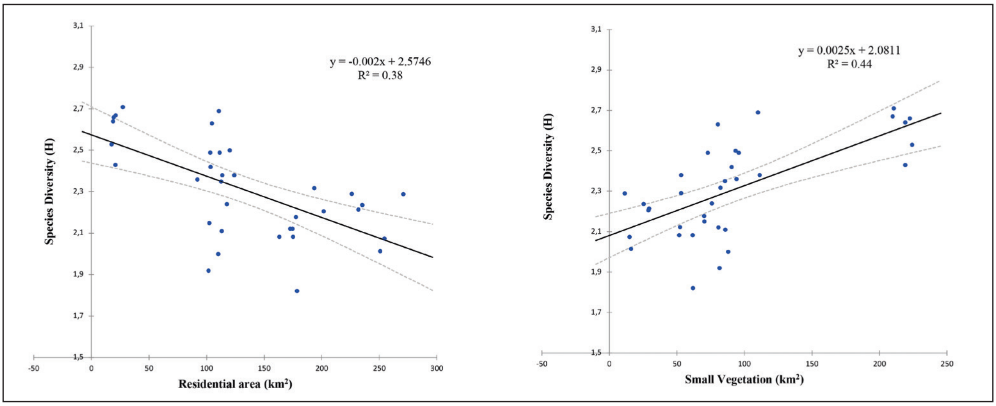


Figure 5. Regression model showing relationship between bird diversity and residential area and small vegetation

5. ábra Regressziós modellek illeszkedése a fajgazdagság és változatosság összefüggésére a különböző vegetáció borítottságú területekkel

and water bodies along a rural-urban gradient. The urban birds viz., *Columba livia domestica*, *Acridotheres ginginianus*, *Corvus splendens* and *Milvus migrans* showed association with residential areas. Three bird species viz., *Merops orientalis*, *Spilopelia senegalensis* and *Riparia riparia* showed a relationship with moderate residential area and woody plantation. Biplot depicted that *Psittacula krameri*, *Dicrurus macrocercus* and *Passer domesticus* showed relationship with shrubby and low vegetation cover. Low vegetation cover seemed to be a good habitat for bird species viz., *Pycnonotus cafer*, *Motacilla alba*, *Acridotheres tristis* and *Bubulcus ibis* with cropland habitat associated with water bodies *(Figure 7)*.

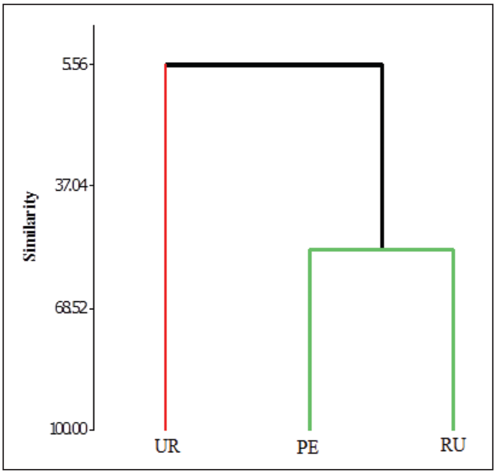


Figure 6. Dendrogram (UPGMA, average linkage between groups) based on Euclidean distances between sites showing UR, PE and RU clusters separately with respect to bird species diversity

6. ábra Euklidészi távolságon alapuló dendrogram a madarak fajgazdagsága közötti hasonlóság értékelésére. UR – városi, PE – városhoz közeli, RU – vidéki

Discussion

The present research supported our first hypothesis proposing significant variations in density along rural-urban gradient because of variable response of birds towards increasing urbanization. The density of common birds which can find food in anthropogenic resources was highest in UR than PE and RU areas (Beissinger & Osborne 1982). However, the bird diversity and richness was least in UR areas. Bird communities were evenly distributed in UR than

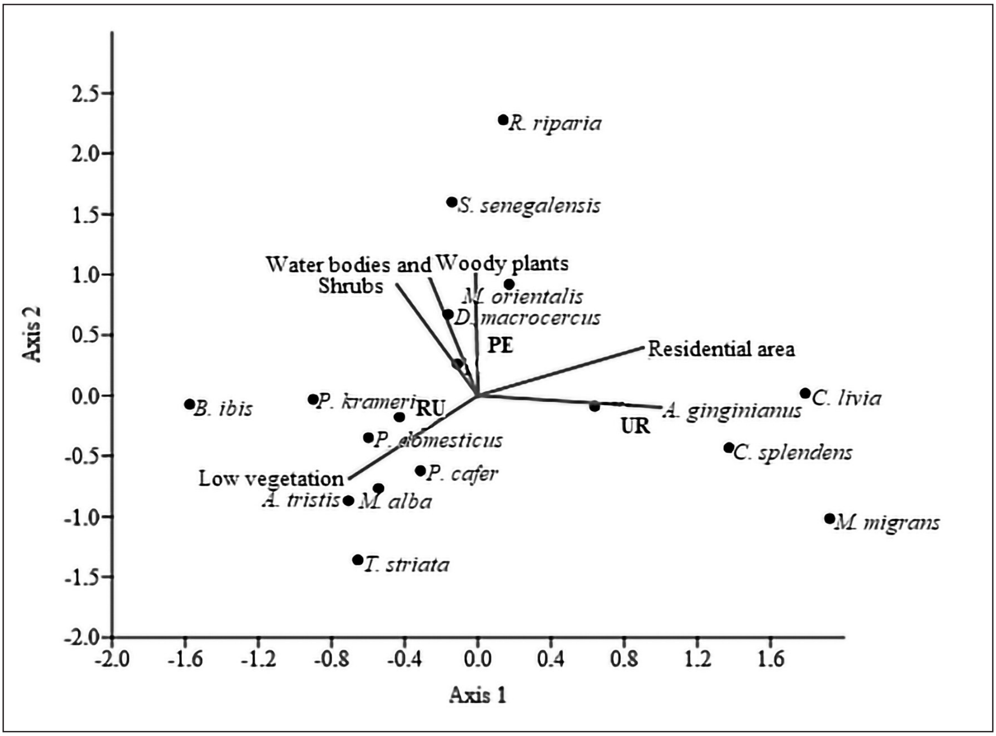


Figure 7. Triplot showing association of dominant bird species with different landscape class along rural- urban gradient

7. ábra A domináns madárfajok és a különböző vegetáció borítottságú területek összefüggése. UR – városi, PE – városhoz közeli, RU – vidéki

adjoining areas. These findings were in line with the study of Marzluff and Ewing (2001). Blair (2001) also supported the evidence that avian diversity and richness declined as developments proceeded along the rural-urban gradient. Diversity and richness of bird species also have shown a positive relationship with the diversity of trees and shrubs in all habitats.

The avian community structure showed variation along the rural-urban gradient. The analysis of the functional group illustrated resource based distribution of avian communities along a rural-urban gradient. The functional groups viz., frugivores and carnivores dominated in the rural areas which provide higher resource availability, e.g. trees and open areas as compared to urban areas. Rural communities were more evenly distributed as compared to urban areas, which had high dominance of omnivorous species like house crows and common myna. Whereas, urban areas corroborate more omnivore birds (Emlen 1974, Lancaster & Rees 1979, Beissinger & Osborne 1982, Mills *et al.* 1989, Kluza *et al.* 2000, Fraterrigo & Wiens 2005, Chace & Walsh 2006). Expectedly again, the percentages of omnivores abundances were found to be higher due to their close association with residential areas (Fraterrigo & Wiens 2005, Chiari *et al.* 2010).

The present study analyzed that avian community varied with variations in land cover classes viz., residential area, small vegetation, woody trees / bushes. Chace and Walsh

(2006) and Friesen (1998) analyzed impacts of urbanization on structure and composition of avifauna. The evidences supported that increasing structural complexity in habitat structure provided larger degrees of heterogeneity that enables birds to occupy more niches (Poulsen 2002, Machtans & Latour 2003, Loyola & Martins 2008, Shochat *et al.* 2010). The studies emphasized that *C. splendens* and *M. migrans* had shown association with UR and PE areas. These areas provided sufficient roosting and foraging sites due to natural and anthropogenic sources (Sergio *et al.* 2003). Many studies showed that these birds are attracted towards public and commercial buildings because of availability of food from anthropogenic source (Rajashekara & Venkatesha 2014, Manjula *et al.* 2015, Pattnaik *et al.* 2016, Katuwal *et al.* 2018). *A. ginginanus* primarily prefers farmland habitat that is adapted to urban habitat due to behaviorally flexible foraging habits (Kler 2009). The highest adaptability potential of *C. livia domestica* was observed among invasive urban bird species. This bird was primarily an inhabitant of cliffs while urban area cliffs of building structures provide a substitute of natural cliffs (Tiwary & Urfi 2016).

Nearly 50% of the avian population of PE was composed of just two bird species viz., *C. splendens* and *P. domesticus.* In this regard, urban adopters *(D. macrocercus, N. murina, M. orientalis)* were actually inhabitants of PE but had shown tendency to move towards UR. The present data depicted a strong association between *D. macrocercus* and *S. senegalensis* in PE. It is worth mentioning here that PE acts as a transitional zone which contains a mixed avian assemblage of both habitats of UR and RU (Dearborn & Kark 2010). Main roosting sites for *D. macrocercus* in urban area were electric wires, cables, lightning pools, and human source provide them a variety of food items (Sekercioglu 2012).

Species, such as *P. domesticus*, *A. tristis* and *P. cafer* represented 56% of avian assemblage associated with RU. Granivores get a maximum opportunity of grain food from agriculture habitat but have shown the tendency of adaptability towards UR. Peacock *et al.* (2007) reported that these birds has adaptability potential for UR because buildings can provide nesting/roosting sites and human resources provide a variety of food items. High density of *P. krameri* in maize and cereal crops in agriculture habitat has been reported (Khan *et al.* 2004). The high density and diversity of *B. ibis* was recorded near the water bodies (Changder *et al.* 2015).

This study showed response of birds to resource availability at various levels of urban development. It will help to explore the suitable conditions for wildlife in urban areas. In this connection, restoration of urban areas of vegetation will definitely help in conservation of avian fauna in urban habitat.

Conclusions

Avian assemblage has also shown pronounced variations in abundance and richness along the rural-urban gradient. It is noteworthy that the proportion of non-native species (urban exploiters) becomes more common towards the urban core. This research indicated that residential area provided roosting and nesting sites and organic waste as food from anthropogenic source to these birds. It could be inferred that human solid waste could be one of the major sources of attraction for urban birds. So, proper management of city solid waste material will be helpful in bringing back native bird species. Urban adapter birds mainly adapted to city outskirts where extensive re-vegetation facilitate the restoration of ecological succession. The present study provides public biodiversity education that could be effective in promoting an understanding of concept such as "ecological succession" and role of different landscape classification in promoting native avian diversity along a rural-urban gradient of Gujranwala city (Punjab: Pakistan).

References

Abbasi, N. A., Khan, M. U., Jaspers, V. L. B., Chaudhry, M. J. I. & Malik, R. N. 2015. Spatial and interspecific variation of accumulated trace metals between remote and urbane dwelling birds of Pakistan. – Ecotoxicology and environmental safety 113(2): 79–286. DOI: 10.1016/j.ecoenv.2014.11.034

Ali, A., Altaf, M. & Khan, M. S. H. 2016. Winter survey of birds at Keti Bunder, district Thatha, Pakistan. – Punjab University Journal of Zoology 31(2): 3–208.

Ali, S. & Ripley, S. D. 1983. Handbook of the birds of India and Pakistan. Compact edition. – Oxford University Press, New Delhi and Oxford

Ali, S., Rakha, B. A., Hussain, I., Nadeem, M. S. & Rafique, M. 2013. Ecology of Feral Pigeon *(Columba livia)* in urban areas of Rawalpindi/Islamabad, Pakistan. – Pakistan Journal of Zoology 45(5): 1229–1234.

Altaf, M., Javid, A., Khan, A. M., Khan, M., Umair, M. & Ali, Z. 2018. Anthropogenic impact on the distribution of the birds in the tropical thorn forest, Punjab, Pakistan. – Journal of Asia-Pacific Biodiversity 11(2): 229–236. DOI: 10.1016/j.japb.2018.03.001

Anjum, W., Ahmad, S., Sanaullah, M., Majid, Z. & Mirza, K. 2016. Geographic information system and modeling approach for groundwater systems of Rechna Doab, Pakistan. – Pakistan Journal of Science 68(4): 470–476.

Aronson, M. F., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S., Cilliers, S. & Clarkson, B. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. – Proceedings of the Royal Society B: Biological Sciences 281(1780): 201–330. DOI: 10.1098/rspb.2013.3330

Aynalem, S. & Bekele, A. 2008. Species composition, relative abundance and distribution of bird fauna of riverine and wetland habitats of Infranz and Yiganda at southern tip of Lake Tana, Ethiopia. – Tropical Ecology 49(2): 199–209.

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

Bellanthudawa, B., Nawalage, N., Subanky, S., Panagoda, P., Weerasinghe, H., Tharaka, L., Handapangoda, H., Silva, H., Dissanayake, D. & Abeywickrama, M. 2019. Composition and diversity variation of avifauna, along different vegetative habitat types in a human-modified area, University of Kelaniya, Sri Lanka. – International Journal of Zoology, pp. 1–16. DOI: 10.1155/2019/9727609

Blair, R. B. 2001. Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous fauna? – Biotic Homogenization, Springer, pp. 33–56. DOI: 10.1007/978-1-4615-1261-5_3

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

Changder, S., Adhurya, S., Roy, U. S. & Banerjee, M. 2015. A report on midwinter bird diversity from Mangalajodi Wetland, Odisha. – ZOO's Print Journal 30(12): 1–5.

Chiari, C., Dinetti, M., Licciardello, C., Licitra, G. & Pautasso, M. 2010. Urbanization and the more-individuals hypothesis. – Journal of Animal Ecology 79(2): 366–371. DOI: 10.1111/j.1365-2656.2009.01631.x.

Clergeau, P., Jokimäki, J. & Snep, R. 2006. Using hierarchical levels for urban ecology. – Trends in Ecology & Evolution 21(12): 660–661. DOI: 10.1016/j.tree.2006.09.006

Dallimer, M., Rouquette, J. R., Skinner, A. M., Armsworth, P. R., Maltby, L. M., Warren, P. H. & Gaston, K. J. 2012. Contrasting patterns in species richness of birds, butterflies and plants along riparian corridors in an urban landscape. – Diversity and Distributions 18(8): 742–753. DOI: 10.1111/j.1472-4642.2012.00891.x

Davidar, P., Yoganand, T., Ganesh, T. & Joshi, N. 1997. An assessment of common and rare forest bird species of the Andaman Islands. – Forktail 12: 135–142. DOI: 10.1046/j.1365-2699.2001.00584.x

Dearborn, D. C. & Kark, S. 2010. Motivations for conserving urban biodiversity. – Conservation Biology 24(2): 432–440. DOI: 10.1111/j.1523-1739.2009.01328.x.

Emlen, J. T. 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. – The Condor 76(2): 184–197. DOI: 10.2307/1366729

Fernandez-Juricic, E. & Jokimäki, J. 2001. A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. – Biodiversity & Conservation 10(12): 2023–2043. DOI: 10.1023/A:1013133308987

Fraterrigo, J. M. & Wiens, J. A. 2005. Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. – Landscape and Urban Planning 71(2–4): 263–275. DOI: 10.1016/j.landurbplan.2004.03.008

Friesen, L. 1998. Impacts of urbanization on plant and bird communities in forest ecosystems. – The Forestry Chronicle 74(6): 855–860. DOI: 10.5558/tfc74855-6

Garaffa, P. I., Filloy, J. & Bellocq, M. I. 2009. Bird community responses along urban-rural gradients: does the size of the urbanized area matter? – Landscape and Urban Planning 90(1–2): 33–41. DOI: 10.1016/j.landurbplan.2008.10.004.

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

Hansen, A. J. & Urban, D. L. 1992. Avian response to landscape pattern: the role of species' life histories. – Landscape Ecology 7(3): 163–180. DOI: 10.1007/BF00133308.

Hensley, C. B., Trisos, C. H., Warren, P. S., MacFarland, J., Blumenshine, S., Reece, J. & Katti, M. 2019. Effects of urbanization on bird assemblages in three southwestern US cities. – Frontiers in Ecology and Evolution 7: 71. DOI: 10.3389/fevo.2019.00071

Hostetler, M. 2001. The importance of multi-scale analyses in avian habitat selection studies in urban environments. – In: Marzluff, J. M., Bowman, R. & Donnelly, R. (eds.) Avian Ecology and Conservation in an Urbanizing World. – Springer, Boston, MA. DOI: 10.1007/978-1-4615-1531-9_7

Jongman, R., Braak, C. & Van Tongeren, O. 1995. Data Analysis in Community and Landscape Ecology. – Cambridge University Press, Cambridge, UK. DOI: 10.2307/2531665

Joshua, G. & Ali, Z. 2011. Avian diversity with the varying urban congestions of Lahore. – Journal of Animal and Plant Sciences 21(4): 21–482.

Katuwal, H. B., Pradhan, N. M. B., Thakuri, J. J., Bhusal, K. P., Aryal, P. C. & Thapa, I. 2018. Effect of urbanization and seasonality in bird communities of Kathmandu Valley, Nepal. – Proceedings of the Zoological Society 71: 103–113. DOI: 10.1007/s12595-018-0265-z

Kent, M. & Coker, P. 1992. Vegetation Description and Analysis: A Practical Approach. – Belven Press, London. DOI: 10.2307/3451427

Khan, H. A., Beg, M. A. & Khan, A. A. 2004. Breeding habitats of the Rose-ringed Parakeet *(Psittacula krameri)* in the cultivations of Central Punjab. – Pakistan Journal of Zoology 36: 133–138.

Khan, M. Z., Tabbassum, F., Ghalib, S. A., Zehra, A., Hussain, B., Siddiqui, S., Yasmeen, G., Gabol, K., Mahmood, N. & Khan, I. S. 2014. Distribution population status and conservation of the birds in Karachi Sindh, Pakistan. – Canadian Journal of Pure and Applied Sciences 8(1): 2697–2713. DOI: 10.6000/1927-5129.2012.08.01.05.

Kler, T. 2009. Some observations on the breeding activities of the Pied Myna *Sturnus contra* (Linn.). – Environment and Ecology 27(1): 213–215.

Kluza, D. A., Griffin, C. R. & DeGraaf, R. M. 2000. Housing developments in rural New England: effects on forest birds. – Animal Conservation Forum 3: 15–26. DOI: 10.1111/j.1469-1795.2000.tb00083.x.

Lancaster, R. K. & Rees, W. E. 1979. Bird communities and the structure of urban habitats. – Canadian Journal of Zoology 57(12): 2358–2368. DOI: 10.1139/z79-307

Leveau, L. M. & Leveau, C. M. 2016. Does urbanization affect the seasonal dynamics of bird communities in urban parks? – Urban Ecosystems 19(2): 631–647. DOI: 10.1007/s11252-016-0525-5.

Lim, H. C. & Sodhi, N. S. 2004. Responses of avian guilds to urbanisation in a tropical city. – Landscape and Urban Planning 66(4): 199–215. DOI: 10.1016/S0169-2046(03)00111-7.

Loyola, R. D. & Martins, R. P. 2008. Habitat structure components are effective predictors of trap-nesting Hymenoptera diversity. – Basic and Applied Ecology 9(6): 735–742. DOI: 10.1016/j.baae.2007.06.016

Luck, G. W. & Smallbone, L. T. 2010. Species diversity and urbanisation: patterns, drivers and implications. – In: Kevin, J. G. (ed.) Urban Ecology. – Cambridge University Press, pp. 88–119. DOI: 10.1017/CBO9780511778483.006.

Machtans, C. S. & Latour, P. B. 2003. Boreal forest songbird communities of the Liard Valley, northwest territories, Canada. – The Condor 105(1): 27–44. DOI: 10.1093/condor/105.1.

Manjula, M., Mohanraj, R. & Devi, M. P. 2015. Biomonitoring of heavy metals in feathers of eleven common bird species in urban and rural environments of Tiruchirappalli, India. – Environmental Monitoring and Assessment 187(5): 4502. DOI: 10.1007/s10661-015-4502-x.

Marzluff, J. M. & Ewing, K. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. – Restoration Ecology 9(3): 280–292. DOI: 10.1046/j.1526-100x.2001.009003280.x

McKinney, M. L. 2002. Urbanization, biodiversity and conservation. The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. – BioScience 52(10): 883–890. DOI: 10.1641/0006-3568(2002)052[0883:UBAC]

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. – Biological Conservation 127(3): 247–260. DOI: 10.1016/j.biocon.2005.09.005

McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. – Urban Ecosystems 11(2): 161–176. DOI: 10.1007/s11252-007-0045-4.

Mehmood, H., Sajjad, S. & Shirazi, S. 2017. Spatio-temporal trends and patterns of urban sprawl in Gujranwala city, Punjab, Pakistan. – Pakistan Journal of Science 69(1): 63–68.

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

Mills, G. S., Dunning, Jr. J. B. & Bates, J. M. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. – The Condor 91(2): 416–428._DOI: 10.2307/1368320.

Ortega-Álvarez, R. & MacGregor-Fors, I. 2009. Living in the big city: Effects of urban land-use on bird community structure, diversity, and composition. – Landscape and Urban Planning 90(3–4): 189–195. DOI: 10.1016/j.landurbplan.2008.11.003

Parsons, H., Major, R. E. & French, K. 2006. Species interactions and habitat associations of birds inhabiting urban areas of Sydney, Australia. – Austral Ecology 31(2): 217–227. DOI: 10.1111/j.1442-9993.2006.01584.x

Pattnaik, P., Das, M. & Parida, S. P. 2016. Preliminary study of avifauna diversity of Utkal University Campus, Bhubaneswar, Odisha, India. – Current Life Sciences 2(1): 20–26.

Peacock, D. S., van Rensburg, B. J. & Robertson, M. P. 2007. The distribution and spread of the invasive alien Common Myna, *Acridotheres tristis* L. (Aves: Sturnidae), in southern Africa. – South African Journal of Science 103(11–12): 465–473.

Peck, H. L., Pringle, H. E., Marshall, H. H., Owens, I. P. & Lord, A. M. 2014. Experimental evidence of impacts of an invasive parakeet on foraging behavior of native birds. – Behavioral Ecology 25(3): 582–590. DOI: 10.1093/beheco/aru025.

Peh, K. S-H. 2010. Invasive species in Southeast Asia: the knowledge so far. – Biodiversity and Conservation 19(4): 1083–1099. DOI: 10.1007/s10531-009-9624-4.

Poulsen, B. O. 2002. Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. – Biodiversity & Conservation 11(9): 1551–1566. DOI: 10.1023/A:1016839518172

Rajashekara, S. & Venkatesha, M. 2014. Insectivorous bird communities of diverse agro-ecosystems in the Bengaluru region, India. – Journal of Entomology and Zoology Studies 2(5): 142–155.

Rottenborn, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. Biological Conservation 88(3): 289–299. DOI: 10.1016/S0006-3207(98)00128-1

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

Seress, G. & Liker, A. 2015. Habitat urbanization and its effects on birds. – Acta Zoologica Academiae Scientiarum Hungaricae 61(4): 373–408. DOI: 10.1007/s10336-012-0869-4

Sergio, F., Pedrini, P. & Marchesi, L. 2003. Adaptive selection of foraging and nesting habitat by Black Kites *(Milvus migrans)* and its implications for conservation: a multi-scale approach. – Biological Conservation 112(3): 351–362. DOI: 10.1016/S0006-3207(02)00332-4.

Shochat, E., Lerman, S. & Fernández-Juricic, E. 2010. Birds in urban ecosystems: population dynamics, community structure, biodiversity, and conservation. – Urban Ecosystem Ecology 55(2010): 75–86. DOI: 10.2134/agronmonogr55.c4

Sol, D., González-Lagos, C., Lapiedra, O. & Díaz, M. 2017. Why are exotic birds so successful in urbanized environments? – In: Murgui, E. & Hedblom, M. (ed.) Ecology and Conservation of Birds in Urban Environments. – Springer, pp. 75–89. DOI: 10.1007/978-3-319-43314-1_5. 75.

Tiwary, N. & Urfi, A. 2016. Spatial variations of bird occupancy in Delhi: The significance of woodland habitat patches in urban centres. – Urban Forestry & Urban Greening 20(3): 38–347. DOI: 10.1016/j.ufug.2016.10.002

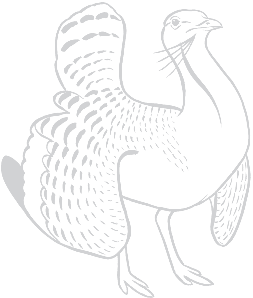
Trammell, E. J. & Bassett, S. 2012. Impact of urban structure on avian diversity along the Truckee River, USA. – Urban Ecosystems 15(4): 993–1013. DOI: 10.1007/s11252-012-0251-6.

van Rensburg, B. J., Peacock, D. S. & Robertson, M. P. 2009. Biotic homogenization and alien bird species along an urban gradient in South Africa. – Landscape and Urban Planning 92(3–4): 233–241. DOI: 10.1016/j.landurbplan.2009.05.002.

Villegas, M. & Garitano-Zavala, Á. 2010. Bird community responses to different urban conditions in La Paz, Bolivia. – Urban Ecosystems 13(3): 375–391. DOI: 10.1007/s11252-010-0126-7.

White, J. G., Antos, M. J., Fitzsimons, J. A. & Palmer, G. C. 2005. Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. – Landscape and Urban Planning 71(2–4): 123–135. DOI: 10.1016/j.landurbplan.2004.02.006.

Yap, C. A. & Sodhi, N. S. 2004. Southeast Asian invasive birds: ecology, impact and management. – Ornithological Science 3(1): 57–67. DOI: 10.2326/osj.3.57



sciendo

Ornis Hungarica 2020. 28(1): 65–75.
DOI: 10.2478/orhu-2020-0005

Data on the postbreeding migration of marked Romanian Great White Pelicans (*Pelecanus onocrotalus* Linnaeus, 1758)

Botond J. Kiss*, Vasile Alexe, Alexandru C. Doroşencu & Mihai, E. Marinov

Received: April 26, 2020 – Revised: May 14, 2020 – Accepted: May 15, 2020

Kiss, J. B., Alexe, V., Doroşencu, C. A. & Marinov, E. M. 2020. Data on the postbreeding migration of marked Romanian Great White Pelicans (*Pelecanus onocrotalus* Linnaeus, 1758). – Ornis Hungarica 28(1): 65–75. DOI: 10.2478/orhu-2020-0005

Abstract Between 1931 and 2018 in the Danube Delta, 1,171 Great White Pelican (*Pelecanus onocrotalus* Linnaeus 1758) were ringed (731 with metal rings, 440 with coloured plastic rings) at breeding sites. The majority of the captured birds were flightless young individuals. From the ringed birds, 25 (2.13%) were reported as recaptured. Most were reported from Israel (28%), and the rest from 8 other countries. Recovery distance varied between 50 and 3,000 km. 19 birds (76%) were reported within half year after ringing, 2 birds (8%) within a year, and further 4 individuals (16%) were reported after a year. With the exception of a single photographed individual, all the others perished: they were shot or fell victims to accidents. These cases suggest high mortality in the young age cohort. Very little knowledge is available about the African wintering grounds; there are only two reports from Egypt and one from Southern Sudan. Traditional ringing yields little information for this species. Considerably more exact data could be expected from satellite tracking, use of other modern locating techniques and use of genetic methods. The ringing of nestlings is only possible if we can apply less aggressive methods then used to date. Besides its scientific value, the intense research on the still numerous Great White Pelican population would be justified by the outstanding faunistic, economic and cultural importance of this species.

Keywords: Great White Pelican, Romania, ringing, reported ringing recoveries, *Pelecanus onocrotalus*

Összefoglalás A Duna-deltában 1931 és 2018 között 1171 rózsás gödényt (*Pelecanus onocrotalus* Linnaeus 1758) (fémgyűrűvel 731 példány, színes műanyag gyűrűvel 440 példány) jelöltek meg fészektelepen, csekély kivétellel röpképtelen fiatalokat. Közülük 25 madárról (2,13%) érkezett megkerülési adat. A legtöbbet (28%) Izraelből jelentettek vissza, a többit nyolc másik országból. A megkerülési távolságok 50 és 3000 km között változtak. A gyűrűzés utáni első félévben 19 madár (76%), félév-egy év között két madár (8%), egy éven felül 4 (16%) példány került meg. Egy lefényképezett egyed kivételével a többi elpusztult, lelőtték, vagy baleset áldozatává vált. Mindez nagy fiatalkori mortalitásra utal. Az afrikai telelőhelyekről keveset tudunk, csupán két egyiptomi és egy dél-szudáni visszajelentésünk van. E faj esetében a hagyományos gyűrűzés kevés adatot szolgáltat. Lényegesen több és pontosabb eredmények várhatók a műholdas követés és más *hightech* eszközök alkalmazásától, valamint a faj genetikai kutatásától. A fiókagyűrűzés akkor jöhet számításba, ha kevésbé agresszív technikát alkalmaznánk, mint eddig. A Duna-delta még nagyszámú gödény állományának vizsgálatát – a tudományos eredmények mellett – kiemelt faunisztikai, gazdasági és kulturális értéke is indokolja.

Kulcsszavak: színes gyűrű, Románia, gyűrűzés, rózsás gödény, visszajelentett gyűrű

Danube Delta National Institute for Research-Development 165, Babadag RO–828112, Tulcea, Romania, e-mail: jbkiss03@yahoo.com
**corresponding author*

Introduction

The world populations of Great White Pelicans (*Pelecanus onocrotalus* Linnaeus 1758) (further referred to as GWP) are divided into two separated stocks. One of them nests in Southeast Europe and Western Asia, while the other in Central Africa. The populations breeding in the Palearctic are long-distance migrants, while the Africans are residents, though they disperse widely in Africa (Crivelli & Schreiber 1984, Crivelli *et al.* 1991a, del Hoyo *et al.* 1992).

Our knowledge of the size of the Palearctic GWP populations is limited, and contradictory data are available. Smaller populations breed around the Mediterranean Sea in Turkey and Greece (Crivelli *et al.* 2000). Around half of the Palearctic populations breed in the territory of the former USSR. At the end of the 20th century, the number of breeding pairs was estimated at 3,120–6,550 (Krivenko *et al*. 1994), or 3,070–4,300 (Crivelli *et al*. 1994). Later their number was changed to 2,553–31,124 pairs (Crivelli *et al.* 1997). The world population was estimated at 7,345–10,500 pairs (Crivelli 1994, Crivelli *et al*. 1991, 2000, del Hoyo *et al*. 1992). From the start of the 21st century, a positive trend was described: the estimated number grew to 6,790–11,300 pairs (IUCN 2001). Based on the census and estimations carried out in 2011–2012, the number of breeding pairs was 4,702–5,175 in the populations breeding at the colonies in Southeast Europe and Turkey (Catsadorakis *et al*. 2015, Catsadorakis 2016), and a year later the Red List quoted 4,900–5,600 pairs (IUCN 2018). At the end of the 20th century, their number in Romania was estimated to be 3,500 pairs (Crivelli 1997), and at the beginning of the 21st century still 3,500 pairs are mentioned (Plattheeuw *et al.* 2001). Then 460–3,500 pairs were given by Schogolev *et al*. (2005) and 3,650–4,000 pairs were estimated by Kiss *et al*. (2015) and 4,100–4,500 by Petrovici (2015), The BirdLife International (2018) mentions 4,100–4,480 pairs, which is 82% of the European population, and the tendency of change is stable. All these data probably seriously underestimated the real number of GWPs, as with the use of drone technology from 2016 at a single large colony located in the Danube Delta, the number of breeding pairs was estimated to 16,000–19,000 (17,000 GWP on average) (Marinov e*t al*. 2016, Kiss *et al.* 2019b).

The migration, and especially the wintering grounds, of this species are even less studied (Crivelli *et al*. 1991a, del Hoyo *et al*. 1992, Izhaki *et al*. 1994, 2002, Catsadorakis 2002). As there have not been intense GWP ringing efforts in the Danube Delta since 1996, and it hinders the chance of reports of recaptured birds, this paper aims to summarise and elaborate the recovery data of ringed GWPs. Here, we should emphasize that we use the term ‘recovery report’ for both the rings found on corpses, or the visual observation and report of marked birds, or any other information source, such as newspaper / press announcements (Kiss 2018).

Materials and Methods

With two exceptions – when we ringed two pelicans outside the colony – we ringed flightless nestlings at the strictly protected Roşca-Buhaiova Area. This is the largest GWP colony in Europe. This area is one of the most valuable parts of the Danube Delta Biosphere Reserve of UNESCO’s list of World Heritage Sites. The strictly protected area is located at the north-eastern part of the Delta consisting of 9,625 hectares open water surface and reed beds that form floating islands. These islands follow the water level changes and are not linked to dry land. Woody vegetation is represented by grey willow *(Salix cinerea)* bushes. The area is dissected by several old canals that have silted up. The GWP colony *(Figure 1)* is located on the two adjacent lakes named Buhaiova-Hrecisca (Andone *et al*. 1969, Kiss 2002, Ceico 2003, Platteuw *et al*. 2004, Kiss *et al.* 2019b).

To catch the flightless nestlings we applied two methods, both of them were technically and ethically approved then. Both of these methods are based on utilizing the short time window, when the nestlings reach maximum size and aggregate into nurseries*,* when they swim around in groups, but do not fly at all, or their flight is very weak. As breeding is highly synchronised in the whole colony, the nestlings are more or less the same age. In the Danube Delta, the beginning and (to a lesser degree) the middle of August seem to be the most appropriate for ringing. The first method was the following: the targeted individual was followed with a light fishing boat, with a low number of crew on board, and the nestling was captured with a long-handled lifting fishing net. The other method was to create a large 'V'-shaped seine net tunnel fixed to long poles pushed into the lake bottom, and the nestlings were driven by boats into the tunnel. The capture boats were waiting for the GWP nestlings at the narrow throat of the tunnel. The advantage of this method is the relatively short duration of disturbance and more efficient ringing, but it requires the coordinated work of at least 4–5 boats and 10–12 skilled persons.

Up to the date of writing our paper, from the 731 metal and 440 colour ringed GWPs only 25 were reported, and part of these reports were data deficient or inaccurate. Two of them were rings from bird corpses found by the national park rangers. The highest number of

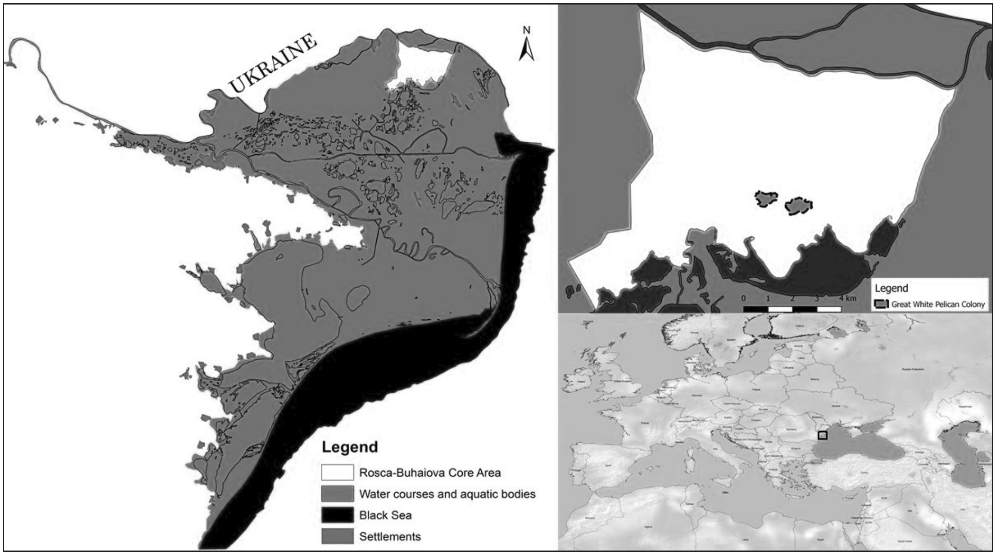


Figure 1. The lakes Buhaiova and Hrecisca in the strictly protected Roşca-Buhaiova Reserve in the Danube Delta, Romania (Graphic: Doroșencu C. Alexandru)

1. ábra A Buhaiova és Hrecisca tavak a romániai Duna-deltában, a Roşca-Buhaiova szigorúan védett rezervátumban reports were published in the reports of the Romanian Ornithological Centre (Kiss 1992, Kiss & Condac 1992, Radu 1994, Cătuneanu 1999, Akriotis & Handrinos 2004). From the metal ringed birds, 9 (1.23%) recovery reports were published (Crivelli *et al*. 1991, Cătuneanu 1999), and later an additional 4 reports arrived, so the sum grew to 1.78%. From the 440 coloured plastic rings used from 1989 (2.72%), 12 were reported. The cumulative recovery report of all metal and plastic ringed birds is 2.14%. Only a single colour ring was observed in the field, and reported. The rest of the cases were recovered from dead or shot birds.

If the recovery report was not precise regarding the date of ringing, we used the middle of August for the given ringing year as a starting point. If the original ringing report did not specify the location, or only Danube Delta or the city of Tulcea is given, we gave the coordinates of the largest colony of the Delta (it is specified from 1934 as a location). If the data on ringing date was missing, we calculated the time spans from the middle of August based on our experience and literature data.

Results

With the exception of three individuals, all the Danube Delta GWP recoveries were reported from the southward migration period. Seven (28%) reached Israel, from where they were

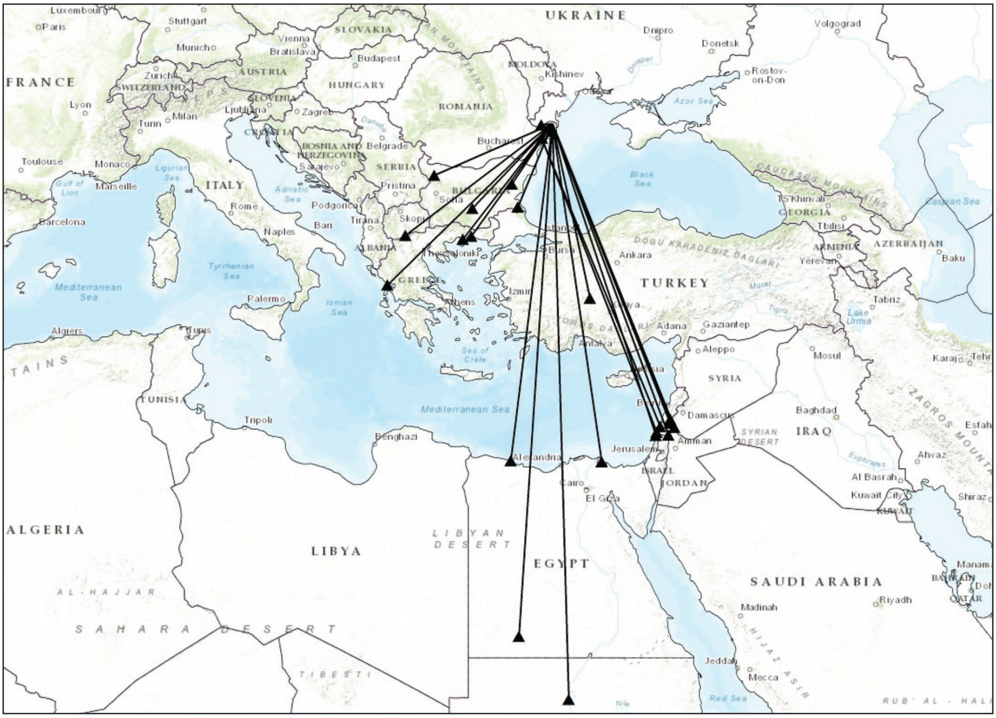


Figure 2. Recapture locations of Great White Pelicans *Pelecanus onocrotalus* (n = 25) ringed in the Danube Delta (Romania)

2. ábra A Duna-deltában megjelölt rózsás gödények (n = 25) megkerülései reported, and the rest from 8 countries on 3 continents *(Figure 2)*. The exceptions are: one bird turned back and was reported from Ukraine, one was collected in Greece at the middle of March, most probably on its return passage from the wintering ground, and one individual was found in May in Israel.

Although few data are available, it seems that birds start both southeast and southwest from the Danube Delta (Fülöp *et al.* 2018). This is further supported by the spatial pattern of later recoveries. Birds using the southeastern flyway were recovered from Turkey, Syria, Israel, Egypt and Sudan, while the birds heading to the other (southwestern) flyway were recovered in Bulgaria and Greece. The Ukrainian data cannot be clearly assigned to either route.

The majority of recoveries were within a short period of time. Juvenile mortality is high. Within half a year after ringing, 19 GWPs (76%) were either shot or fall victim to accidents. Between half a year and one year, a further 2 individuals (8%) were reported, and recoveries more than a year after ringing amounted to 4 individuals (16%).

Discussion

The method of bird ringing, invented by the Danish ornithologist H. Ch. Mortensen in 1899 for the study of migration, still yields remarkable results, especially when using plastic colour ring combinations that can be identified from a long distance with a scope. The application of modern technologies, such as the solar- or battery-powered satellite tracking, opened a new era of bird migration research. In Romania, with the exception of a single satellite transmitter study of GWP migration that was initiated to follow the movement of birds around the breeding colonies planned for three month duration (Kiss & Nichersu 2002), only ringing yielded data on the spatial and temporal pattern of GWP migration, a strictly protected bird of outstanding faunistic and economic importance.

The first GWP ringed in Romania was recovered in 1935 in Egypt, and then, until the 1940s, there were no data from Romania on GWP ringing. Between 1940 and 1970, a total of 731 metal rings were put on flightless nestlings (Crivelli *et al.* 1991a, Cătuneanu 1999). Blue plastic colour rings with 4–5 characters were used from 1989. Until today, our working group marked 440 birds with these plastic rings, and the overwhelming majority (99.6%) of them were also flightless young birds at breeding colonies. Only two individuals were caught outside the colonies, and both of them were recovered later.

During the autumn migration, GWPs fly towards the African wintering grounds along the Eastern shores of Europe and Asia Minor in the Eastern Mediterranean Sea region. Thus following the *Via Pontica*, between 1979 and 2003 on average 20,946 and maximum 37,703 individuals flew through Bulgaria. The number of birds observed shows an increasing trend (Michev *et al.* 2004, 2011, 2012, 2018, Iankov 2014). In the last years of the 20th century, a similar increasing trend was reported from Israel, where autumn records were between 70,000–80,000 observed individuals (Crivelli *et al.* 1991b, Izhaki 1994), while the average was 71,421 per year (Leshem & Yom-Tov 1996, Shmueli *et al.* 2000a, 2000b). In the last decade of the 20th century on average 36,923 overflying GWPs were calculated (Alon *et al.* 2004). Later, these numbers were raised to 40,000±9,000 GWPs (Hadzofe 2014).

According to the Israel Nature & Parks Authority (INPA), between 1999 and 2013, on average 39,395±8,201 GWPs per year were estimated (Labinger & Hadzoffe 2015). It is worth mentioning that according to the IUCN Red List the Wetlands International – Waterbird Population Estimates, the total number of GWPs in 2015 was 265,000–295,000 individuals in the world (BirdLife International 2018).

The fact that the majority (28%) of GWPs ringed in Romania were recovered in Israel can be explained, first of all, by the location of the country. Several important passage routes transect Israel, among them many of piscivorous species. These seriously impact the intensely managed fisheries of Israel, and hence are an important factor in the fish industry.

GWPs not only migrate through these countries but due to global climate change (Doxa *et al.* 2012), overwintering of some individuals or even groups becomes more and more common, which has economic, epidemiological and other consequences. This phenomenon results in more intense applied ornithological research, and more effort and financial funds invested into GWP research (Crivelli *et al*. 1991b, Izhaki 1994, Leshem & Yom Tov 1996, Smueli *et al*. 2000a, 2014, Izhaki *et al*. 2002, Alon *et al.* 2004, Artzi & Oron 2014). At the same time, intense fishery production necessitates the use of advanced infrastructure and fish stock protection measures. These measures significantly increase GWP mortality, and at the same time result in more ringing recovery reports (Shmueli *et al.* 2000a, 2000b).

GWPs are large soaring birds, and therefore, when flying around the Mediterranean Sea, they follow the shorelines using the uplift of thermals. It is less likely that some flocks would directly cross the Mediterranean Sea. There is a migration route that starts to the southeast from Greece, by which GWP flocks from the western part of the Balkan Peninsula can join the circumpontic flocks (Crivelli *et al*. 1991a, Izhaki & Dagan-Shmueli 1994, Catsadorakis 2002).

It is already known that the migration of GWPs follow the Nile from Egypt (Crivelli *et al*. 1991a, del Hoyo *et al*. 1992, Izhaki *et al*. 2002, Chege 2014, Shmueli *et al*. 2014). The most faraway point (2,820 air kilometres from the site of capture) reached by any GWP ringed in Romania is located at Arduan (El Dean) in the valley of the White Nile, coordinates: 19°56' N, 30°25' (Cătuneanu 1991, Crivelli *et al*. 1991a).

In the last decades, it has been proven that some GWP populations do not migrate to the classic wintering grounds in Africa. This phenomenon is more characteristic for immature GWPs that disperse in the Balkan and the eastern part of the Mediterranean in Turkey, and especially in Israel, where they overwinter and hence can shorten their autumn migration (Crivelli *et al.* 1991a, Izhaki *et al*. 1994, 2002, Leshem & Yom-Tov 1996, Shmueli *et al.* 2000a, 2000b, 2014, Arzi & Oron 2014, Onmuş 2014). For example, a bird equipped with a satellite transmitter in Israel spent the winter in Israel, from where it returned to Europe in the spring in two consecutive years (Izhaki *et al*. 1994, 2002).

The African wintering grounds of the GWP are not exactly identified, but there are confirmed data that at least 5% of the European population cross the Red Sea at Gebel El Zeit (Hilgerloh *et al*. 2011), reach South Sudan, and then follow the water way of the White Nile and later, along the lake system of the Great Rift Valley, get to the equatorial part of Africa (Crivelli *et al*. 1991a, del Hoyo *et al*. 1992, Izhaki *et al*. 2002, Chege 2014, Shmueli *et al*. 2014). Location data from birds tagged in Israel with satellite transmitters arrived from the water bodies of Nasser and Jebel Aula Dam on the White Nile, and from the Sudd Swamp in South Sudan, from Lake Rosaires on the Blue Nile, and through the lakes of the Rift Valley to Kenya to Lake Turkana. Only a single Danube Delta GWP's data fits into this pattern, recovered in South Sudan (Cătuneanu 1991, Crivelli *et al*. 1991).

Compared to other large water birds ringed by us, the recovery rate of GWPs ringed in the Danube Delta is very low: only 2.13%. These differences are mainly due to the different anatomy and behaviour of the ringed species (del Hoyo *et al.* 1992). From the 215 ringed Great Cormorant *(Phalacrocorax carbo)*, 32 (14.89%), from the 219 ringed Eurasian Spoonbill *(Platalea leucorodia)*, 35 (15.99%) were recovered (Kiss *et al*. 2007, Sándor *et al*. 2011, Kiss *et al.* 2019a). The rings can be easily observed on the long tarsus of the Spoonbills when they are feeding in the shallow water or rest on trees. Great Cormorants often bask on prominent points. But the tarsus of the pelicans is relatively short, and they most often stand in shallow water, and hence it is impossible to observe and photograph the colour rings.

Ringing recoveries are similarly low for the GWPs marked in other countries. For example, between 1925 and 1989 in the Soviet Republic of Dagestan, 256 GWP were ringed, and only juveniles (1.56%) were recovered, and from the approximately 2,000 ringed juveniles at Lake Balhas, only 7 (0.35%) were recovered. From the 2,116 individuals ringed in Iran, only 30 were recovered (1.42%). Based on the period when these birds were marked, we can safely assume that only metal rings were used. From the 731 GWPs marked with metal rings in Romania, 8 individuals were recovered: this constitutes 1.09% (using the data from Crivelli *et al*. 2001). With recoveries in later years, the ratio grew to 1.78%. The use of coloured plastic rings by which the bird can be identified from a greater distance has considerably improved the recovery rate: from the 440 colour ringed birds, the recovery of 12 (2.13%) was reported.

There is another explanation for the low recovery in the case of the GWP. Ringing recovery rate, or the returned information, does not only depend on the size of the bird and the ringing effort, but also on the human population density, (research) infrastructural, cultural and economic properties of the countries along the migration route, and also on the presence (or lack) and density of scavenger animals, and other factors (Underhill *et al.* 1999). The GWPs ringed in the Danube Delta migrate through the Balkan towards Asia Minor, from where the main source of recovery data is Israel. Afterwards, they disappear almost without any trace in Africa.

As classic ringing did not yield enough data on the migratory routes and the exact locations of the wintering grounds of GWPs, the use of other, technologically more advanced methods seems more promising. The results from Israel show that the use of battery-powered satellite transmitter techniques is especially promising. These develop very fast and provide data with a resolution and exactness formerly not possible. To achieve a similar amount of information through conventional ringing, the marking of birds in numbers at a higher magnitude would be necessary. The related costs and required time invested would be considerably higher and, even worse, the capture and ringing of birds becomes more problematic. We should stress here that during the one and a half century long ornithological research in the Danube Delta, there has never been a project fully dedicated to the marking of GWPs and research into their migration. Our knowledge mainly comes from collateral sources. If we take into account the positive population dynamic trends of this species, this in itself should be the topic of research projects. For example, the application of drone technology in the census showed a four times higher number of breeding pairs than conventional techniques (Marinov *et al*. 2016, Kiss *et al*. 2019b). A population increase of such magnitude would cause problems in several countries on three continents. GWPs have outstanding importance not only in terms of biological diversity, but also in terms of culture, fisheries and tourism. Therefore it is inevitable that their research deserves special attention. It is also clear that our knowledge regarding the exact mapping of their migration routes and localising their wintering grounds can only be achieved through an international large-scale project. It must also involve African countries that based on our present knowledge are part of the migration routes from Southeast Europe to equatorial Africa. The project should prioritise satellite tracking and long-term monitoring of GWPs belonging to different age cohorts.

Genetic analyses of moulted feathers could yield similarly valuable data, and could shed light on the reasons of the sharp decline in population numbers detected in recent years. As we cannot rule out that African migrants might mix among the GWPs migrating towards Europe (Crivelli *et al.* 1991a, Kiss 1992, Kiss & Condac 1992, Michev *et al.* 2018), this method can only work if moulted feathers are collected both at the starting points and wintering grounds. It could also give evidence on the genetic origin of these birds. The classic ringing at breeding areas gives only data on the last location of the given individual, and other marking techniques prove only useful for gaining results if the birds were captured accidentally. It would be advantageous to use modern capture techniques in the course of organised capture campaigns both at the breeding grounds and African wintering grounds. Preferably, the feeding and roosting areas of GWP should be used for the capture. If the lack of other methods would necessitate the capture of flightless young individuals, one of the smaller water bodies in the Danube Delta in their present state would be a possible site, but a capture technique should be used which would cause the least disturbance for the whole population. Besides leg rings, wing tags with colour letter and character codes could also be a good solution.

Special attention must be paid in the project to set up a framework of disseminating information on the migration of GWP along the whole migration route. It should also facilitate the sharing of information on the migration and wintering of GWPs. Based on the outstanding importance of GWP in biodiversity, but also its key role in the fish industry, tourism and culture, organising an international project dedicated to the research and conservation of the GWP would be especially timely and reasonable.

Acknowledgements

We would like to express our gratitude to Giorgos Catsadorakis (IUCN SSC Pelican Specialist Group, Greece), A. J. Crivelli (Station Biologique de la Tour du Valat, France), Ohad Hadzofe (Israel Nature & Parks Authority) and Sándor D. Attila (USAMV – Cluj) for sharing their recapture data with us. We would also like to thank László Haraszthy and Tibor Csörgő for their valuable help in improving the manuscript.

References

Akriotis, T. & Handrinos, G. 2004. Bird Ringing Report (1985–2004). – Hellenic Bird Ringing Centre, p. 26.

Alon, D., Granit, B., Shamoun-Baranes, J., Leshem Y., Kirwan, G. M. & Shirihai, H. 2004. Soaring bird migration over northern Israel in autumn. – British Birds 97: 160–182.

Andone, Gh., Almăşan, H., Radu, D., Andone, L., Chiriac, E. & Scărlătecu, G. 1969. Cercetări asupra păsărilor ihtiofage [Research on fish-eating birds]. – Studii şi Cercetări ICSP. 27(2): 133–183. (in Romanian)

Artzi, Y. & Oron, T. 2014. Pelican Watch: monitoring autumn migration of pelicans in Israel. – Summary of the International Workshop, Hula Valey, Pastoral Hotel, Kfar Blum, Israel, 27–29 October 2014.

BirdLife International 2018. *Pelecanus onocrotalus*. The IUCN Red List of Threatened Species 2018: e. T22697590A132595920.en. Wetlands International 2020. "Waterbird Population Estimates". – wpe.wetlands.org on Monday 16 Mar 2020.

Catsadorakis, G. 2002. The book of pelicans. – The Society from the Protection of Prespa, pp. 9–179.

Catsadorakis, G. 2016. An update of the two *Pelecanus* species in the Mediterranean – Black Sea region. – In: Yésou, P., Sultana, J., Walmsley, J. & Azafzaf, H. (eds.) Proceedings of the UNEP-RAC/SPA symposium – Hammamet, Tunisia, 20 to 22 February 2015, pp. 47–52.

Catsadorakis, G., Onmuş¸ O., Bugariu, S., Gül, O., Hatzilacou, D., Hatzofe, O., Malakou, M., Michev, T., Naziridis, Th., Nikolaou, H., Rudenko, A., Saveljic, D., Shumka, S., Sıkı, M. & Crivelli, A. J. 2015. Current status of the Dalmatian Pelican and the Great White Pelican populations of the Black Sea/Mediterranean flyway. – Endangered Species Research 27: 119–130.

Cătuneanu, I. I. 1999. Istoricul cercetărilor efectuate pe teritoriul României asupra migraţiei păsărilor prin metoda inelărilor, până la înfiinţarea Centralei Ornitologice Române, şi fazele acesteia de dezvoltare în perioada 1939–1970 [History and development of migratory bird studies by banding in Romania between 1939–1970]. – Publicaţiile Societăţii Ornitologice Române 8: 61. (in Romanian)

Ceico, T. 2003. Tatarozás a gödénytelepen [Restoration at the pelican colony]. – Madártávlat 3: 3–4. (in Hungarian)

Chege, A. 2014. The Role of the "Kenya Lake System" in the conservation of the Great White Pelican *(Peleacanus onocrotalus)*. – Summary of the International Workshop, Hula Valey, Pastoral Hotel, Kfar Blum, Israel, 27–29 October 2014.

Crivelli, A. J. 1994. The importance of the former USSR for the conservation of pelican populations nesting in the Palearctic. – In: Crivelli, A. J., Krivenko, V. G. & Vinogradov, V. G. (eds.) Pelicans in the former USSR. – IWRB Special Publication, No. 27., p. 14.

Crivelli, A. 1997. *Pelecanus onocrotalus* White Pelican. – In: Hagemeijer, W. J. M. & Blair, M. J. (eds.) The EBCC Atlas of European breeding birds. – T & AD Poyser, London, p. 32.

Crivelli, A. J., Catsadorakis, G., Hatzilacou, D., Hulea, D., Malakou, M., Marinov, M., Michev, T., Nazirides, T., Peja, N., Sarigul, G. & Siki, M. 2000. Status and population development of Great White Pelican *Pelecanus onocrotalus* and Dalmatian Pelican, *P. crispus* breeding in the Palearctic. – In: Yesou, P. & Sultana, J. (eds.) Monitoring and conservation of birds, mammals and sea turtles of the Mediterranean and Black Seas. – Ministry of Environment, Environment Protection Department, Malta, pp. 38–46.

Crivelli, A. J., Catsadorakis, G. Jerrentrup, H., Hatzilacos, D. & Mitchev, T. 1991a Conservation and management of pelicans nesting in the Palearctic. – In: Salathé, T. (ed.) Conservation of migratory birds. – ICBP Technical Publication 12: 137–152.

Crivelli, A. J., Catsadorakis, G. & Naziridis, T. 1997. *Pelecanus onocrotalus* white pelican. − Birds West Palaearctic Update 1: 144−148.

Crivelli, A. J., Leshem, Y., Mitchev, T. & Jerrentrup, H. 1991b Where do palearctic Great White Pelicans *(Pelecanus onocrotalus)* presently overwinter? – Revue d'Ecologie (La Terre et la Vie) 46: 145–171.

Crivelli, A. J. & Schreiber, R. W. 1984. Status of Pelecanidae. – Biological Conservation 30(2): 147–156. DOI: 10.1016/0006-3207(84)90063-6

del Hoyo, J., Elliott, A. & Sargatal, J. 1992. Handbook of the Birds of the World, Ostrich to Ducks. – Lynx Edicions, Barcelona, p. 309.

Doxa, A., Robert, A., Crivelli, A., Catsadorakis, G., Naziridis, T., Nikolaou, H., Jiguet, F. & Theodorou, K. 2012. Shifts in breeding phenology as a response to population size and climatic change: a comparison between short- and long-distance migrant species. – Auk 129: 753–762. DOI: 10.1525/ auk.2012.11213

Fülöp, A., Daróczi, S. J., Dehelean, A. S., Dehelean, L. A., Domahidi, Z., Dósa, A., Gyékény, G., Hegyeli, Z., Kis, R. B., Komáromi, I. S., Kovács, I., Miholcsa, T., Nagy, A. A., Nagy, A., Ölvedi S. Z., Papp, T., Pârâu, L. G., Sándor, A. K., Sos, T. & Zeitz, R. 2018. Autumn passage of soaring birds over Dobrogea (Romania): a migration corridor in Southeast Europe. – Ardea 106: 61–77. DOI: 10.5253/arde.v106i1.a3

Hadzofe, O. 2014. Pelicans and fisheries conflict management – lesson learned? – Summary of the International Workshop, Hula Valey, Pastoral Hotel, Kfar Blum, Israel, 27–29 October 2014.

Hilgerloh, G., Michalik, A. & Raddatz, B. 2011. Autumn migration of soaring birds through the Gebel El Zeit Important Bird Area (IBA), Egypt, threatened by wind farm projects. – Bird Conservation International 21(4): 365–375. DOI: 10.1017/S0959270911000256

Iankov, P. 2014. Pelicans (*Pelecanus onocrotalus* and *P. crispus*) and fisheries in Bulgaria. – Summary of the International Workshop, Hula Valey, Pastoral Hotel, Kfar Blum, Israel

Izhaki, I. 1994. Preliminary data on the importance of Israel for the conservation of the White Pelican *Pelecanus onocrotalus* L. – Ostrich 65: 213–217. DOI: 10.1080/00306525.1994.9639684

Izhaki, I. & Dagan-Shmueli, M. 1994. The biology and ecology of the Great White Pelican during migration over Israel. – The Torgos 24: 30–43.

Izhaki, I., Shmueli, M., Arad, Z., Steinberg, Y. & Crivelli, A. 2002. Satellite tracking of migratory and ranging behavior of immature Great White Pelicans. – Waterbirds 25(3): 295–304. DOI: 10.1675/1524-4695(2002)025[0295:STOMAR]2.0.CO;2

Kiss, J. B. 1992. Noi regăsiri de inele de pelicani comuni – *Pelecanus onocrotalus* [Recently recovered rings from Great White Pelicans]. – Buletin de Informare SOR. Mediaş 2: 4. (in Romanian)

Kiss, J. B. 2002. Mesterséges fészkelőhelyek biztosítása a rózsás gödények (*Pelecanus onocrotalus* L.) számára a Duna-Deltában [Establishment of artificial nesting grounds for Great White Pelicans *(Pelecanus onocrotalus)* in the Danube Delta]. – Múzeumi Füzetek 13: 92–94. (in Hungarian with English Summary)

Kiss, J. B. 2018. Hol telelnek a Duna-Delta gödényei? [Where do the pelicans of the Danube Delta winter?]. – Állatvilág 6: 18–19. (in Hungarian)

Kiss, J. B. & Condac, M. 1992. Inelări la pelicani şi evaluarea sincronă a ornitofaunei acvatice peteritoriul RB-DD executată de către Corpul de Pază şi Inspecţie Tulcea [Banding of pelicans and synchronous surveys of waterbirds within the RBDD protectorate by the Guard and Inspection Body of Tulcea]. – Analele Stiinţifice ale Institului Delta Dunării. Delta Dunării, Tulcea, pp. 167–170. (in Romanian)

Kiss, J. B. & Nichersu, I. 2002. Satellite telemetry of birds route for automatic data logging of Pelicans deal behaviour. – Analele Stiinţifice, Scientific Annals, INCDDD, Tulcea, Editura Technică, pp. 106–111. (in Romanian)

Kiss, J. B., Sándor, A., Marinov, E. M. & Overdijk, O. 2007. New data regarding the migration of Spoonbills *(Platalea leucorodia)* in the Danube Delta, based on colour ring resightings. – Scientific Annals of the Danube Delta Institute, Tulcea, 13: 45–49.

Kiss, J. B., Marinov, M. Jr., Dorosencu, A., Alexe, V. & Tamiris, P. 2015. The Great White Pelican *(Pelecanus onocrotalus)* in Romania: Current status, monitoring and conservation measures. – Summary of the International Workshop, Hula Valey, Pastoral Hotel, Kfar Blum, Israel, 27–29 October 2014.

Kiss, J. B., Alexe V., Marinov, M., Doroşencu, A. & Sándor, D. A. 2019a Post-breeding dispersion and migratory routes of Dalmatian Pelican *(Pelecanus crispus)*, Great Cormorant *(Phalacrocorax carbo)* and Eurasian Spoonbill *(Platalea leucorodia)* from the North of Sinoe Lagoon (Danube Delta). – Scientific Annals of the Danube Delta Institute Tulcea, Romania 24: 51–62.

Kiss, J. B., Doroşencu, C. A. V. & Marinov, E. M. 2019b Data regarding fluctuations in the Great White Pelican (*Pelecanus onocrotalus* Linnaeus 1758) population in the Danube Delta (Romania) between the 1950–2016. – Muzeul Olteniei Craiova, Oltenia, Studii şi comunicări. Ştiinţele Naturii 35(2): 129–140.

Krivenko*,* V. G., Crivelli, A. J. & Vinogradov, V. G. 1994. Historical changes and present status of pelicans in the former USSR: a synthesis with recommendations for their conservation. – In: Crivelli, A. J., Krivenko, V. G. & Vinogradov, V. G. (eds.) Pelicans in the former URSS. – IWRB Special Publication, Slimbridge, No. 27., pp. 132–151.

Labinger, Z. & Hatzofe, O. 2015. Summary of the International Workshop Great White Pelican Migration over Israel: Management of Ecological Demands and Conflicts with Inland Fisheries Hula Valley, Pastoral Hotel, Kfar Blum, Israel, 27–29 October 2014. – www.wetlands.org/wp-content/uploads/2015/11/pelican-Conference-summary

Leshem,Y. & Yom-Tov, Y. 1996. The magnitude and timing of migration by soaring raptors, pelicans and storks over Israel. – Ibis 138: 667–674. DOI: 10.1111/j.1474-919X.1996.tb04328.x

Marinov, M., Pogan, T., Doroşencu, A., Nichersu, I., Alexe, V., Trifanov, C., Bozagievici, R., Tošić, K. & Kiss, J. B. 2016. Monitoring the Great White Pelican (*Pelecanus onocrotalus* Linnaeus, 1758) breeding population using drones in 2016 – the Danube Delta (Romania). – Scientific Annals of the Danube Delta Institute Tulcea, Romania 22: 41–52.

Michev, T. M., Profirov, L. A., Dimitrov, M. & Nyagolov, K. 2004. Birds of Lake Atanasovsko, Status and Check List. 2nd ed. – Bourgas Wetlands Publication Series 5: 6–12.

Michev, T., Profirov, L. A., Nyagolov, K. & Dimitrov, M. 2011. The autumn migration of soaring birds at Bourgas Bay, Bulgaria. – British Birds 104: 16–37.

Michev, T., Profirov, L. A., Karaivanov, N. & Michev, B. 2012. Migration of soaring birds over Bulgaria. – Acta Zoologica Bulgarica 64(1): 33–41.

Michev, T. M., Profirov, A. L., Michev, B. T., Hristov, L. A., Ignatov, A. L., Stoynov, E. H. & Chipev, N. H. 2018. Long-term changes in autumn migration of selected soaring bird species at Burgas Bay, Bulgaria. – Acta Zoologica Bulgarica 70(1): 57–68.

Onmuş, O. 2014. Great White Pelicans *(Pelecanus onocrotalus)* from past to present in Turkey: Their status, distribution, migration, key sites and threats. Great White Pelican migration over Israel: Management of ecological demands and conflicts with inland fisheries. Summary of the International Workshop, Hula Valey, Pastoral Hotel, Kfar Blum, Israel, 27–29. October 2014.

Petrovici, M. 2015. Atlas al speciilor de păsări de interes comunitar din Romania [Atlas of Bird species of communal interest in Romania]. – Proiect co-finanțat din Fondul European de Dezvoltare Regională. Editor: Fundația Centrul Național pentru Dezvoltare Durabilă, pp. 82–83. (in Romanian)

Platteuw, M., Kiss, J. B., Sadoul, N. & Zhmud, M. Y. 2004. Colonial waterbirds and their habitat use in the Danube Delta. – RIZA Report 2004.002. pp. 3–168.

Radu, D. 1994. Raport al C.O.R. asupra inelărilor şi regăsirilor de păsări inelate 1975–1988, 1988 [C.O.R. report regarding bird banding and ring recovery between 1975–1988]. – Publicațiile S.O.R. Cluj. 4: 11. (in Romanian)

Sándor, D. A., Kiss, J. B., Alexe, V., Marinov, M. & Domșa, C. 2011. The Danube Delta at the crossroads of migrating Great Cormorants *Phalacrocorax carbo*. – Wetlands International Cormorant Research Group Bulletin 7: 26–32.

Schogolev, I., Rudenko, A. & Crivelli, A. J. 2005. Status of pelicans and cormorants on the northern Black Sea. – Bird Conservation International 15(1): 63–71. DOI: 10.1017/S0959270905000055

Shmueli, M., Izhaki, I., Arieli, A. & Arad, Z. 2000a Energy requirements of migrating Great White Pelicans *Pelecanus onocrotalus*. – Ibis 142: 208–216. DOI: 10.1111/j.1474-919X.2000.tb04860.x

Shmueli, M., Izhaki, I., Zinder, O. & Arad, Z. 2000b The physiological state of captive and migrating Great White Pelicans *(Pelecanus onocrotalus)* revealed by their blood chemistry. – Comparative Biochemistry and Physiology Part A 125: 25–32. DOI: 10.1016/S1095-6433(99)00162-2

Shmueli, M., Arad, Z. & Izhaki, I. 2014. Satellite tracking of the Great White Pelican migrating between Europe and Africa through Israel. – Summary of the International Workshop, Hula Valey, Pastoral Hotel, Kfar Blum, Israel, Conference 27–29 October 2014.

IUCN 2001. IUCN Red List Categories and Criteria, version 3.1. – IUCN Species Survival Commission. IUCN, Gland, Switzerland, and Cambridge, United Kingdom. – www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria

Underhill, L. G., Tree, A. J., Oscadleus, H. D. & Parker, V. 1999. Review of ring recoveries of waterbirds in Sothern Africa. – Avian Demography Unit, University of Cape Town, pp. 103–106.

Ornis Hungarica 2020. 28(1): 76–91.
DOI: 10.2478/orhu-2020-0006

The role of reedbeds in secondary habitats during the migration and breeding of reed warblers

László Bozó

Received: April 21, 2020 – Revised: May 28, 2020 – Accepted: May 29, 2020

Bozó, L. 2020. The role of reedbeds in secondary habitats during the migration and breeding of reed warblers. – Ornis Hungarica 28(2): 76–91. DOI: 10.2478/orhu-2020-0006

Abstract The reedbeds provide essential habitat for many *Acrocephalus* and *Locustella* species during both breeding and migration periods. The nesting and the migration of these species have been the subject of detailed research over the past half century in the Carpathian Basin. However, these studies have focused primarily on natural habitats and large reedbeds and thus, little is known about the role of smaller habitat fragments in the migration and nesting of these species. During my work, I studied the spring and autumn migration of five passerines in a landscape dominated by agricultural land in Southeast Hungary. Field observations were carried out to survey the populations of different species between 2010–2019. To study their migration, I used the method of bird ringing between 2016–2019 in an oleaster forest and a drainage canal. I was able to determine the migration periods of the species and in autumn, to calculate the time spent in the research area based on the recaptures. In conclusion, reedbeds in secondary habitats play a similar role in the migration of the most common *Acrocephalus* and *Locustella* species as in the natural habitats in different regions of the Carpathian Basin. There are differences among species in the timing of migration, the length of time spent here, and the accumulated fat stores. As these species nest in small numbers in the area, primarily individuals from more distant populations occur here during the migration.

Keywords: *Acrocephalus*, agricultural lands, drainage canal, habitat conservation, *Locustella*, Southeast Hungary

Összefoglalás A nádasok nélkülözhetetlen élőhelyet jelentenek a különböző *Acrocephalus* és *Locustella* fajok számára a költési és vonulási időszakban egyaránt. Vonulásukat és költésüket részletesen tanulmányozták az elmúlt fél évszázadban a Kárpát-medencében, de ezek a kutatások elsősorban természetes élőhelyekre és nagy kiterjedésű nádasokra koncentrálódtak. A fragmentált és kis kiterjedésű, másodlagos élőhelyeken alig foglalkoztak ezen kérdések vizsgálatával. Jelen dolgozatban Délkelet-Magyarországon, egy mezőgazdasági területek által dominált tájban öt, nádasban élő énekesmadár faj tavaszi és őszi vonulási és fészkelési időszakban gyűjtött adatait dolgoztam fel. Az adatgyűjtés 2016–2019 között egy ezüstfás erdőben és egy belvízelvezető csatornában zajlott a madárgyűrűzés módszerével, 2010–2019 között terepi megfigyelésekkel. A jelölés-visszafogás adatok segítségével meghatároztam a fajok vonulási időszakait, és a madarak által a területen eltöltött időt. Az eredmények szerint a másodlagos élőhelyeken található kis kiterjedésű nádasok hasonló szerepet töltenek be a nádi énekesek vonulásában, mint a Kárpát-medence más területein található természetes élőhelyek nádasai. A fajok vonulásának időzítésében, az itt töltött idő hosszában és a felhalmozott zsírraktárakban különbségek vannak. Mivel a térségben ezek a fajok csak kis számban fészkelnek, így a vonulás során elsősorban távolabbi populációk egyedei fordulnak itt elő.

Kulcsszavak: *Acrocephalus*, mezőgazdasági területek, belvízelvezető csatorna, *Locustella*, Délkelet-Magyarország

Eötvös Loránd Tudományegyetem, Állatrendszertani és Ökológiai Tanszék, 1117 Budapest, Pázmány Péter sétány 1/c, e-mail: bozolaszlo91@gmail.com

Introduction

Reedbeds provide very important resting, feeding and nesting area for many bird species (Bíró 2007). Highly protected bird species, such as the Great Egret *Ardea alba*, Spoonbill *Platalea leucorodia* or Glossy Ibis *Plegadis falcinellus* breed in these habitats. They provide home not only for the large birds but also for the songbirds (Haraszthy 2013). Many of them use these habitats during migration and wintering, and they occur in different parts of the reedbeds during breeding (Csörgő 1995, Báldi & Kisbenedek 1999, Preiszner & Csörgő 2008). However, the extent of reedbeds across Europe is declining due to tourism and improper management. One of the many harmful interventions that reduce the area of reedbeds is the fragmentation and the lack of old reeds, which affects the populations of most of the songbirds breeding here (Haraszthy 2013). As a result, in recent times, there was a decline in the number of many species, and without proper conservation efforts, these species can easily disappear along with reedbeds. It is particularly disadvantageous for those species which only settle in old, unharvested reedbeds and those which require large, continuous patches. In contrast, certain species, such as Great Reed Warbler, does not necessarily need large, non-harvested habitats, but a small lakeside reed spot is enough for them to settle (Csörgő 1998a).

The reedbed is important not only during the breeding period but also during the migration period for many species. Habitat use, migration patterns and population changes of these species have been the subject of numerous studies in the Carpathian Basin (Gyurácz & Csörgő 1994, Gyurácz & Bank 1997, Csörgő *et al.* 1998, Gyurácz *et al.* 1998, Gyurácz *et al.* 2003, Vadász *et al.* 2008, Nagy *et al.* 2009, Czikkelyné Ágh 2014) within the framework of bird ringing programs working in reedbeds of fishponds and natural habitats.

However, reedbeds occur not only in natural but also in secondary habitats, such as at the edges of pit lakes and along inland drainage canals. Permanent water cover is not necessarily needed for reedbeds, as it can be found in dry habitats, usually in the steppes. These are the so-called dry reeds, which cause serious problems in the conservation of nature due to their prevalence against native vegetation (Haraszthy 2013).

The breeding and migration of songbirds have not yet been studied in detail in these types, although in some landscapes these are the dominant reed habitats. The southern part of Békés County is also one of these, since it is a plain covered by infusion loess, with only one stream flowing in the area (Száraz-ér) and with no natural standing water at all (Jakab & Deli 2012). Although small reed patches can be found nearby small, artificial quarry ponds and drainage canals, the most important reedbeds can be found in lawns (Bozó 2017).

During my work, I examined the nesting population and migration of four *Acrocephalus* and one *Locustella* species associated with reedbeds. I was looking for the role of these secondary reedbeds in the breeding and migration of the studied species, with particular reference to their stopover ecology.

Material and Methods

I carried out my research in the area of Kevermes and Lőkösháza in the southern part of Békés County *(Figure 1)*. There were two methods of sampling. For the breeding population survey, simple field observations were made on the 5000 hectares area of the two settlements. During the binocular observations, I cycled through the area. I have observation data from 439 different days between April and August from 2010 to 2019. The central areas of the surveys were the quarry ponds in Kevermes and the Turai lawn in Lőkösháza, but I regularly visited all the canals and other reedbeds in other areas as well. For a detailed description of the areas, see the work of Bozó (2017). In the case of this paper, it should be emphasized that only small reed patches can be found in the quarry ponds as well as along canals. In contrast, the Turai lawn has an approx. 25 hectares of reedbeds, which, in the deeper parts of the flat, form a habitat mixed with bulrush and other swamp vegetation. Since only a part of the area is mown regularly, the reedbeds also appear in smaller or larger patches on the protected vegetation of the lawn. The data collected during the spring migration are also primarily based on field observations, but since 2012, I have been able to use occasional bird ringing data. These come from the Kevermes gravel mine. For a detailed description of the area and non-standard ringing work, see Bozó (2016). During the autumn seasons from 2016 to 2019, I was ringing in a 0.5 hectare patch of the former Pheasant station (EOV 815638 123876) with a seven-meter long and twelve pieces of twelve-meter long Japanese-type mist nets. It is a bushy area, where in addition to the dominant oleaster *Elaeagnus*

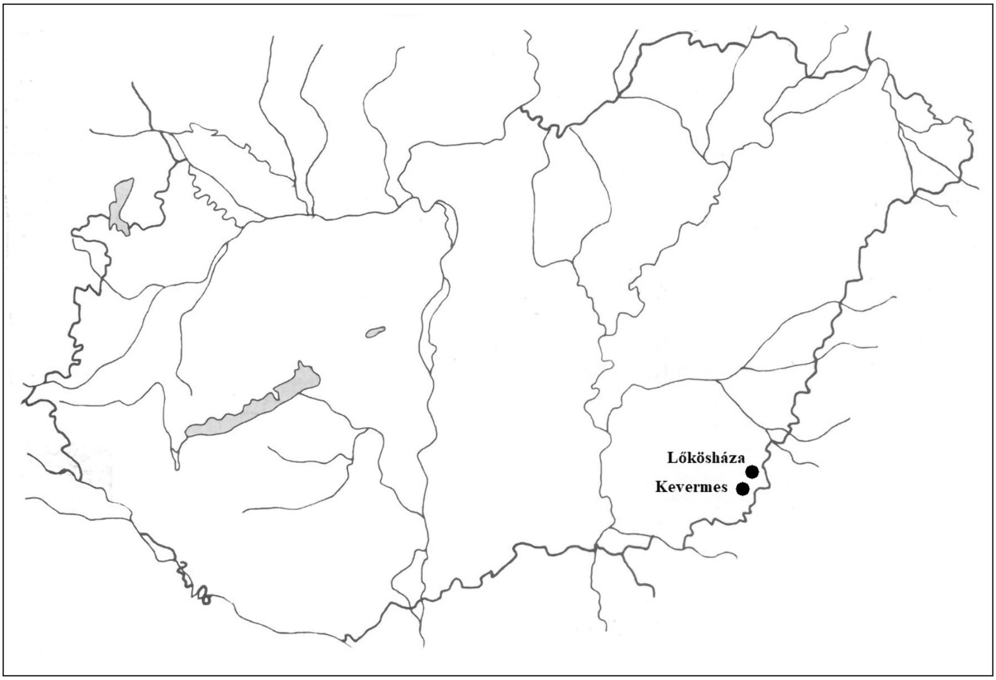


Figure 1. The location of the study area within Hungary
1. ábra A kutatási terület Magyarországon belüli elhelyezkedése

angustifolia, some taller elms *Ulmus* sp., black locust *Robinia pseudoacacia* and wild pear *Pyrus pyraster* can also be found. The shrub level consisted of black elder *Sambucus nigra* and blackthorn *Prunus spinosa*, while at lower levels, blackberry *Rubus caesius* was common. At the edge of the forest, the vegetation was denser, with reeds and weeds. Behind the forest, there was a drainage canal with southeast-northwestern orientation (Tulkánéri canal), with young willows *Salix* sp. on its shores, and dense reedbed on the shore and in the riverbed. During the ringing, I collected different biometric data (wing length, subcutaneous fat, weight) according to Eck *et al.* (2011), I determined the age and the sex of the birds by Svensson (1992), and then released them. The work took place between the beginning of August and the end of October for two days a week (16 working hours).

I used the minimum stopover length – the number of days between the first capture and the last recapture of an individual – as an estimate for true stopover duration (Yosef & Chernetsov 2005, Polak & Szewczyk 2007). To calculate the minimum stopover length, I only used the data of the recaptured birds. Also, I examined the stopover duration and the body mass changes by intervals of “10-day periods” to learn the changes of these items. Differences among stopover duration in subsequent periods were tested using Kruskal-Wallis test. Intervals with less than 10 individuals per species were excluded from my analysis. I estimated the change of body mass during stopover as the percentage of the initial body mass (Yosef & Chernetsov 2004, Polak & Szewczyk 2007). To compare the amount of accumulated fat between ringing and recapture, I used the Mann-Whitney U test. I used Spearmans’s rank correlation to relate the body mass and fat with the number of days elapsed since the first capture. To test the possible differences in body mass change among the periods, I used one-way ANOVA. Statistical analyses were carried out using Past 3.14 (Hammer *et al.* 2001).

Results

Marsh Warbler *(Acrocephalus palustris)*

Regular and common breeder and a migratory species. The largest population can be found along the canals, but it also frequently breeds in abandoned gardens and weedy areas. The population density along the Tulkánéri canal can reach two pairs within 100 meters. It has a small population on the Turai lawn, and it is only an occasional breeder in the quarry ponds.

In spring between 2013–2019, I observed the first individuals between 2 May and 10 May *(Table 1)*. During the non-standard ringing, birds migrating through the area were caught between 6–17 May.

The members of the local population disappear from the nesting sites until late July. In some years (e.g. 2019), singing males can be heard even in mid-July.

In autumn, a total of 217 individuals were caught and 48 of these individuals were recaptured (22.1%). Of the ringed birds, seven were adult and 210 juveniles (3.2% and 96.8%).

The migration took place between 1 August and 28 September, with a median date of 20 August *(Figure 2)*. There was a significant difference between years, as the median of migration was later in both 2017 and 2018 ($H = 17.06$, $p = 0.0006$) *(Figure 3)*. Differences in

Table 1. Spring arrival dates of the study species between 2013–2019
1. táblázat A vizsgált fajok tavaszi visszaérkezési idejei 2013–2019 között

Species	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**
Marsh Warbler	9 May	9 May	10 May	6 May	7 May	5 May	2 May
Eurasian Reed Warbler	16 April	27 April	16 April	12 April	23 April	12 April	18 April
Sedge Warbler	11 April	8 April	16 April	5 April	10 April	8 April	18 April
Great Reed Warbler	23 April	26 April	16 April	18 April	20 April	17 April	24 April
Savi's Warbler	11 April	8 April	16 April	5 April	10 April	8 April	18 April

migration between adult and juvenile birds could not be examined due to the low sample size of the adults.

The minimum stopover duration of Marsh Warblers was on average 3.8 days (median = 2 days, range = 1–15 days, *SD* = 3.7 days.)

Concerning stopover duration, significant differences were found between subsequent periods (*Kruskal-Wallis test*, $H = 7.246$, $p = 0.0487$) *(Figure 4)*, and their body mass also changed significantly among the periods. The birds captured between 21–30 August have significantly higher body mass than birds captured in any other weeks (*one-way ANOVA*, $F = 5.541$, $p = 0.001$).

The body mass of recaptured individuals did not change during the stopover at the study area (on average 0.9 g, 8.1% of the initial body mass; $N = 24$, $t = -1.223$, $p = 0.226$). In detail, of recaptured birds, 70.8% showed a body mass gain and 29.2% showed a body mass loss.

There was a significant correlation between the body mass change and the number of days elapsed between the first capture and the recapture ($r_s = 0.5767$, $p = 0.0025$), i.e. the birds that spent more time in the study area changed their body mass greater.

The amount of fat of the birds at ringing was significantly lower than at recapture (*Mann-Whitney U test*, $U = 1123$, $z = -2.3734$, $p = 0.017$). Changes in fat were higher in parallel with the number of days elapsed between ringing and recapture ($r_s = 0.538$, $p < 0.0001$).

There were also individuals that showed mixed identification characters with the Eurasian Reed Warbler mainly in the color of the plumage, but they were usually distinguishable by biometric parameters. In the first part of the migration period, at the beginning of August, we caught almost exclusively typical birds that were definite by all identification characters. Then, by the second half of the month, these individuals have disappeared, and individuals with mixed characters appeared.

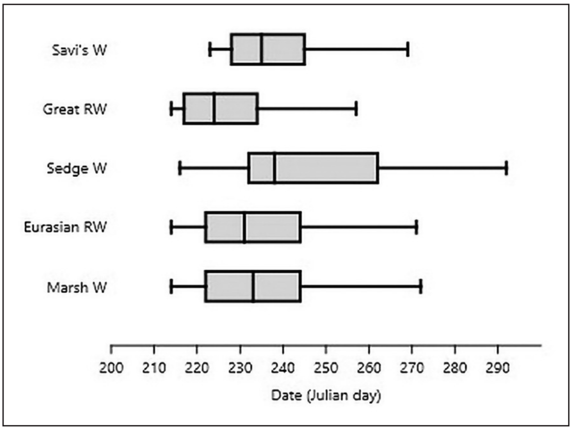


Figure 2. The timing of autumn migration of the study species
2. ábra A vizsgált fajok őszi vonulásának időzítése

Eurasian Reed Warbler *(Acrocephalus scirpaceus)*

Regular, but small number breeder and common migrant. In the study area, a small population of 3–4 pairs regularly breeds in the reedbeds of the Turai lawn. Occasionally, it can be also found as a breeder in the largest reedbed of the Cigányka canal called Jérce lawn.

In spring, I noticed the first singing birds between 12–27 April *(Table 1)*. According to six individuals ringed in the area of the quarry ponds, its migration continues even in mid-May. The first non-local recapture of the species comes also from the spring season. This individual was ringed as a juvenile bird in Farmos (Pest County) on 1 September 2015 and recaptured on 18 May 2016 in the area of the quarry ponds.

Nesting birds typically leave the breeding area by the end of July, but for example, on 7 August 2019, I heard a singing male on the Turai lawn.

In autumn, a total of 122 individuals were ringed and 27 of these individuals were recaptured (22.1%). Of the ringed birds, two were adults and 120 were juveniles (1.6% and 98.4%).

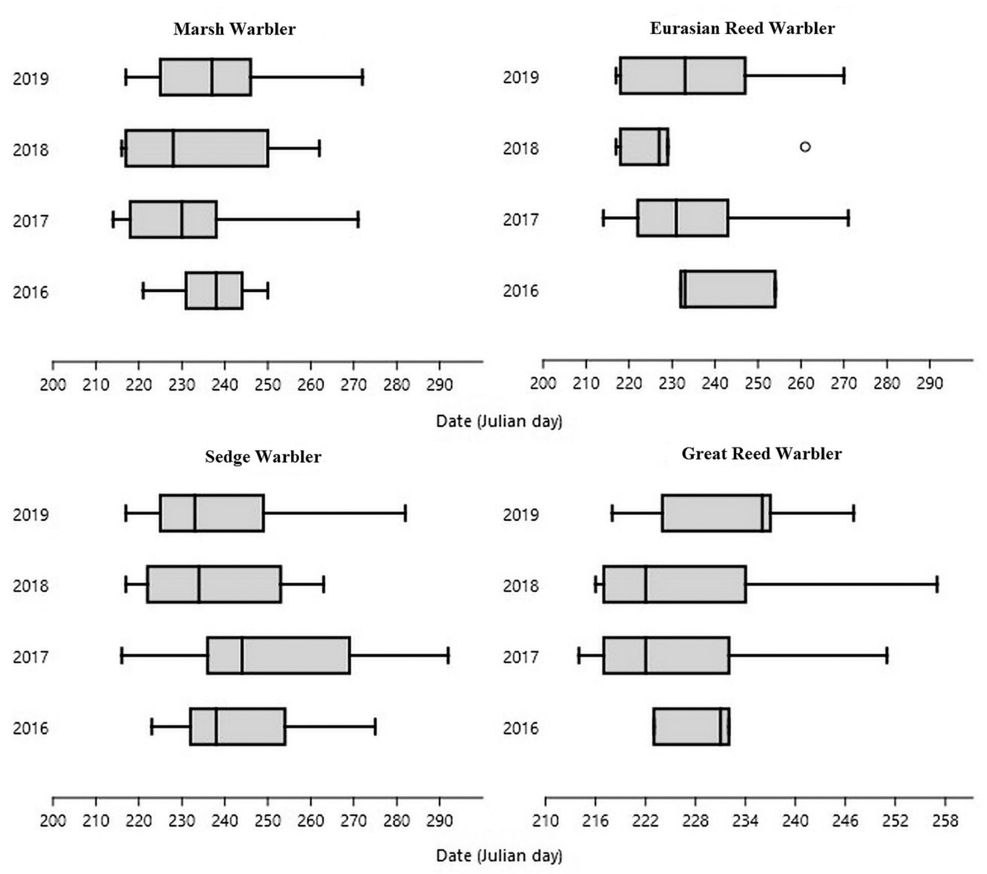


Figure 3. The differences in autumn migration timing between years
3. ábra A vizsgált fajok őszi vonulási időzítésének évenkénti összehasonlítása

The migration took place between 1 August and 27 September, with a median date on 18 August *(Figure 2)*. The latest data is from 27 September 2017. There were no significant differences among years (*H* = 3.714, *p* = 0.293) *(Figure 3)*. Differences in migration between adult and juvenile birds could not be examined due to the low sample size of the adults.

The minimum stopover duration of Eurasian Reed Warblers was on average 3.1 days (median = 2 days, range = 1–14 days, *SD* = 3.1 days).

Concerning stopover duration, no significant differences were found between subsequent periods (*Kruskal-Wallis test*, *H* = 2.184, *p* = 0.6377), however, their body mass did not change significantly between the periods (*one-way ANOVA*, *F* = 1.649, *p* = 0.1687) *(Figure 4)*.

The body mass of recaptured individuals did not change during the stopover at the study area (on average 0.4 g, 10.1% of the initial body mass; *N* = 14, *t* = -0.3942, *p* = 0.696). In detail, of recaptured birds, 42.9% showed a body mass gain, and 57.1% showed a body mass loss.

There was no significant correlation between the body mass change and the number of days elapsed between the first capture and the recapture (r_s = 0.4296, *p* = 0.1252).

The amount of fat of the birds did not change significantly between the first capture and the recapture (*Mann-Whitney U test*, *U* = 399.5, *z* = -1.1551, *p* = 0.248). Changes in fat

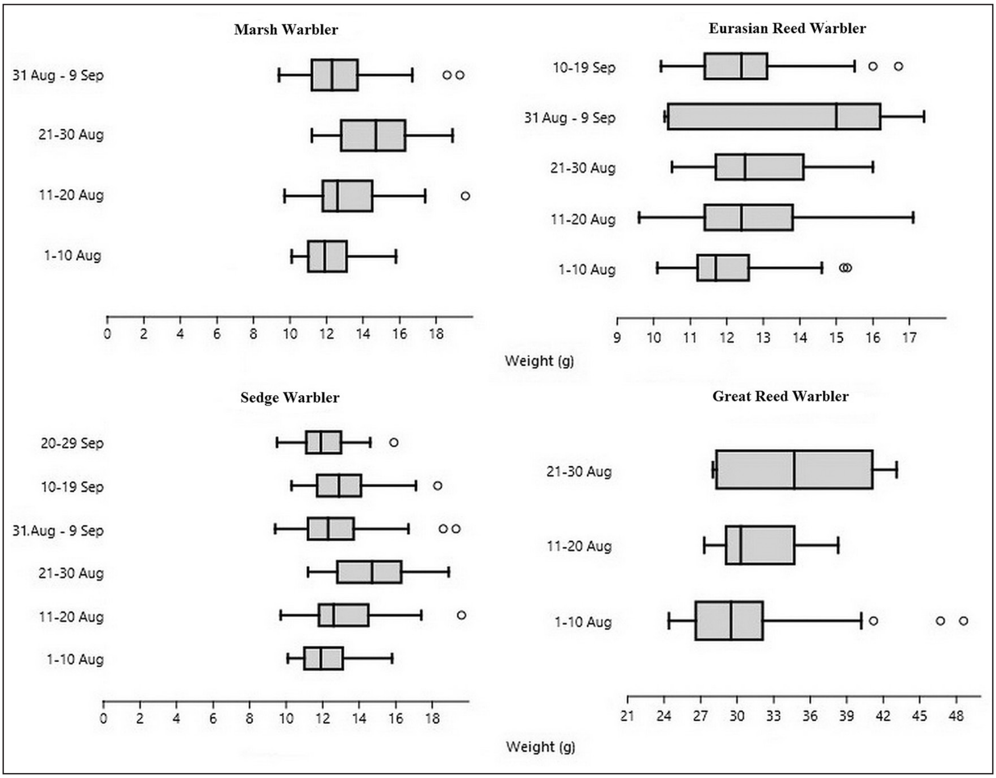


Figure 4. The body mass change of the study species between decades
4. ábra A vizsgált fajok testtömeg-változása dekádonként

were greater in parallel with the days elapsed between ringing and recapture ($r_s = 0.475$, $p = 0.007$).

The second non-local recapture was from the autumn period. A juvenile bird ringed in Komárom-Esztergom County on 6 August 2017 was recaptured on 30 August 2017.

Sedge Warbler *(Acrocephalus schoenobaenus)*

This is the most numerous breeding and migratory species among all studied species. The highest population (app. 25–30 pairs) breed in the reedbeds of the Turai lawn. Some pairs can also be found regularly along the canals in smaller reedbeds. Occasionally breeds in grasslands, and in agricultural lands mixed with johnson grass *Sorghum halepense* and reed. The population of the Turai lawn was stable, with the exception of 2017, when the population decreased to 15 pairs.

In spring, the first singing individuals were observed between 5–18 April *(Table 1)*. My last observation in the quarry ponds was on 8 May, but between the second part of April and early May, it was a regular migrant.

Breeding typically ends by the middle of July, after feeding the young individuals until early in the month (rarely in the middle of the month) and leaving the nesting areas around 20 July. However, 2019 was an extraordinary year due to the significant rainfall in the summer and birds could be observed while feeding the nestlings even in early August (Bozó 2020).

In autumn, a total of 293 individuals were ringed and 20 of these individuals were recaptured (6.8%). Of the ringed birds, 51 were adults and 242 juveniles (17.4% and 82.6%).

The migration took place between 1 August and 17 October with a median date on 25 August *(Figure 2)*. The latest data is from 17 October 2017. There was a significant difference among the years (*Kruskal-Wallis test*, $H = 14.29$, $p = 0.0025$) *(Figure 3)*. Adults migrated significantly earlier than juveniles (*Kruskal-Wallis test*, $H = 12.68$, $p = 0.0003$, median adults: 24 August, median juveniles: 31 August).

The minimum stopover duration of Sedge Warblers was on average 2.6 days (median = 1 day, range = 1–8 days, $SD = 2.6$ days).

Concerning stopover duration, no significant differences were found (*Kruskal-Wallis test*, $H = 1.88$, $p = 0.5814$). Their body mass changed significantly between the periods (*one-way ANOVA*, $F = 5.11$, $p < 0.0001$).

The body mass of recaptured individuals did not change during the stopover at the study area (on average 0.9 g, 6.3% of the initial body mass, $t = -0.6370$, $p = 0.5343$) *(Figure 4)*. In detail, of recaptured birds, 50% showed a body mass gain, and 50% showed a body mass loss.

There was a significant correlation between the body mass change and the number of days elapsed between the first capture and the recapture ($r_s = 0.7864$, $p = 0.0333$), i.e. the birds that spent more time in the study area changed their body mass greater.

The amount of fat of the birds did not change significantly between the first capture and the last recapture (*Mann-Whitney U test*, $U = 285.5$, $z = -0.5257$, $p = 0.599$). Changes in fat were higher in parallel with the number of days elapsed between ringing and recapture ($r_s = 0.611$, $p = 0.001$).

Great Reed Warbler *(Acrocephalus arundinaceus)*

The Great Reed Warbler is the second most common breeder among the studied species in the study area. The largest population breeds in the reedbeds of the quarry ponds. In addition, it is also common breeder along the canals (app. 2 pairs/100 meters along the Cigányka canal) as well as in the villages. However, it is a rare breeder in the Turai lawn with a total population of 8–10 pairs. There have been no fluctuations in the species' population over the past decade.

In spring, the first singing birds were observed between 16–26 April *(Table 1)*. The data of non-standard ringing revealed that some individuals migrate even in mid-May.

Breeding typically ends by the second half of July. The latest observation regarding adults feeding nestlings was on 21 July 2014.

In autumn, a total of 65 individuals were ringed and 18 of these individuals were recaptured (27.7%). Of the ringed birds, seven were adult and 58 juveniles (10.8% and 89.2%).

Migration took place between 1 August and 13 September with a median date on 11 August *(Figure 2)*. The latest data is from 13 September 2018. There were no significant differences among the years (*Kruskal-Wallis test*, $H = 7.41$, $p = 0.0587$) *(Figure 3)*. Differences in migration between adult and juvenile birds could not be examined due to the low sample size of the adults.

The minimum stopover duration of Great Reed Warblers was on average 3.4 days (median = 1 day, range = 1–18 days, $SD = 4.2$ days).

Concerning stopover duration, no significant differences were found between subsequent periods (*Kruskal-Wallis test,* $H = 0.2858$, $p = 0.84$). Their body mass did not change significantly between the periods (*one-way ANOVA,* $F = 1.793$, $p = 0.1772$) *(Figure 4)*.

The body mass of recaptured individuals did not change during the stopover at the study area (on average 1.1 g, 3.1% of the initial body mass, $t = -0.751$, $p = 0.4662$). In detail, of recaptured birds, 35.7% showed a body mass gain, and 64.3% showed a body mass loss.

There was a significant correlation between the body mass change and the number of days that elapsed between the first capture and the recapture ($r_s = 0.6203$, $p = 0.018$), i.e. the birds that spent more time in the study area changed their body mass greater.

The body mass of recaptured individuals did not change during the stopover at the study area (*Mann-Whitney U test*, $U = 111.5$, $z = -0.\ 021$, $p = 0.983$). There was no correlation between the change of fat amount and the number of days elapsed between the first capture and the recapture ($r_s = 0.128$, $p = 0.649$).

It should be noted that an individual was seen on 2 October 2013 on the field, which is the latest occurrence of the species in the study area.

Savi's Warbler *(Locustella luscinioides)*

Regularly breeds and migrates through the area in small number. The only place where the species regularly breeds is the Turai lawn. In 2014, the pairs bred in the reedbed of the Tulkán law and the Jérce lawn.

The first singing birds were observed between 5–18 April *(Table 1)*. I do not have information on its spring migration due to the lack of ringing data.

The nesting pairs are on the breeding ground until mid-July, however, it is not uncommon that the adults feed the nestlings in this period. They typically disappear from the area by the end of the month. However, 2019 was an exception, as on 7 August, I observed nestlings fed by the parents, and even on 11 September, I observed specimens moving in the area.

In autumn, a total of eight individuals were ringed and two of these individuals were recaptured (25%).

The migration took place between 10 August and 25 September with a median date on 22 August *(Figure 2)*. The latest data is from 25 September 2017.

Both recaptured individuals were caught two times after ringing (five and thirteen, and one and seven days elapsed between the ringing and the recaptures).

Discussion

Among the bird species examined in my study, the local nesting populations of Sedge Warbler, Marsh Warbler and Great Reed Warbler were proportional to the number of captured individuals during the autumn migration. This can be compared with the assertion that the number of birds in a given resting and feeding place during the migration season correlates significantly with the size of the local breeding population (Safriel & Lavee 1991). In this case, it can be interpreted as the number of birds trapped in the canal and oleaster forest in autumn is in parallel with their breeding population in the region. However, in the case of the Eurasian Reed Warbler, which has the smallest local breeding population, we caught far more birds than we should have by this logic. The reason for this is probably the fact that the canal plays an important role in the migration of the species, it is a migration corridor, so the individuals of the more distant populations migrate here. This was also assumed for other species migrating mainly during daytime by Bozó *et al.* (2017) and Schupkégel *et al.* (under revision).

The relative lack of Eurasian Reed Warbler in the landscape also makes it likely that individuals with mixed phenological characters can arrive from further geographic regions. The two species can hybridize only in habitats where they breed close to each other (Lemaire 1977). The Marsh Warbler breeds mainly in the edges of reedbeds, along canals and other weedy plant communities (Csörgő 1998b, Végvári 2008a, Haraszthy 2019), while the Eurasian Reed Warbler breeds in the larger, more closed reedbeds (Csörgő 1998c, Végvári 2008b, Haraszthy 2019). Individuals with mixed characters tend to occur later in the migratory period, whereas in early-August, I trapped birds with almost typical, clear, species-specific characters.

There are similarities and differences in the timing of the autumn migration of the five species. The earliest species was the Great Reed Warbler, followed by the Marsh and Eurasian Reed Warbler, while the latest species was the Sedge Warbler. This is similar to the one described by Gyurácz and Csörgő (1991) in Ócsa and Sumony. The lengths of migration periods are also similar to those: the shortest for Great Reed Warbler, followed by Marsh Warbler and Common Reed Warbler, while the Sedge Warbler has the longest migration period. This is probably due to the fact that the Sedge Warbler has a much larger and more northern distribution area than other species (BirdLife International 2020), so the birds reach and migrate through the Carpathian Basin, which is an important resting place, in wider intervals (Csörgő & Gyurácz 2009a).

The median date of migration of the Marsh Warbler was on 20 August. This coincides with the date when 90% of the birds in Ócsa left the area (Gyurácz & Csörgő 1991). In the Carpathian Basin, the peak of the species' migration is at the end of July and beginning of August (Csörgő & Gyurácz 2009b), that is three weeks before the median date of the migration of the birds in my study site. One of the reasons for this difference might be that in the Actio Hungarica camps they started ringing in mid-July, two weeks before the work started in Kevermes. However, this does not explain the three-week difference, because in the beginning of August we would have had to catch a much larger number of the Marsh Warblers. It should be noted, that there was ringing every day in the Actio Hungarica camps, and only two days a week in the present study, therefore this may also skew the results of any comparisons. There is also a possibility that local agricultural areas are less suitable for the breeding of the species than natural habitats, and that is why I trapped mainly migrating birds from northern populations. The migration dynamics of birds with mixed characters also seems to support this.

However, in the case of Eurasian Reed Warbler, comparisons with data from the Carpathian Basin are likely to be made, as the migration begins later than that of the Marsh Warbler (Csörgő & Gyurácz 2009c). According to the results, this species seems to migrate later in the region than in Ócsa and Sumony, probably for the same reason as the Marsh Warbler. Because of the absence of suitable habitats, the species do not breed in large numbers in the region, thus their number only increases with the arrival of individuals of further populations. Also, it should be emphasized, that the northern populations migrate through the Carpathian Basin only in small numbers (Csörgő & Gyurácz 2009c), so the birds I trapped in mid-August may have come from within the Carpathian Basin. This may be supported by the fact that the species is very rare in the second half of September and has no data at all in October, although it occurs in Hungary by mid-October (Csörgő & Gyurácz 2009c). Based on the two long-term recaptures, the birds follow the southeast-northwest direction, which is similar to the birds breeding in or migrating through the Carpathian Basin (Gyurácz *et al.* 2004).

The median date of migration of Sedge Warbler was on 25 August. In Ócsa, this was on 17 August, in Fenékpuszta on 19 August, and in Sumony on 16 August (Gyurácz & Csörgő 1994). The difference is probably due to the differences in the start of the work and the number of working days of these locations and may ringing station. The same might be true for the Great Reed Warbler, where the difference is similar (Csörgő & Gyurácz 2009d). The migration of adult birds peaked a week earlier than that of juveniles, which is similar to data published from different places in Hungary (Gyurácz & Csörgő 1991, Gyurácz & Bank 1997, Csörgő & Gyurácz 2009d).

The migration of the Savi's Warbler was studied in Sumony, Southern Hungary between 1993–2002 (Mátrai *et al.* 2006). Their results show that the migration of the species falls in late July and early August, but there were still migratory individuals in September and early October. Based on biometric data, two migration waves were identified with a border line on 16 August. The individuals migrating in the second wave had longer wings, so they may have come from more northern populations. As only a few specimens were ringed in the autumn during my study, I do not have accurate information on the autumn migration of the species, but based on Mátrai *et al.* (2006) and the typical ringing time after mid-August, it is likely that the majority of birds come from more northern areas. The peak period of the spring migration in Hungary is in mid-April, and the last local birds arrive in the first days of May (Gyurácz & Csörgő 2009). This is also similar to my results.

However, when dealing with migration phenology when comparing studies covering longer time periods, the effects of climate change should not be forgotten either. As a result of ringing in Ócsa between 1987–2004, it was found that the migration of the Savi's Warbler shifted earlier in the fall, while the migration of the other species I studied shifted later over the decades (Miholcsa *et al.* 2009). They also found a significant difference between the different age groups in case of Marsh Warbler: adults migrated earlier, while migrated later in the study area. Also, studies in Ócsa between 1989–2009 showed one- or two-week delay for Eurasian Reed Warbler, Marsh Warbler and Sedge Warbler in autumn, while in spring, Eurasian Reed and Sedge Warbler returned 6.5 and 7.5 days earlier in the end of this period (Kovács *et al.* 2012). In this regard, no significant change in the timing of the spring migration was found for Marsh Warbler. These results call attention to the fact that the results of articles on migration phenology published a few years or decades ago can be used with caution when evaluating the results of recent researches.

Among the species studied, the Sedge Warbler spent the shortest time in the area. In addition to this, there were far fewer recaptures than in the case of the other species. The reason for this phenomenon is that the Sedge Warbler migrates faster than other species and therefore spends less time on other stopover sites (Csörgő & Gyurácz 2009a). It usually migrates with high fat reserves, but only a minority of birds resting in the Carpathian Basin increase their fat reserves (Csörgő & Gyurácz 2009a). This is supported by my results as neither the body weight of the birds nor the body fat category changed significantly during the time spent here.

The Marsh Warbler had the most fat reserves of all the species studied, and body fat values also increased during the stopover. All of this is related to the fact that the species flies through larger barriers such as mountains, and therefore accumulates high fat reserves (Csörgő *et al.* 2000, Csörgő & Gyurácz 2009a). Conversely, the Eurasian Reed Warbler crossed the area with very little stored fat and did not increase its reserves significantly during its stay. The reason for the low fat reserves is that the species migrates in short steps and use the large Mediterranean peninsulas, so it does not need much fat reserve (Csörgő & Gyurácz 2009c).

The ringed Great Reed Warblers, however, had higher fat reserves, though they did not increase these fat reserves during the stopover. With regard to the stopover duration, the individuals of the Marsh Warbler spent more in the area over time during the migratory season, while in the case of the other species, there was no change in this respect. This may be because Marsh Warblers have the highest fat reserves and they increase this during their stay. However, as time passes, the amount of available food may decrease due to degradation of herbaceous vegetation and therefore, the birds require more time to accumulate sufficient amounts of fat. Similar to the Marsh Warbler, the Sedge Warbler had a higher body weight at the end of the migratory period than at the beginning. The body weight of both species was highest in the end of August during the migration peak. All this can clearly be related to the assumption that the birds leave with the greatest possible reserves. The migration peak will be when most birds are able to reach critical mass. For the other two species, there was no difference in this respect. The Marsh Warbler migrates with much less fat and its amount does not change during the whole migration period. The Eurasian Reed Warbler, however, moves in such a concentrated, narrow period that it cannot develop different fat accumulation strategies.

The earliest spring migrant is the Sedge Warbler followed by the Marsh Warbler, Savi's Warbler and Great Reed-warbler in mid-April. The Marsh Warblers return to the breeding grounds the latest. The reason for the temporal differentiation is the different nesting sites. The first four species breed in reedbeds (Csörgő 2009b, 2009c, 2009d, 2009e, Végvári 2008b, 2008c, 2008d, 2008e, Haraszthy 2019), whilst the Marsh Warblers build their nest in the herbaceous vegetation (Csörgő 1998a, Haraszthy 2019). However, herbaceous plants reach their proper height and density much later than reeds (Csörgő & Gyurácz 2009b), so birds need to arrive later. It is clear from some spring ringing and field observation data that while some of the local birds are already in the territories, other birds are still migrating. My assumed migration periods for each species overlap with those described in the literature (Csörgő & Gyurácz 2009a, 2009b, 2009c, 2009d, Gyurácz & Csörgő 2009).

Overall, reedbeds in secondary habitats play a similar role in the migration and nesting of the most common passerines of this habitat in the southeastern part of Hungary as the natural habitats of other areas in the Carpathian Basin. This is particularly important because, for example, in the case of the European Robin *Erithacus rubecula*, Gyimóthy *et al.* (2011) found that the species used different migration strategies in optimal and suboptimal habitats in terms of feeding and resting. The studies were carried out by comparing data from several different ringing station in the Carpathian Basin highlighted that using the data from only one habitat in a migration dynamics study is not enough because the data are influenced by the geographical location and vegetation structure of the area. Studies in the coast of Baltic Sea also support that Eurasian Reed Warblers spend much more time in the optimal habitats (reedbeds) than in shrubs in coastal dunes, and have to devote less energy to obtaining food than in suboptimal habitats (Ktitorov *et al.* 2010). All these highlight the important shortcoming that the results of Hungarian researches are based almost exclusively on data from natural habitats, so they do not necessarily give a realistic picture of the migratory characteristics of these species in Hungary. More comparative research would be needed between the optimal and suboptimal habitats. The species-specific differences show that due to the limited number of suitable breeding sites available in the area, migrating individuals are from further geographical areas. As emphasized in other works (Bozó *et al.* 2017, Bozó 2018, Schupkégel *et al.* under revision), these secondary habitats play a key role in the migration of birds through the agricultural landscape, and their conservation and protection, on at least a local level, are important tasks. This is particularly important because the diversity and bird populations of agricultural areas are rapidly declining across Europe (Chamberlain & Fuller 2000, Donald *et al.* 2006), so secondary habitats may be very important in the conservation of certain species.

Acknowledgements

I am grateful to Tibor Csörgő for his helpful comments on the early version of the manuscript. I am also grateful to Nikolett Olajos for checking and improving the English language of the text.

References

Báldi, A. & Kisbenedek, T. 1999. Species-specific distribution of reed-nesting passerine birds across reed-bed edges: effects of spatial scale and edge type. – Acta Zoologica Academiae Scientiarum Hungaricae 45(2): 97–114.

BirdLife International 2020. IUCN Red List for birds. – http://www.birdlife.org on 13/03/2020.

Bíró, I. 2007. Biharugrai-halastavak [Biharugra fishponds]. – In: Tardy, J. (ed.) A magyarországi vadvizek világa [The wildlife of Hungarian wetland habitats]. – Alexandra Kiadó, Pécs (in Hungarian)

Bozó, L. 2016. A madárgyűrűzés eredményei a kevermesi sóderbánya területén 2012–2016 között [Results of bird ringing at the querry ponds in Kevermes between 2012–2016]. – A Száraz-ér társaság kutatásai 2011–2015 között, pp. 35–38. (in Hungarian)

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

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

Bozó, L. 2020. A szélsőséges időjárás hatása a madarak fészkelésére [The impact of the extreme weather conditions on the breeding of some bird species]. – Madártávlat 27(1): 29. (in Hungarian)

Bozó, L., Bozóné Borbáth, E. & Tar, L. 2017. Énekesmadarak őszi vonulása csatornaparti fasoron [Songbird migration in a channel-sided alley]. – Természetvédelmi Közlemények 23: 1–13. DOI: 10.20332/tvk-jnatconserv.2017.23.1 (in Hungarian with English Summary)

Chamberlain, D. E. & Fuller, R. J. 2000. Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. – Agriculture, Ecosystems & Environment 78(1): 1–17. DOI: 10.1016/S0167-8809(99)00105-X

Csörgő, T. 1995. A nádas zonációk és szegélyvegetációk énekesmadarai [Niche segregation and microhabitat preference of warblers within a reed stand]. – In: Vásárhelyi, T. (ed.) A nádasok állatvilága [The animals of reed beds in Hungary]. – Magyar Természettudományi Múzeum, Budapest, pp. 138–143. (in Hungarian with English Summary)

Csörgő, T. 1998a Nádirigó [Great Reed-warbler]. – In: Haraszthy, L. (ed.) Magyarország madarai [Birds of Hungary]. – Mezőgazda Kiadó, Budapest, pp. 306–307. (in Hungarian)

Csörgő, T. 1998b Énekes nádiposzáta [Marsh Warbler]. – In: Haraszthy, L. (ed.) Magyarország madarai [Birds of Hungary]. – Mezőgazda Kiadó, Budapest, p. 304. (in Hungarian)

Csörgő, T. 1998c Cserregő nádiposzáta [Eurasian Reed Warbler]. – In: Haraszthy, L. (ed.) Magyarország madarai [Birds of Hungary]. – Mezőgazda Kiadó, Budapest, p. 305. (in Hungarian)

Csörgő, T. 1998d Nádi tücsökmadár [Savi's Warbler]. – In: Haraszthy, L. (ed.) Magyarország madarai [Birds of Hungary]. – Mezőgazda Kiadó, Budapest, p. 299. (in Hungarian)

Csörgő, T. 1998e Foltos nádiposzáta [Sedge Warbler]. – In: Haraszthy, L. (ed.) Magyarország madarai [Birds of Hungary]. – Mezőgazda Kiadó, Budapest, pp. 302–303. (in Hungarian)

Csörgő, T., Karcza, Zs. & Palkó, S. 1998. Környezeti változások monitorozása énekesmadarakkal [Monitoring of environmental changes with passerine birds]. – Ornis Hungarica 8(Suppl. 1): 17–26. (in Hungarian with English Summary)

Csörgő, T., Miklay, Gy. & Halmos, G. 2000. Migration of *Acrocephalus* species along the coast of the Black Sea. – Ornis Hungarica 10: 141–147.

Csörgő, T. & Gyurácz, J. 2009a Foltos nádiposzáta [Sedge Warbler]. – 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. 483–488. (in Hungarian with English Summary)

Csörgő, T. & Gyurácz, J. 2009b Énekes nádiposzáta [Marsh Warbler]. – 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. 494–496. (in Hungarian with English Summary)

Csörgő, T. & Gyurácz, J. 2009c Cserregő nádiposzáta [Eurasian Reed Warbler]. – 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. 489–493. (in Hungarian with English Summary)

Csörgő, T. & Gyurácz, J. 2009d Nádirigó [Great Reed-warbler]. – 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. 499–501. (in Hungarian with English Summary)

Czikkelyné Ágh, N. 2014. Nádiposzáta fajok őszi vonulásának kor-és ivarfüggő mintázatai [Age and sex related autumn migration phenology of the Reed, Marsh and Sedge Warbler]. – Szakdolgozat, Szent István Egyetem, Állatorvos-tudományi Kar Biomatematikai és Számítástechnikai Tanszék, Biológiai Intézet (in Hungarian)

Donald, P. F., Sanderson, F. J., Burfield, I. J. & Van Bommel, F. P. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. – Agriculture, Ecosystems & Environment 116(3–4): 189–196. DOI: 10.1016/j.agee.2006.02.007

Eck, S., Fiebig, J., Fiedler, W., Heynen, I., Nicolai, B., Töpfer, T., van den Elzen, R., Winkler, R. & Woog, F. 2011. Vögel vermessen/measuring birds. – Deutsche Ornithologen-Gesellschaft, Minden, Christ Media Natur

Gyimóthy, Zs., Gyurácz, J., Bank, L., Bánhidi, P., Farkas, R., Németh, Á. & Csörgő, T. 2011. Autumn migration of Robins *(Erithacus rubecula)* in Hungary. – Biologia 66(3): 548–555. DOI: 10.2478/s11756-011-0039-9

Gyurácz, J. & Csörgő, T. 1991. Az öreg és a fiatal madarak őszi vonulása közti különbségek négy nádiposzáta (*Acrocephalus* spp.) fajnál [Differences between autumn migration of adult and juvenile birds in four reed warbler (*Acrocephalus* spp.) species]. – MME III. Tudományos Ülése, Szombathely, pp. 164–171. (in Hungarian with English Summary)

Gyurácz, J. & Csörgő, T. 1994. Autumn migration dynamics of the Sedge Warbler *(Acrocephalus schoenobaenus)* in Hungary. – Ornis Hungarica 4: 31–37.

Gyurácz, J. & Bank, L. 1997. Spatial distribution of migrating Sedge Warblers *(Acrocephalus schoenobaenus)* in a Hungarian reed bed. – Ornis Hungarica 7: 43–47.

Gyurácz, J., Bank, L. & Horváth, G. 2004. Studies on the population and migration dynamics of five reed warbler species in a South Hungarian reed bed. – Aquila 111: 105–129.

Gyurácz, J. & Csörgő, T. 2009. Nádi tücsökmadár [Savi's Warbler]. – 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. 473–475. (in Hungarian with English Summary)

Gyurácz, J., Horváth, G., Csörgő, T., Bank, L. & Palkó, S. 2003. Influence of macrosyoptic weather situation on the autumn migration of birds in Hungary. – Ring 25(1–2): 18–20.

Gyurácz, J., Károssy, Cs., Csörgő, T., Bank, L. & Palkó, S. 1998. A makroszinoptikus időjárási helyzetek hatása a foltos nádiposzáta *(Acrocephalus schoenobaenus)* őszi vonulásdinamikájára [Influence of the macrosynoptical weather situations on the autumn migration dynamics of the Sedge Warblers *(Acrocephalus schoenobaenus)*]. – Ornis Hungarica 8(Suppl. 1): 163–168. (in Hungarian with English Summary)

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

Haraszthy, L. 2013. Értékőrző gazdálkodás Natura 2000 területeken [Farming in Natura 2000 areas]. – Pro Vértes Természetvédelmi Közalapítvány, Csákvár (in Hungarian)

Haraszthy, L. 2019. Magyarország fészkelő madarainak költésbiológiája. 2. kötet. Sárgarigóféléktől a sármányfélékig [Breeding biology of Hungarian nesting birds. Vol. 2. Passeriformes]. – Pro Vértes Nonprofit Kft., Csákvár, pp. 448–453. (in Hungarian)

Jakab, G. & Deli, T. 2012. A Dél-Tiszántúl természetföldrajzi viszonyai [The natural characteristic of the South-Tiszántúl]. – In: Jakab, G. (ed.) A Körös-Maros Nemzeti Park növényvilága [The Flora of the Körös-Maros National Park]. – Körös-Maros Nemzeti Park Igazgatóság, Szarvas, pp. 24–33. (in Hungarian)

Kovács, Sz., Fehérvári, P., Nagy, K., Harnos, A. & Csörgő, T. 2012. Changes in migration phenology and biometrical traits of Reed, Marsh and Sedge Warblers. – Central European Journal of Biology 7(1): 115–125. DOI: 10.2478/s11535-011-0101-1

Ktitorov, P., Tsvey, A. & Mukhin, A. 2010. The good and the bad stopover: behaviours of migrant Reed Warblers at two contrasting sites. – Behavioral Ecology and Sociobiology 64(7): 1135–1143. DOI: 10.1007/s00265-010-0929-9

Lemaire, F. 1977. Mixed song, interspecific competition and hybridization in the Reed and Marsh Warblers *A. scirpaceus* and *A. palustris*. – Behaviour 3: 215–240.

Mátrai, N., Gyurácz, J. & Bank, L. 2006. A nádi tücsökmadár *(Locustella luscinioides)* őszi vonulása egy dél-magyarországi nádasban [Autumn migration of Savi's Warblers *(Locustella luscinioides)* in a southern Hungarian reed-bed]. – Állattani Közlemények 91(1): 19–28.

Miholcsa, T., Tóth, A. & Csörgő, T. 2009. Change of timing of autumn migration in *Acrocephalus* and *Locustella* genus. – Acta Zoologica Academiae Scientiarum Hungaricae 55(2): 175–185.

Nagy, K., Csörgő, T., Harnos, A. & Kovács, Sz. 2009. A cserregő és az énekes nádiposzáta *(Acrocephalus scirpaceus, A. palustris)* vonulásának fenológiai változásai [Changes in the migration phenology of Reed and Marsh Warbler *(Acrocephalus scirpaceus*, *A. palustris)*]. – Természetvédelmi Közlemények 15: 434–445. (in Hungarian with English Summary)

Polak, M. & Szewczyk, P. 2007. Relation between stopover length and time and body parameters of European Robin *Erithacus rubecula* (L., 1758) during autumn migration (Central Poland). – Polish Journal of Ecology 55(3): 511–517.

Preiszner, B. & Csörgő, T. 2008. Habitat preference of Sylviidae warblers in a fragmented wetland. – Acta Zoologica Academiae Scientiarum Hungaricae 54(Suppl. 1): 111–122.

Safriel, U. N. & Lavee, D. 1991. Relative abundance of migrants at a stopping-over site and the abundance in their breeding ranges. – Bird Study 38(1): 71–72. DOI: 10.1080/00063659109477069

Schupkégel, B., Bozó, L. & Tölgyesi, Cs. (under revision). The role of the water canals and secondary forests in bird migration. – Ring

Svensson, L. 1992. Identification guide to European passerines. – Svensson, Stockholm

Vadász, Cs., Németh, Á., Karcza, Zs., Loránt, M., Biró, Cs. & Csörgő, T. 2008. Study on breeding site fidelity of *Acrocephalus* warblers in Central Hungary. – Acta Zoologica Hungarica 54(Suppl. 1): 167–175.

Végvári, Zs. 2008a Énekes nádiposzáta [Marsh Warbler]. – In: Hadarics, T. & Zalai, T. (eds.) Magyarország madarainak névjegyzéke – Nomenclator Avium Hungariae. – Magyar Madártani és Természetvédelmi Egyesület, Budapest, p. 188.

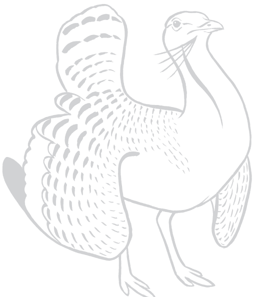
Végvári, Zs. 2008b Cserregő nádiposzáta [Eurasian Reed Warbler]. – In: Hadarics, T. & Zalai, T. (eds.) Magyarország madarainak névjegyzéke – Nomenclator Avium Hungariae. – Magyar Madártani és Természetvédelmi Egyesület, Budapest, p. 188.

Végvári, Zs. 2008c Nádirigó [Great Reed-warbler]. – In: Hadarics, T. & Zalai, T. (eds.) Magyarország madarainak névjegyzéke – Nomenclator Avium Hungariae. – Magyar Madártani és Természetvédelmi Egyesület, Budapest, p. 189.

Végvári, Zs. 2008d Nádi tücsökmadár [Savi's Warbler]. – In: Hadarics, T. & Zalai, T. (eds.) Magyarország madarainak névjegyzéke – Nomenclator Avium Hungariae. – Magyar Madártani és Természetvédelmi Egyesület, Budapest, p. 186.

Végvári, Zs. 2008e Foltos nádiposzáta [Sedge Warbler]. – In: Hadarics, T. & Zalai, T. (eds.) Magyarország madarainak névjegyzéke – Nomenclator Avium Hungariae. – Magyar Madártani és Természetvédelmi Egyesület, Budapest, p. 187.

Yosef, R. & Chernetsov, N. 2005. Longer is fatter: body mass changes of migrant Reed Warblers *(Acrocephalus scirpaceus)* staging at Eilat, Israel. – Ostrich 76(3–4): 142–147. DOI: 10.2989/00306520509485486



Ornis Hungarica 2020. 28(1): 92–103.
DOI: 10.2478/orhu-2020-0007

Woodcock (*Scolopax rusticola* L.) nestings in Carpatian Basin from the second half of the 19th century to present days

Attila Bende[1*] & Richárd László[2]

Received: February 25, 2020 – Revised: March 15, 2020 – Accepted: March 16, 2020

Bende, A. & László, R. 2020. Woodcock (*Scolopax rusticola* L.) nestings in Carpatian Basin from the second half of the 19th century to present days. – Ornis Hungarica 28(1): 92–103. DOI: 10.2478/orhu-2020-0007

Abstract In this study, we summarized and evaluated nesting data of 300 Woodcocks in both historic and present Hungary recorded from the 19th century until now that appeared in 108 ornithological and hunting literature including the results of Vönöczky Schenk's study (1908–1917). We acquired a comprehensive picture of Woodcock nestings in the Carpathian Basin as we drew nesting maps based on previously collected data analysis. We classified those significant regions where nesting data of this sparsely nesting species were registered. It is ascertainable that the distribution of Woodcock nestings concentrated in certain regions of the country both before and after the First World War. Nesting data collected before 1921 concentrated to higher areas especially the well forested regions of the Carpathian Mountains where 3 main nesting regions can be distinguished with 72% of all nesting data. The most significant nesting area is the region of the North Carpathian Mountains (36%) (Pest-Pilis-Solt-Kiskun, Esztergom, Hont, Nógrád, Borsod, Gömör and Kis-Hont, Abaúj-Torna, Zólyom, Liptó, Sáros, Zemplén and Ung counties). The second main nesting region is situated on the ranges of the East and South Carpathian Mountains (26%) (Máramaros, Beszterce-Naszód, Maros-Torda, Udvarhely, Kisküküllő, Nagyküküllő, Brassó, Fogaras, Szeben, Alsó-Fehér, Torda-Aranyos counties). The third important nesting region can be found in the west part of Historic Hungary (10%) (Moson, Győr, Sopron, Vas, Zala counties). The distribution of nesting observations – based on data collected between 1921–2019 – can be connected well to mountainous nesting regions in the Kingdom of Hungary where nesting conditions were more favourable. Many of these regions are abroad now. Apart from sparse nestings on the Great Hungarian Plain, breeding grounds concentrate in well forested areas such as in North Hungarian counties (63%) (Pest, Nógrád and Borsod-Abaúj-Zemplén) and in some Transdanubian counties (31%) mainly in Győr-Moson Sopron, Vas, Veszprém and Baranya counties.

In the dominant nesting regions this species typically do not join to higher altitudes, however, in the south margin of their nesting region in the Carpathian Basin – based on 170 years nesting data (n=704) – it can be stated that they rather nest in woodlands of higher altitudes due to their more favourable (cool and rainy) climatic features.

Keywords: Woodcock, *Scolopax rusticola* L., nesting, nesting sites, nesting regions, Carpathian Basin

Összefoglalás Tanulmányunkban összefoglaltuk és értékeltük a történelmi Magyarország és jelenlegi országhatáraink területére vonatkozóan – a XIX. század közepétől napjainkig – a magyar ornitológiai és vadászati szakirodalomban közölt 108 publikáció közel 300 erdei szalonka fészkelésre vonatkozó adatát, valamint a Vönöczky Schenk-féle felmérés (1908–1917) eredményeit. Az elkészített fészkelési térképek alapján meghatároztuk azokat a jelentős régiókat, ahol e Magyarországon szórványosan fészkelő faj költési adatait regisztrálták. Megállapítható, hogy az erdei szalonka fészkelések az első világháborút megelőző időszakban és azt követően is az ország egyes régióiban koncentrálódtak. A fészkelési adatok súlypontjai zömében a magasabb térszintek, különösen a Kárpátok hegyvidéki régióinak erdősült területeire tehetők. Az összes fészkelési adat 72%-a három fő régióból származott: 1. Északi-Kárpátok (36%) (Pest-Pilis-Solt-Kiskun, Esztergom, Hont, Nógrád, Borsod, Gömör és Kis-Hont, Abaúj-Torna, Zólyom, Liptó, Sáros, Zemplén, Ung vármegye), 2. Keleti- és Déli-Kárpátok (26%) (Máramaros, Beszterce-Naszód, Maros-Torda, Udvarhely, Kisküküllő, Nagyküküllő, Brassó, Fogaras, Szeben, Alsó-Fehér, Torda-Aranyos vármegye), 3. Nyugat-Dunántúl (10%) (Moson, Győr, Sopron, Vas, Zala vármegye).

A mai Magyarországon 1921–2019 közötti időszakban gyűjtött adatok alapján a költési megfigyelések területi eloszlása jól kapcsolódik a Magyar Királyság – mára jelentős részben határon kívülre került – kedvezőbb hegyvidéki fészkelőterületeihez. A ritka alföldi szórványfészkelést leszámítva azokban a régiókban koncentrálódnak a fészkelések, ahol kiterjedt erdőterületek vannak: 1. Északi-középhegység területe (63%) (Pest, Nógrád, Borsod-Abaúj-Zemplén megye). 2. Dunántúli régió (31%) (Győr-Moson-Sopron, Vas, Veszprém, Baranya megye).

A faj domináns fészkelőterületein jellemzően nem kötődik a magasabb térszintekhez, viszont a fészkelőterületének déli peremén, a Kárpát-medencében több mint 170 év fészkelési adata (n=704) alapján megállapítható, hogy a kedvezőbb klimatikus adottságok (hűvösebb, csapadékosabb) miatt inkább a magasabb térszintek erdőterületein fészkel.

Kulcsszavak: erdei szalonka, *Scolopax rusticola,* fészkelés, fészkelőhelyek, fészkelési régiók, Kárpát-medence

[1] *Institute of Wildlife Management and Vertebrate Zoology, Faculty of Forestry, University of Sopron, Sopron, Bajcsy-Zsilinszky utca 4., 9400 Hungary, e-mail: bende.attila.tibor@phd.uni-sopron.hu*
[2] *Institute of Wildlife Management and Vertebrate Zoology, Faculty of Forestry, University of Sopron, Sopron, Bajcsy-Zsilinszky utca 4., 9400 Hungary*
** corresponding author*

Introduction

Woodcocks nest in Hungary year after year but only sparsely and in small numbers, no more than 10–60 pairs, according to estimations (Hadarics & Zalai 2008). During their spring (March-April) and autumn (September-October) migrations, they are observable in larger numbers. So far, only few people have made attempts to summarize the peculiarities of Woodcock's nesting habits. The first comprehensive study in this topic was written by Vönöczky Schenk in 1944. Since the birth of Vönöczky Schenk's study almost a century has passed, nevertheless, no detailed retrospective study – that could provide data summary on Woodcock nestings in Hungary from the 19th century – has appeared. As we have very little data of Woodcock nesting, the question raises, whether we can interpret the phenomenon of breeding stock here in Hungary. Authors report rather nestings of those Woodcocks that are either left behind in their spring migration or late arrivals. The reason why we are short of data might be the fact that this mysterious bird hides both its nest and eggs. In this study, we attempted to analyze literature appeared in the last 174 years and to provide a clear picture of Woodcocks nesting regions in Hungary.

Sources and methods

Beside data summary from different hunting reports and publications that deal with both nesting and young breeding habits of Woodcocks we also used never published verbal information. Altogether they form the basis of our examination. The following data sources were used during our work:

Woodcock briding in the Kingdom of Hungary between 1846–1921.
The following reports provide data of found nests:
Széchényi (1879), Lovassy (1884), Anonim (1885), Chernel (1885), Sárkány (1885), Szidnay (1885), Anonim (1886), Lakatos (1886), Orlovszky (1889), Anonim (1891a), Lovassy

(1891), Anonim (1893), Teschler (1893), Anonim (1896), Ertl (1897), Egerváry (1898), Gy. Takách (1901), Ertl (1902), Ertl (1903), Lakatos (1903), Matolai (1906), Anonim (1907), Sugár (1916), Veress (1916), Preuszler (1917), Chernel (1918), Károlyi (1921), Kiskárpáti (1935), Lokcsánszky (1935b), Vönöczky Schenk (1944), Fuisz *et al*. (2015), Haraszthy and Viszló (2010), Haraszthy *et al.* (2015).

Data on chick directing Woodcock hens or Woodcock chicks appeared in the following studies:
Anonim (1871a), Anonim (1871b), Széchényi (1871), Chernel (1885), Deák (1885), Lakatos (1886), Anonim (1889), Anonim (1891b), Egerváry (1895), Anonim (1898), Bod (1901), Borsiczky (1901), Gy. Takách (1901), Anonim (1902b), Dorning (1903), Lakatos (1903), Matolai (1906), Anonim (1910), Sőreghy (1912), Breuer (1929), Kiskárpáti (1935), Lokcsánszky (1935b).

Summer Woodcock rodings data are in the following reports:
Chernel (1885), Anonim (1896), Anonim (1902a), Lakatos (1903), Sőreghy (1912), Réz (1930), Lokcsánszky (1935b).

Woodcock breeding in Hungary between 1921–2019.
The following reports provide data of found nests:
Mérey (1928), Réz (1928), Dorner (1930), Réz (1930), Schenk (1930), Steiner (1931), Csele (1932), Szurmay (1933), Bársony (1935), Farkas (1935), Kozarits (1935), Lokcsánszky (1935a, 1935b, 1935c), Parragh (1935), Réz (1935), Anonim (1936), Boroviczény (1936), Csete (1936), Kiriczi (1936), Vásárhelyi (1936), Say (1937), Anonim (1938), Berényi (1938), Agárdi (1939), Zsilinszky (1943), Szilágyi (1948), Szomjas (1950), Csiba (1959), Szabó (1964 in Hungarian Bird Ringing Databank), Varga (1966, 1968, 1975, 1977, 1979, 1980, 1985), Agárdi (1968), Csaba (1974), Bársony (1985), Faragó (1987), M. Mester (2011), Haraszthy (2012, 2015), Solti *et al.* (2015), Kozma and Vadász (2018), Pukánszki (2018).

Data on chick directing Woodcock hens or Woodcock chicks appeared in the following studies:
Polgár (1922), Janisch (1924), Réz (1928, 1930), Dorner (1930), Réz (1932 in Hungarian Bird Ringing Databank), Várady (1932), Veress (1932), Kozarits (1935), Lokcsánszky (1935a, 1935b), Réz (1935), Lengyel (1937), Berényi (1938), Várkonyi (1938), Parragh (1941), Gyapay (1943), Zsilinszky (1943), Anonim (1947), Szilágyi (1948), Hoffmann (1950), Gárdonyi (1958 in Hungarian Bird Ringing Databank), Győry (1958 in Hungarian Bird Ringing Databank), Varga (1966), Csaba (1967), Varga (1968, 1973, 1979), Csaba (1974), Bársony (1985), Faragó (1987), Fenyősi (1993), Fenyősi and Stix (1993), ifj. Reményfy pers. comm. (2019, not published).

Summer Woodcock rodings data are in the following reports:
Réz (1930), Sárvári (1933), Farkas (1935), Unger-Ullmann (1935), Kiriczi (1936), Vidonyi (1941), Zsilinszky (1943), Szilágyi (1948), Horváth (1989), Fenyősi and Stix (1993).

We visualized the suitable information from the articles with the use of ArcGIS 10.3 software. We created our maps in county settings based on observation data (nesting n=204) like chick directing hens or immature birds (n=91). We also used data from Vönöczky Schenk's map published in 1944. These maps refer both to the historical and present country.

Results

Woodcock nesting in the Kingdom of Hungary between 1846–1921.

Reports on Woodcock nestings in the Kingdom of Hungary are known from 1846. We can state that the division of nesting data in certain regions of the country before the World War I. was not equable either. The focus of nesting data was put mainly on woodlands of higher altitude *(Figure 1)*.

Woodcocks insist on woodlands during nesting. Numerous nesting data are known from deciduous, coniferous or mixed woods. Woodcock nests in Hungary were found in 90 m above the sea level (Sarkadremete, Békés county) (Faragó 1987) as well as in higher altitude 1600 above sea level (Garamfő – now Telgárt, Slovakia) (Lokcsánszky 1935a) in woods in the mountains, hills or flat areas in different exposures or sloping conditions. Yet,

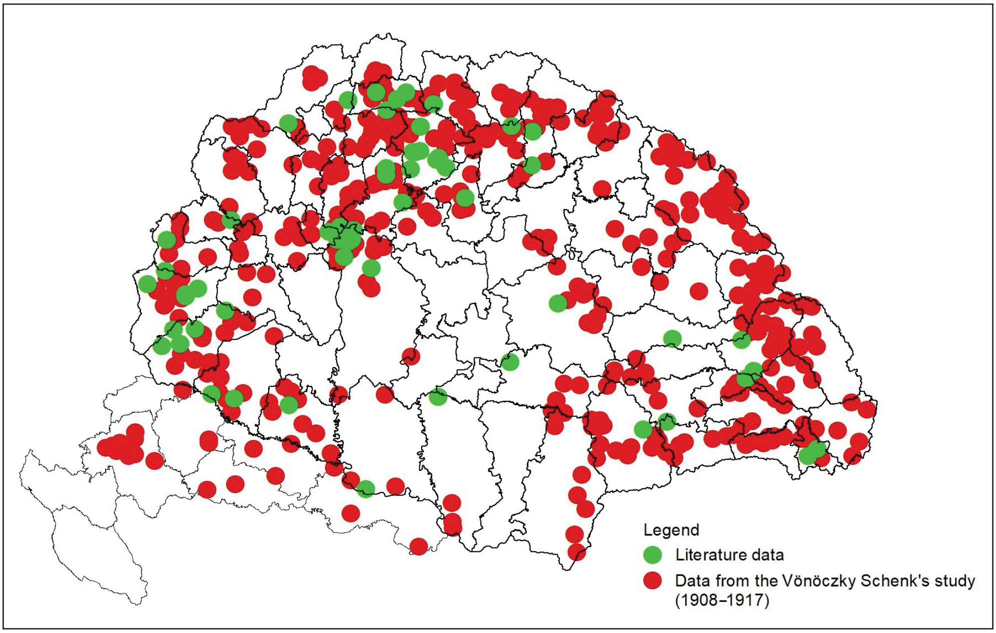


Figure 1. Observation data of Woodcock nests (n=70), hens directing chicks, Woodcock chick (n=36) in the area of the Kingdom of Hungary between 1846 and 1921 and data of Vönöczky Schenk's study (1944) (n=409)

1. ábra Erdei szalonka fészkek (n=70), csibéket vezető szalonka tyúkok, illetve szalonka csibék (n=36), a Magyar Királyság területén 1846 és 1921 között, valamint a Vönöczky Schenk-féle felmérés (1944) (n=409) adatai the majority of nesting data came from woods in the Carpathian Mountains during the era of the Kingdom of Hungary. Most data arrived from the North Carpathian Mountains but it is true that we also have data from every part of the ranges of the Carpathians. Other important nesting regions are the North-east and the East Carpathian Mountains the Transylvanian Mountain and the South Carpathians with a lot of hatching data. Though Woodcocks regularly hatch in these regions (Lokcsánszky 1935a, 1935b, Vönöczky Schenk 1944) their hatchings cannot be considered frequent. The west border regions of Historical Hungary – the east ranges of the Austrian Alps – are also important nesting places. According to Vönöczky Schenk (1944), wood-covered regions in Transdanubia seem to be favourable for nesting but their low altitude and unfavourable climate make these regions less popular for Woodcocks. We have a lot of nesting data from certain parts of the North Hungarian Mountain, especially from the Pilis region. We also have data about sparse nestings from flatlands but these came from wood-covered areas apart from a few exceptions. Nesting data also arrived from the Croatian-Slavonia mountainous woodlands.

In accordance with the information we mentioned above nesting observations focus on 3 regions in the land of Historical Hungary *(Figure 2)*. The most important nesting area is situated in the North-Carpathian region (36%) (Pest-Pilis-Solt-Kiskun, Esztergom, Hont, Nógrád, Borsod, Gömör and Kis-Hont, Abaúj-Torna, Zólyom, Liptó, Sáros, Zemplén and Ung counties). The diversity of elevation and the rather large extension of Pest-Pilis-Solt-Kiskun county slightly distort this picture. Only 1–2 nesting cases are known from the flat south area of the region while the majority of nests are in the north wood-covered hilly

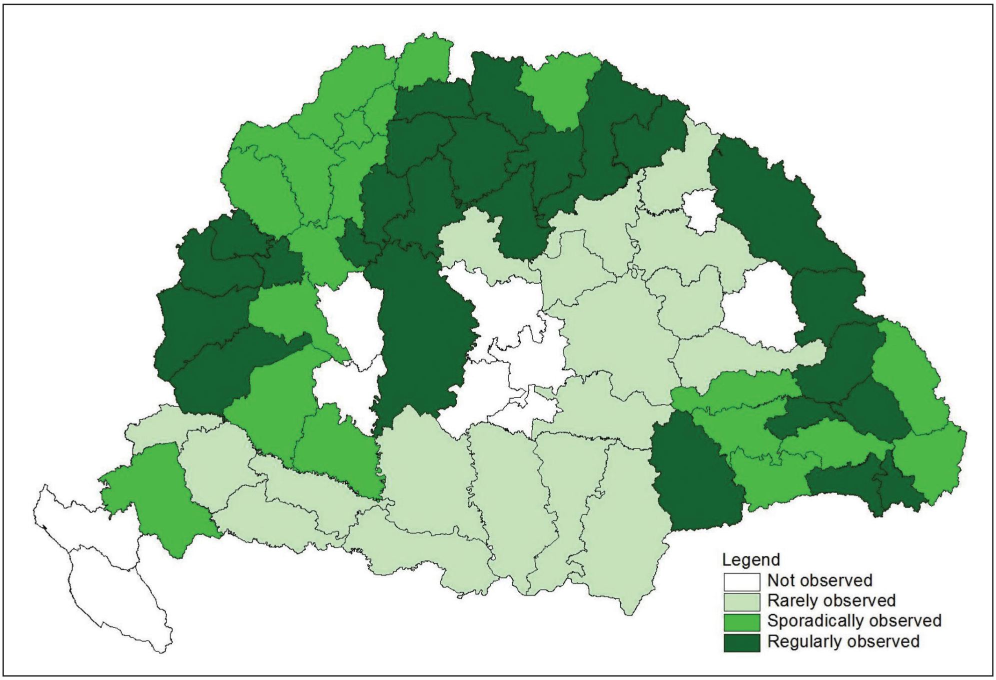


Figure 2. Frequency of Woodcock nestings in the area of the Kingdom of Hungary before 1921
2. ábra Erdei szalonka fészkelések gyakorisága a Magyar Királyság területén 1921 előtt

parts. The area which belongs to the north nesting region and has sparse nesting data is situated in the west part of the North Carpathian Mountains with some counties such as Pozsony, Nyitra, Bars, Trencsén, Turóc and Árva. The second nesting region having importance involves the ranges of the East and the South Carpathian Mountains (26%) (Máramaros, Beszterce-Naszód, Maros-Torda, Udvarhely, Kisküküllő, Nagyküküllő, Brassó, Fogaras, Szeben, Alsó-Fehér, Torda-Aranyos counties). Neither their geomorphological features nor the lack of vast woodlands can explain the low-representation of Nagyküküllő, Szeben, Alsó-Fehér and Torda-Aranyos counties in sparse nesting data. We believe that the nearness of both the Transylvanian Mountain and the East Carpathian Mountains mean positive influence for this species when providing more favourable nesting conditions for these birds. This statement is justified by the dot-map, because those nesting places which were documented in these counties are situated relatively close to those areas where many nesting data came from. Similarity can be experienced in the low altitude Bereg county located between the first two nesting regions. Beside the nesting regions we mentioned previously in the west region of Historical Hungary there is an important nesting area, too. Moson, Győr, Sopron, Vas and Zala counties shared 10% from the west Hungarian counties. From the neighbouring counties such as Somogy, Veszprém and Komárom we have sparse nesting data. The higher share of Baranya county in south Transdanubia can be explained with the favourable nesting opportunities in the well-forested higher areas in Mecsek mountain. We have no nesting data from the karstic lands south from Sava river or from the higher areas of lands not far from the sea (Modrus-Fiume, Lika-Korbava counties) due to the submediterranean climate zone which did not belong to these birds' hatching places.

Woodcock nestings in Hungary from 1921 to 2019

Examining Woodcock nesting data collected during the last hundred years we conclude that nestings concentrate in those parts of the country where the land is well forested. These inland areas cover well the nesting regions in Historical Hungary and join to those regions that are abroad now. So the prime role of west and south Transdanubia has not changed (31%). Besides, the north Hungarian region is the most important because 63% of observations happened there. In the land between the Danube and Tisza rivers and plains eastward from Tisza nestings were observed only occasionally (6%) due to the low rate of woodlands. We can state that Vönöczky Schenk's report (1944) is valid for the present situation, so the importance of regions is the same. But it is also important to add that the size of wood-covered area doubled during the last 100 years *(Figure 3)*. According to data of nesting frequency Győr-Moson-Sopron, Vas and Veszprém counties in Transdanubia are still significant (16%), and join well to data coming from the east Austrian counties (Niederösterreichischer Landesjagdverband 2012). The role of Baranya county is still considerable and we described its reasons in the Historical Hungary previously. Beside this area, spare nestings were also reported from Zala and Somogy counties. Central and north Hungar ian counties (61%) such as Pest, Nógrád and Borsod-Abaúj-Zemplén counties are significant while Heves county that also belong to this region is only sparse nesting areas. It is important to convey that the nesting importance of Pest county is distorted by its diverse geomorphology.

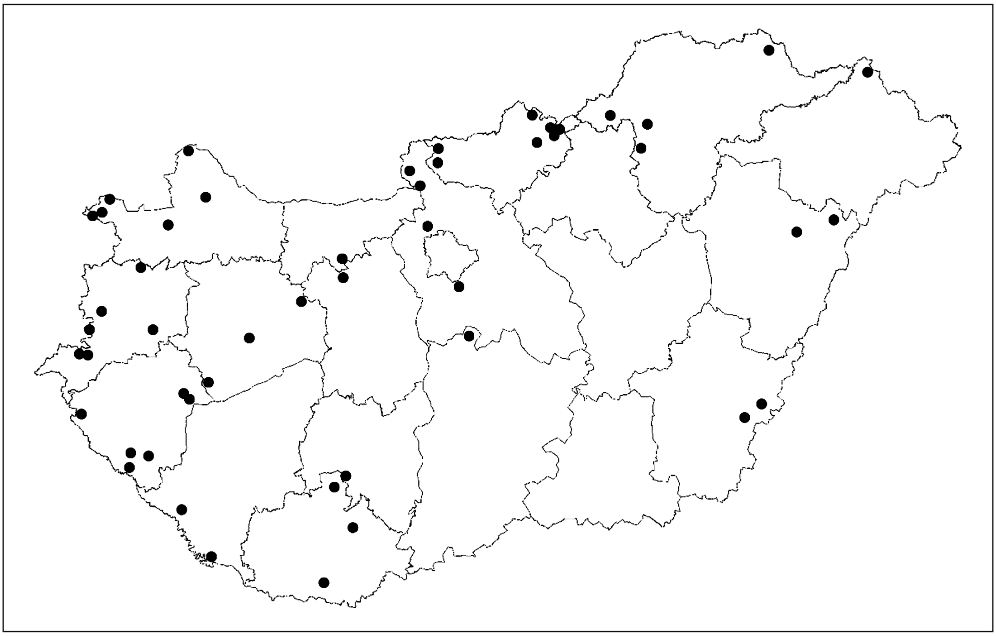


Figure 3. Observation data of Woodcock nests (n=133), hens directing chicks, Woodcock chick (n=55) in the area of Hungary between 1921–2019

3. ábra Erdei szalonka fészkelések (n=133), csibéket vezető szalonka tyúkok, illetve szalonka csibék (n=55) megfigyelési adatai alapján, Magyarország területén 1921–2019 között

The rare forested flat areas between the Danube and Tisza rivers are not suitable for nesting, so the majority of data arrived from the north part of the county. From the central region of the Great Hungarian Plain (Jász-Nagykun-Szolnok and Csongrád counties) we have no data of hatching observations, that is why these places can be considered unfavourable for Woodcocks. Around the east border (Békés, Hajdú-Bihar and Szabolcs-Szatmár-Bereg counties) only small number of Woodcock hatchings were reported. The role of Békés county is outstanding and it can be explained with the larger extension of forests in the Körös river area. These lands may join well to the sparse nesting data of west Rumanian counties. Going eastward, higher altitude and forested areas provide much more favourable nesting conditions for this species even today.

Observing summer flights

Observation data of summer Woodcock flights are important in the light of little nesting data, when we intend to describe national nestings. We suppose nestings of this species even in such places where no hatchings were ever reported. Observed flights from May to October show similarities with bridal flights. During springlike nice flights at nights or at dawn many authors write about Woodcocks that twissick and grunt during ther flights (Anonim 1896, Borsiczky 1901, Anonim 1902a, Farkas 1935, Unger-Ullmann 1935, Zsilinszky 1943, Horváth 1989). According to Zsilinszky (1943) the second mating season starts in June which

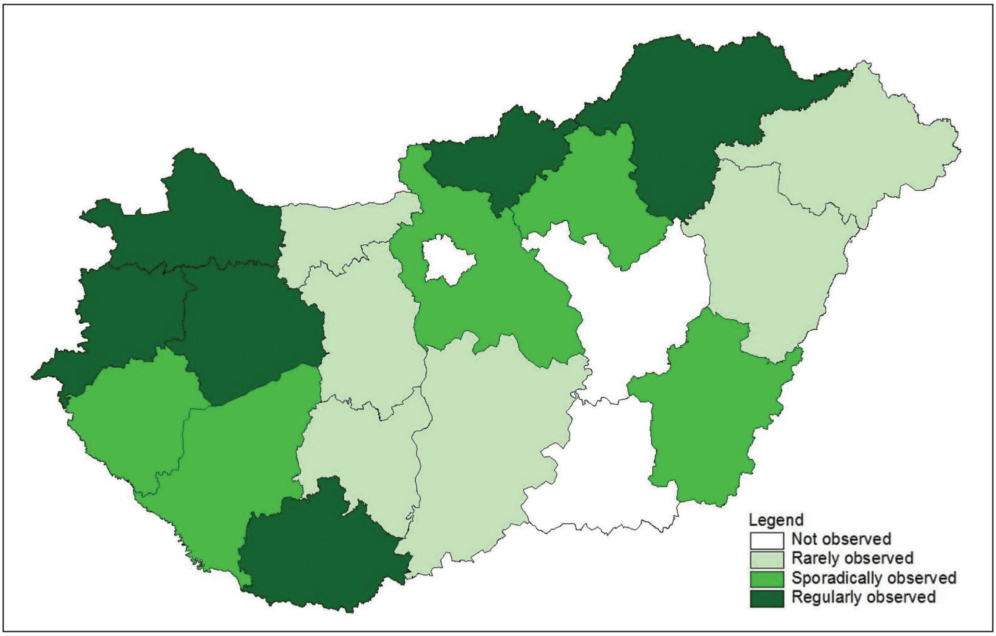


Figure 4. Frequency of Woodcock nestings in the area of Hungary between 1921–2019
4. ábra Az erdei szalonka fészkelési gyakorisága megyénként Magyarország területén 1921–2019 között

happens in the same way as the first one in April. According to Horváth (1989) summer flight observations prove nestings. We state that data of summer observations on their own are insufficient for describing real nestings, but we may suppose in case of summer Woodcock mating flights that the species really nests in that area. It was proved by observations of Fenyősi and Stix (1993) in the protected area in Barcs (30th June 1988 and 9th June 1989). They supposed nesting on the grounds of summer flights and finally it was proven in the spring of 1992 when a nesting Woodcock was found there.

Request

The list of our knowledge on Woodcock nesting and habits of breeding chicks is not perfect so the authors of this study welcome any new information in this topic.

Acknowledgement

This article was made in frame of the „EFOP-3.6.1-16-2016-00018 – Improving the role of research+development+innovation in the higher education through institutional developments assisting intelligent specialization in Sopron and Szombathely.

References

Agárdi, E. 1939. A Keleti Mecsek madárvilága – Die Vogelwelt des östlichen Mecsek-Gebirges [The bird world of the Eastern Mecsek Mountains]. – Aquila 46–49: 269–284., 285–299. (in Hungarian and German)

Agárdi, E. 1968. *Scolopax rusticola* második költése – Second hatching of *Scolopax rusticola*. – Aquila 75: 285., 297. (in Hungarian and English)

Anonim. 1871a Adat az erdei szalonka életrajzához [Data regarding ecology of the Woodcock]. – Vadász és Versenylap 15(18): 133. (in Hungarian)

Anonim. 1871b Még egy pár adat a szalonkáról [Just a couple more data about the Woodcock]. – Vadász és Versenylap 15(20): 143. (in Hungarian)

Anonim. 1885. A szalonka-idény utóhangjai [Echoes of the Woodcock hunting season]. – Vadász és Versenylap 6(15): 204. (in Hungarian)

Anonim. 1886. Az erdei szalonkákról [About the Woodcock]. – Vadász és Versenylap 6(15): 204. (in Hungarian)

Anonim. 1889. Vadtenyésztés és vadászat [Game breeding and hunting]. – Vadász-Lap 10(17): 217. (in Hungarian)

Anonim. 1891a Az erdei szalonkák [The Woodcocks]. – Vadász-Lap 12(14): 217. (in Hungarian)

Anonim. 1891b Erdei szalonkát fogtak [The Woodcock was caught]. – Vadász-Lap 6(16): 213. (in Hungarian)

Anonim. 1892. Vadtenyésztés és vadászat [Game breeding and hunting]. – Vadász-Lap 13(22): 288. (in Hungarian)

Anonim. 1893. Vadász-levél Gömörből [Hunter's letter from Gömör]. – Vadász-Lap 14(13): 171. (in Hungarian)

Anonim. 1896. Vadtenyésztés és vadászatok [Game breeding and hunting]. – Vadász-Lap 17(16): 212. (in Hungarian)

Anonim. 1898. Felső-Eőr (Vas megye.) júl. 20. [Felső-Eőr (Vas county.) July 20.]. – Vadász-Lap 17(16): 212. (in Hungarian)

Anonim. 1902a Szalonka-huzás nyáron [Woodcock roding in summer]. – Vadász-Lap 23(18): 242. (in Hungarian)

Anonim. 1902b Egy erdei szalonka-fészket talált… [He found a Woodcock nest…]. – Vadász-Lap 23(18): 242. (in Hungarian)

Anonim. 1907. Az erdei szalonkákról [About the Woodcock]. – Vadász-Lap 12(28): 168. (in Hungarian)

Anonim. 1910. Fiatal erdei szalonka a kirakatban [Juvenile Woodcock in the shop window]. – Pécsi Napló 19(100): 7. (in Hungarian)

Anonim. 1936. A Magyar Vadászok Országos Szövetsége hivatalos közleményei. Az igazgatóság javaslata tilalmi idők tárgyában [Official Announcements of the National Association of Hungarian Hunters. Board of Directors' proposal on period of hunting season]. – Magyar Vadászujság 36(14): 219–223. (in Hungarian)

Anonim. 1938. A szalonkák idei húzása a Börzsöny-hegységben [This year's Woodcock roding in the Börzsöny Mountains]. – Nimród Vadászujság 38(12): 187. (in Hungarian)

Anonim. 1947. Szalonka élmény [Woodcock experience]. – Nimród Vadászujság 34(12): 191. (in Hungarian)

Bársony, Gy. 1935. A debreceni erdők madárfaunája – Die Vogelfauna der Debrecener Wälde [Bird fauna of the forests of Debrecen]. – Aquila 38–41: 344–346.,406–407. (in Hungarian and German)

Bársony, I. 1985. Szalonkavarázs III. [Woodcock attraction]. – Nimród 105(3): 101–107. (in Hungarian)

Berényi, V. 1938. Az erdei szalonka [The Woodcock]. – Magyar Vadászujság 38(7): 103–105. (in Hungarian)

Bod, P. 1901. T. Szerkesztőség! [Dear Editorial Staff!]. – A természet 4(17): 10. (in Hungarian)

Boroviczény, A. 1936. Az igazság az erdei szalonka tavaszi vadászatáról [The truth about the Woodcock hunting in spring]. – A természet 32(5): 107–112. (in Hungarian)

Borsiczky, O. 1901. T. Szerkesztőség! [Dear Editorial Staff!]. – A természet 4(16): 10. (in Hungarian)

Breuer, Gy. 1929. *Scolopax rusticola* fészkelése Sopron környékén – Nisten von *Scolopax rusticola* in der Umgehung von Sopron [Nesting of *Scolopax rusticola* around Sopron]. – Aquila 34–35: 386., 428. (in Hungarian and German)

Chernel, I. 1885. Az erdei szalonka költéséhez [For the nesting of the Woodcock]. – Vadász és Versenylap 6(18): 238. (in Hungarian)

Chernel, I. 1918. Adatok Magyarország madárfaunájához – Daten zur Vogelfauna Ungarns [Datas for Hungarian bird fauna]. – Aquila 24: 17–18., 15–24. (in Hungarian and German)

Csaba, J. 1967. Erdei szalonka költése Felsőmarác határában – Woodcock Nesting on the Territory of Felsőmarác. – Aquila 73–74: 179., 195. (in Hungarian and English)

Csaba, J. 1974. Adatok Vas megyéből – Ornitologische Angaben aus dem Komitat Vas [Datas from Vas county]. – Aquila 78–79: 233–234., 241. (in Hungarian and German)

Csele, A. 1932. Madárvonulás [Bird migration]. – Nimród-Vadászlap 20(13): 202. (in Hungarian)

Csete, A. 1936. Palmárum – Trallarum! – Nimród Vadászujság 24(15): 232. (in Hungarian)

Csiba, L. 1959. Kiegészítő adatok dr. Keve András „Adatok a Közép-Duna madárvilágához." c. munkájához – Supplementary data to dr. A. Keve's Paper: „Data to the Ornis of the Middle-Danube." – Aquila 65: 304., 357. (in Hungarian and English)

Deák, J. 1885. A szalonka-idény utóhangjai [Echoes of the Woodcock hunting season]. – Vadász és Versenylap 6(15): 204. (in Hungarian)

Dorner, B. 1930. Mese a szalonkáról [Fairy tale about the Woodcock]. – Nimród Vadászújság 18(12): 199–200. (in Hungarian)

Dorning, H. 1903. Vonulási adatok [Migration data]. – Vadászat és állatvilág 3(11): 161. (in Hungarian)

Egerváry, Gy. 1895. Állatbiológiai gyűjtemény [Animal biological collection]. – Vadász-Lap 16(19): 254. (in Hungarian)

Egerváry, Gy. 1898. Vas vármegye vadászati viszonyairól [About the hunting conditions in Vasvár county]. – Vadász-Lap 19(3): 35. (in Hungarian)

Ertl, G. 1897. Nidologia et Oologia – Erdei szalonka – Waldschnepfe [Nidology and Oology – Woodcock]. – Aquila 4(1–3): 155–159. (in Hungarian and German)

Ertl, G. 1902. Az erdei szalonka fészkeléséhez – Zum Brüten der Waldschnepfe [For the nesting of the Woodcock]. – Aquila 9(1–4): 230., 231. (in Hungarian and German)

Ertl, G. 1903. Más fészkelési különösségek – Andere auffallende Nistfälle [Other breeding specials]. – Aquila 10(1–4): 257. (in Hungarian and German)

Faragó, S. 1987. Adatok az erdei szalonka *(Scolopax rusticola)* fészkeléséhez Magyarországon [Datas of the breeding of Woodcock *(Scolopax rusticola)* in Hungary]. – Madártani Tájékoztató 10: 30–31. (in Hungarian)

Farkas, J. 1935. Az erdei szalonka fészkelése az Alföldön – Nisten der Waldschnepfe im Alföld [Breeding of Woodcock in the Great Hungarian Plain]. – Aquila 38–41: 356., 419. (in Hungarian and German)

Fenyősi, L. 1993. A Barcsi Tájvédelmi Körzet madarai (1983–1993) [Birds of the Landscape Protection Area Barcs (1983–1993)]. – Állattani Közlemények 79: 57–64. (in Hungarian)

Fenyősi, L. & Stix, J. 1993. Adatok az erdei szalonka *(Scolopax rusticola)* fészkeléséhez [Datas for the nesting of the Woodcock *(Scolopax rusticola)*]. – Madártani Tájékoztató 17: 38. (in Hungarian)

Fuisz, T. I., Pereszlényi, Á., Vas, Z. & Haraszthy, L. 2015. A Magyar Természettudományi Múzeum megsemmisült tojásgyűjteményének rekonstruált adatai [The restored data of the perished egg collection of the Hungarian Natural History Museum]. – In: Haraszthy, L. (ed.) Magyarországi tojásgyűjtemények katalógusai [Catalogue of the Hungarian oological collections]. – Pro Vértes Nonprofit Zrt., Csákvár, pp. 133–215. (in Hungarian)

Gyapay, J. 1943. Fészkelő szalonkák [Nesting Woodcocks]. – Nimród Vadászlap 31(20): 316. (in Hungarian)

Gy. Takách, Gy. 1901. A szalonkák fészkelése, pusztulása és csalogatósíppal való vadászata [Woodcock nesting, devastation and hunting with tempting whistle]. – Vadász-Lap 5(1): 7. (in Hungarian)

Hadarics, T. & Zalai, T. 2008. Magyarország madarainak névjegyzéke – Nomenclator Avium Hungariae – An annotated list of the birds of Hungary. – MME, BirdLife International, Budapest, p. 118. (in Hungarian and English)

Haraszthy, L. 2012. A Janus Pannonius Múzeum madártojás- és fészekgyűjteményeinek katalógusa [Catalog of bird eggs and nest collections at the Janus Pannonius Museum]. – Baranya Megyei Múzeumok Igazgatósága, Pécs (in Hungarian)

Haraszthy, L. 2015. Magyarországi tojásgyűjtemények katalógusai [Catalogue of the Hungarian oological collections]. – Pro Vértes Nonprofit Zrt., Csákvár (in Hungarian)

Haraszthy, L., Fuisz, T. I. & Vas, Z. 2015. Cseresnyés Szilárd tojásgyűjteménye a Magyar Természettudományi Múzeumban [The oological collection of Szilárd Cseresnyés in the Hungarian Natural History Museum]. – In: Haraszthy, L. (ed.) Magyarországi tojásgyűjtemények katalógusai [Catalogue of the Hungarian oological collections]. – Pro Vértes Nonprofit Zrt., Csákvár, pp. 39–57.

Haraszthy, L. & Viszló, L. 2010. Máté László tojásgyűjteménye a Madártani Intézetben [László Máté's egg collection at the Ornithological Institute]. – Aquila 116–117: 215–227. (in Hungarian)

Hoffmann, S. 1950. Az erdei szalonka fiahordása – Woodcock carrying its chicks. – Aquila 51–54: 175., 198–199. (in Hungarian and English)

Horváth, L. 1989. Szalonkafészkelés a Hanságban [Woodcock nesting in Hanság]. – Nimród 109(3): 137. (in Hungarian)

Janisch, S. 1924. Szalonka megfigyelések és egyebek [Woodcock observations and others]. – Nimród 2(17): 134–135. (in Hungarian)

Károlyi, L. 1921. Szalonkavadászat [Woodcock hunting]. – Nimród-Vadászlap 9(6): 93. (in Hungarian)

Kiriczi, Z. 1936. Erdei szalonka [Woodcock]. – Nimród Vadászujság 24(32): 508. (in Hungarian)

Kiskárpáti, 1935. Fészkelő erdei szalonkák! [Nesting Woodcocks!]. – Magyar Vadászujság 35(30): 472–474. (in Hungarian)

Kozarits, Gy. 1935. Erdei szalonka fiókák [Woodcock nestlings]. – Nimród Vadászujság 23(17): 271. (in Hungarian)

Kozma, B. & Vadász, Cs. 2018. Az erdei szalonka fészkelése nemesnyárasban [Woodcock nesting in poplar plantation]. – Madártávlat 25(2): 20–21. (in Hungarian)

Lakatos, K. 1886. Az erdei szalonka húzása és költéséről [Roing of Woodcock and about breeeding]. – Vadász-Lap 7(23): 318–320. (in Hungarian)

Lakatos, K. 1903. Az erdei szalonka párosodása és szaporítási viszonyai [Mating and reproduction conditions of Woodcock]. – Természet 10(22): 210–212. (in Hungarian)

Lengyel, E. 1937. Megfigyelések a szalonka családi életéből [Observations from the family life of the Woodcock]. – Nimród Vadászujság 25(14): 224. (in Hungarian)

Lokcsánszky, A. 1935a Adatok erdei szalonkáink fészkeléséhez [Datas for nesting our Woodcocks]. – Magyar Vadászujság 35(23): 355–358 (in Hungarian)

Lokcsánszky, A. 1935b Adatok erdei szalonkáink fészkeléséhez [Datas for nesting our Woodcocks]. – Magyar Vadászujság 35(24): 376–378 (in Hungarian)

Lokcsánszky, A. 1935c Adatok erdei szalonkáink fészkeléséhez [Datas for nesting our Woodcocks]. – Magyar Vadászujság 35(25): 393–394 (in Hungarian)

Lovassy, S. 1884. Adatok Gömörmegye madár-faunájához [Datas for the bird fauna of Gömör county 1883]. – In: B. Eötvös, L. (ed.) Mathematikai és Természettudományi Közlemények vonatkozólag a hazai viszonyokra 18., p. 327. (in Hungarian)

Lovassy, S. 1891. Az ornithologiai kiállítás magyarországi tojás- és fészek gyűjteményének katalógusa [Catalog of the Hungarian egg and nest collection of the ornithological exhibition]. – Magyar Kir. Tud.-egyetemi Könyvnyomda, Budapest

Matolai, E. 1906. Az erdei szalonkák költési idejéről [About the breeding period of the Woodcock]. – Vadász-Lap 27(19): 248. (in Hungarian)

M. Mester, K. 2011. „Feketét el ne ereszd!" Fekete István (1900–1970) és Sólyom kapcsolata [„Don't let go Fekete!" Relationship between István Fekete (1900–1970) and Falcon]. – Nimród Vadászújság 99(1): 48–49. (in Hungarian)

Mérey, A. 1928. Madárvonulási hírek [Bird migration news]. – Nimród Vadászújság 99(1): 48–49. (in Hungarian)

Niederösterreichischer Landesjagdverband 2012. Wildtiermonitoring Waldschnepfe: Projektabschnitt Brutvorkommen 2006 bis 2012 [Wildlife monitoring Woodcock: Project section breeding occurrence 2006 to 2012]. – https://www.noejagdverband.at/wp-content/uploads/Waldschnepfen-Monitoring-Brutvorkommen-2006-bis-2012.pdf. (in German)

Orlovszky, Gy. 1889. Vadtenyésztés és vadászat [Game breeding and hunting]. – Vadász-Lap 10(22): 286. (in Hungarian)

Parragh, J. 1935. Erdei szalonka hírek [Woodcock news]. – Nimród 23(8): 125. (in Hungarian)

Parragh, J. 1941. Szalonkaköltés [Woodcock breeding]. – Nimród Vadászlap 29(16): 254. (in Hungarian)

Polgár, J. 1922. Fiatal erdei szalonka [Juvenile Woodcock]. – Vadászat 5(11): 154. (in Hungarian)

Preuszler, A. 1917. Tanulmányok a szalonkáról [Studies on Woodcock]. – Vadász és Versenylap 38(9): 97–100. (in Hungarian)

Pukánszki, Z. 2018. Erdei szalonka fészkelés Vas megyében [Woodcock nesting in Vas county]. – http://www.szherdeszet.hu/hirek/erdei-szalonka-feszkeles-vas-megyeben.html?page=7. (in Hungarian)

Réz, E. 1928. Erdei szalonka (*Scolopax rusticola* L.) fészkelése [Nesting of Woodcock (*Scolopax rusticola* L.)]. – Kócsag 1(2): 34–37.

Réz, E. 1930. Erdei szalonka (*Scolopax rusticola* L.) fészkelése 1930-ban [Nesting of Woodcock (*Scolopax rusticola* L.) in 1930]. – Kócsag 5(3–4): 112–115.

Réz, E. 1935. Szalonka kérdés [Woodcock question]. – Nimród Vadászujság 23(10): 150–151.

Say, J. 1937. Szalonkafészek a Papodon (Bakony) [Woodcock nest on Papod (Bakony)]. – Magyar Vadászujság 37(12): 190. (in Hungarian)

Sárkány, J. 1885. Az erdei szalonka költéséhez [Data for the nesting of the Woodcock]. – Vadász és Versenylap 6(18): 237–238. (in Hungarian)

Sárvári, 1933. Késői szalonkahúzás [Late Woodcock roding]. – Magyar Vadászujság 33(13): 174. (in Hungarian)

Schenk, J. 1930. Az erdei szalonka tavaszi vonulásának prognózisa Magyarországon – Die Prognose des Frühjahrszuges der Waldschnepfe in Ungarn [Prediction of Woodcock spring migration in Kingdim of Hungary]. – Aquila 36–37: 33–44. (in Hungarian and German)

Solti, B., Rác, P., Štollmann, A. & Haraszthy, L. 2015. Csiba Lajos tojásgyűjteménye [The oological collection of Lajos Csiba]. – In: Haraszthy, L. (ed.) Magyarországi tojásgyűjtemények katalógusai [Catalogue of the Hungarian oological collections]. – Pro Vértes Nonprofit Zrt., Csákvár, pp. 265–281.

Sőreghy, J. 1912. Vadászati tudósítók jelentései [Reports of hunting correspondents]. – Vadászat és Állatvilág 12(1–4): 246–248. (in Hungarian)

Steiner, M. 1931. A csornai Premontrei Kanonokrendi Szent Norbert- Gimnázium 1931–32. évi értesítője [Monastery of St. Norbert-Grammar School of Csorna 1931–32. year bulletin]. – Martineum Könyvnyomda Rt, Szombathely (in Hungarian)

Sugár, K. 1916. Kérelem [Request]. – Vadász-Lap 37(10): 114. (in Hungarian)

Széchényi, F. 1879. Az idei szalonka vadászatok Tarnóczán [This year's Woodcock hunting in Tarnócza]. – Vadász és Versenylap 15(27): 140. (in Hungarian)

Szidnay, L. 1885. Az erdei szalonkák [The Woodcocks]. – Vadász és Versenylap 6(11): 147. (in Hungarian)

Szilágyi, V. 1948. Fészkelő erdei szalonkák a Vértesben [Nesting Woodcocks in the Vértes Mountains]. – Nimród Vadászlap 35(13): 207. (in Hungarian)

Szomjas, L. 1950. Szokatlan fészkelők a Közép-Tiszánál – Unusual breeders on the Middle-Tisza. – Aquila 51–54: 170., 194. (in Hungarian and English)

Szurmay, S. 1933. Szalonka-históriák [Woodcock stories]. – Nimród Vadászújság 21(13): 199–201. (in Hungarian)

Teschler, 1893.Vadtenyésztés, vadászatok [Game breeding, huntings]. – Vadász-Lap 14(17): 224. (in Hungarian)

Unger-Ulmann, E. 1935. Erdei szalonka nyári húzása – Sommerstrich der Waldschnepfe. [Woodcock rooding in summer]. – Aquila 38–41: 356., 419. (in Hungarian and German)

Varga, F. 1966. Az erdei szalonka hazai költéséről… [About the Woodcock nesting in Hungary…]. – Magyar Vadász 19(6): 20. (in Hungarian)

Varga, F. 1968. Erdei szalonka fészkelések, költések Zagyvaróna és Mátraszele környékén 1965–66-ban – Nestling and hatching of the Woodcock in the neighbourhood of Zagyvaróna and Mátraszele, in 1965 and 1966. – Aquila 75: 285–286., 297–301. (in Hungarian and English)

Varga, F. 1973. Adatok az erdei szalonka költéséhez [Datas for the Woodcock breeding]. – Aquila 76–77: 181. (in Hungarian)

Varga, F. 1975. Erdei szalonka *(Scolopax rusticola)* kései költése Zagyvarónán – Spätbrut der Waldschnepfe *(Scolopax rusticola)* in Zagyvaróna [Woodcock *(Scolopax rusticola)* late nesting in Zagyvaróna]. – Aquila 80–81: 286., 304. (in Hungarian and German)

Varga, F. 1977. Adatok az erdei szalonka *(Scolopax rusticola)* költésbiológiájához – Data on the breeding biology of the Woodcock *(Scolopax rusticola)*. – Aquila 83: 283–285., 300–301. (in Hungarian and English)

Varga, F. 1979. Az erdei szalonka újabb fészkelései, költései a Zagyva forrásvidékén [New breeding and nesting of Woodcock in of source area of Zagyva]. – Nimród 99: 30. (in Hungarian)

Varga, F. 1980. Erdei szalonka *(Scolopax rusticola)* fészkelése a Medves hegységben [Woodcock *(Scolopax rusticola)* nesting in Medves Mountains]. – Madártani Tájékoztató 4: 24–25. (in Hungarian)

Varga, F. 1985. Madarász szemmel az erdei szalonkáról *(Scolopax rusticola)* [With ornithologist eyes about the Woodcock *(Scolopax rusticola)*]. – Madártani Tájékoztató 9: 17. (in Hungarian)

Várady, G. 1932. Jelentések a tavaszi madárvonulásról Trencsén megye déli részéből [Reports on spring bird migration from the southern part of Trencsén county]. – Vadász-Lap 37(14): 168. (in Hungarian)

Veress, G. 1916. Jelentések a tavaszi madárvonulásról [Reports on spring bird migration]. – Vadászlap 37(14): 168. (in Hungarian)

Veress, G. 1932. Szalonkavárók [Woodcock waiting]. – Dunántúl 22(65): 4–5. (in Hungarian)

Várkonyi, G. 1938. Az erdei szalonka élete és vadászata [Life and hunting of Woodcock]. – Nimród Vadászujság 38(13): 198–201. (in Hungarian)

Vásárhelyi, I. 1936. Az erdei szalonkáról [About the Woodcock]. – Magyar Vadászujság 36(15): 228–229. (in Hungarian)

Vönöczky Schenk, J. 1944. Az erdei szalonka fészkelő területei a történelmi Magyarországon – Die Nistareale von *Scolopax r. rusticola* L. im historischen Ungarn [Woodcock breeding area in historic Hungary]. – Aquila 50: 310–313., 314–316. (in Hungarian and German)

Vidonyi, Z. 1941. Hozzászólás a szalonkák magyarországi költésének kérdéséhez [Comment on the question of breeding of Woodcock in Hungary]. – Nimród-Vadászlap 29(22): 351. (in Hungarian)

Zsilinszky, 1943. Megfigyeléseimből [Of my observations]. – Vadászújság 3(26): 409–410. (in Hungarian)

sciendo

Ornis Hungarica 2020. 28(1): 104–120.
DOI: 10.2478/orhu-2020-0008

Skull morphometric characters in parrots (Psittaciformes)

Tibor Pecsics[1*], Miklós Laczi[1,3], Gergely Nagy[1], Tamás Kondor[1] & Tibor Csörgő[2]

Received: April 24, 2020 – Revised: June 02, 2020 – Accepted: June 03, 2020

Pecsics, T., Laczi, M., Nagy, G., Kondor, T. & Csörgő, T. 2020. Skull morphometric characters in parrots (Psittaciformes). – Ornis Hungarica 28(1): 104–120. DOI: 10.2478/orhu-2020-0008

Abstract Parrots (Psittaciformes) are a unique and diverse avian group and vary tremendously in size, shape, and colour. Mainly distributed throughout the tropics and subtropics, most species of parrots are largely or exclusively arboreal with several exceptions. The species also differ in diet and habitat, which led to different musculoskeletal adaptations of the skull. However, parrots have conspicuous generalized external features; in this recent study, we tried to increase our knowledge of the cranial shape and foraging habits. 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 diet. The PCs described the relative height of the *cranium*, the relative length and curvature of the beak, differences in the orientation and curvature of the lacrimal bone and the upper margin of orbits, variation in the size and position of the palatine bone and the relative width of the *cranium,* and variation in the relative size of the *neurocranium* compared to the *viscerocranium*. The dietary categories overlap in the morphospace but the analysis in lateral and ventral view resulted in significant differences.

Keywords: cranial morphology, morphometrics, anatomy, jaw, skull, shape, convergent evolution, parrot, diet preference, bill shape

Összefoglalás A papagájalakúak rendje (Psittaciformes) egyedi és jól elkülöníthető madárcsoport, amelybe méretükben és színezetükben rendkívül változatos fajok tartoznak. Néhány kivételtől eltekintve a fajok többsége trópusi, illetve szubtrópusi erdőkben és ligetekben található. Az egyes fajok különböznek méretükben és táplálékpreferenciájuk tekintetében, ennek megfelelő eltéréseket mutatnak koponyájuk csontozatában és izomzatában. Habár a papagájok jól megfigyelhető egyetemes tulajdonságokat mutatnak, jelen vizsgálatunkban a cranialis jegyek és a táplálékpreferencia közötti lehetséges kapcsolatokat kerestük. A geometriai morfometriai vizsgálat során kétdimenziós landmarkok használatával főkomponens-analíziseket végeztünk. A főkomponensek a koponya relatív magasságát, a csőr relatív hosszúságát és görbületét, a könnycsont relatív helyzetét és a szemüreg felső részének ívét, a szájpadcsont viszonylagos helyzetét és nagyságát, valamint az agykoponya és az arckoponya egymáshoz viszonyított nagyságát mutatják. Az egyes táplálkozási csoportok átfednek egymással, azonban a vizsgálatok oldal- és alulnézetben észrevehető különbségeket mutattak.

Kulcsszavak: koponyasajátosságok, morfometria, anatómia, állkapocs, koponya, alak, konvergens evolúció, papagáj, táplálékpreferencia, csőrforma

[1] *Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/C, Hungary*
[2] *Department of Anatomy, Cell- and Developmental Biology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/C, Hungary*
[3] *The Barn Owl Foundation, 8744 Orosztony, Temesvári út 8., Hungary*
**corresponding author, e-mail: nobilis.equus@gmail.com*

Introduction

Parrots (Psittaciformes) are a unique and diverse group of birds. The species vary tremendously in size, shape, and colour. Although there is an extraordinary degree of variation in their external appearance, parrots are one of the most easily recognisable birds due to their conspicuous external features. Prominent and obvious characteristics include the strong curved bill, fleshy cere, proportionately large, broad head, and zygodactyl feet (Forshaw 2010). The parrots are mainly distributed throughout the tropics and subtropics and most species are largely or exclusively arboreal, but there are exceptions. Some species are exclusively terrestrial, inhabit grasslands, or prefer alpine vegetation (Bryant 1994).

This large and diverse order is traditionally classified into four families: Nestoridae (New Zealand parrots), Cacatuidae (cockatoos), Psittacidae (African and NewWorld parrots) and Psittaculidae (Old World parrots) (Christidis & Boles 2008, Hackett *et al.* 2008, Mayr 2010, Jarvis *et al.* 2014, Prum *et al.* 2015, Provost *et al.* 2017). The order contains over 390 species in 74 genera and most of the species are concentrated in the tropical and subtropical regions of the Southern Hemisphere (Barker *et al.* 2004, Homberger 2006, McCormack *et al.* 2013). Diversity in South America and Australasia suggests that the order may have evolved in Gondwana during the Cretaceous period (Cracraft 1973, Barker *et al.* 2004, Cracraft *et al.* 2004, Forshaw 2010). The few early fossils that have been discovered do not have modern parrot-like cranial morphology (Mayr *et al.* 2013). However, parrots possibly evolved in Gondwana; early psittaciform remains have mainly been found in the northern hemisphere and fossil evidence of a stem group in Europe concludes that there was diversification following the Mesozoic era (Dyke & Mayr 1999, Waterhouse 2006).

Parrots are the focus of an increasing number of studies in such areas as vocal communication (Bradbury 2003), brain evolution (Iwaniuk *et al.* 2005, Carril *et al.* 2016) and craniofacial morphology (Tokita 2006, Tokita & Nakayama 2014).

These birds developed novel cranial morphology and show considerable morphological diversity in the cranial musculoskeletal system. This includes two novel structures: the suborbital arch and the *musculus pseudomasseter* (Tokita 2003, Tokita *et al*. 2007). A previous study in geometric morphometric work explored the relationship among skull shape and ecology, which reflected the size and structure of the jaw muscles. Parrots are characterised by their large beaks and are renowned for their ability to produce high bite forces. Factors that influenced the evolution of psittaciform birds' distinctive cranial morphologies were tested (Bright *et al.* 2019).

Although the fundamental pattern of the skull development of birds is conserved in parrots, some differences were observed between parrots and other avian orders. In parrots, the vacuity in the interorbital septum did not emerge throughout ontogeny. This feature is referring to the attachment of the unique jaw muscle at interorbital septum, *musculus ethmomandibularis*. In parrots, the cranio-facial hinge was brought about by secondary transformation of dermal bones. In other groups of birds with a standard prokinetic skull, the nasal-frontal suture directly becomes a hinge of bending. The parrot-specific structures like suborbital arch and cranio-facial hinge are not seen until the juvenile birds leave the nest and can feed alone. These structures are necessary for eating tough food material (Tokita 2003).

Parrots occupy varied dietary niches that require an agile, mobilized, but sturdy feeding apparatus. Cranial kinesis, or the flexibility of intracranial joints, has a central role in the unique feeding apparatus (Cost *et al.* 2017).

Neotropical parrots are ecologically important because of their role as seed eaters and the impact on the structure of tropical forests (Janzen 1969, Terborgh *et al.* 1990, Galetti & Rodrigues 1992). Neotropical species usually forage for nectar, flowers, leaves, fruit pulp, and seeds. Due to the mosaics of the vegetation, these birds use the abundantly available resources. Smaller and larger species foraged on fruits; parakeets largely consumed the pulp, while larger parrot species used pulp and seeds (Ragusa-Netto & Fecchio 2006).

The diversity in morphology, body size, and foraging behaviour are in relation to diet and geographical range. Parrots are granivores rather than seed dispersers and in many cases where they are seen consuming fruit, they are only eating the fruit to get at the seed. The seeds often have poisons or toxins; therefore, the parrots carefully remove coats of the seed. Geographical range and body size explain diet composition rather than phylogeny (Benavidez *et al*. 2018).

The foraging performance and the cranial morphology are functionally linked to numerous vertebrate taxa (Dumont 2003, Anderson *et al*. 2008). The feeding system of most vertebrates produces bite force by the musculoskeletal system of the head (Herrel *et al*. 2005). The feeding methods provide an example of the link between morphological modification and performance (Benkman 2003). Numerous vertebrate taxa show that cranial attributes are related to bite force (Csermely *et al.* 1998, Ward *et al.* 2002, McBrayer 2004, Van der Meij & Bout 2004, Anderson *et al*. 2008, Sustaita & Hertel 2010).

The feeding strategies are highly diverse and the morphological adaptations for feeding are a notable feature of avian evolution (Zweers *et al.* 1994). The avian skull shows a great variety of morphological variation (Zusi 1993). Allometry possibly has a key role in craniofacial form across a range of avian orders (Colwell 2006, Marugán-Lobón & Buscalioni 2006, Kulemeyer *et al*. 2009, Fabbri *et al*. 2017).

Most of the parrot species are omnivorous (Lill 2009) and opportunistic when presented with new feeding opportunities, but sometimes also feed on plants and insects (Clarke 1971, Brejaart 1988).

Lories, lorikeets, hanging parrots, and swift parrots are primarily nectar and pollen consumers. Specialization to nectarivory is associated with radiations within different bird groups. Their shift to nectarivory may have created an ecological opportunity that promotes species proliferation and radiation. Morphological specializations of the feeding apparatus to nectarivory have been described for parrots (Schweizer *et al.* 2014).

Some other examples are more extraordinary than nectarivore species. Pigmy parrots (*Micropsitta* spp.) are suspected to rely heavily on fungi and lichens for food (Rand 1942, Elliott *et al.* 2019). Kea have been reported feeding on chicks and eggs (Temple 1996), mice (Beggs & Mankelow 2002), and domesticated sheep (Marriner 1908) and carrion (Edgar 1974).

The morphology of the skull, the maxillary and mandibular characteristics, and the important details of the skull structure are determinants of the different foraging groups. The two dimensional methods allow size and shape to be considered independently, preserve geometric information, and offer techniques for studying in form (Adams *et al.* 2004).

In this preliminary study, we investigated the cranial and morphological diversity among the different groups. Our objective was to increase our knowledge on the relationship between skull shape and the foraging habits of parrots and possibly find those characteristics that are related to diet and foraging habits. We also tried to find the convergent attributes. The differences in force acting on the beak during feeding may be related to skull geometry and jaw muscles. The significant overlap in skull geometry between the species would suggest that skull geometry has evolved along similar pathways. Differences may reflect selection pressures related to the different foraging habits and mechanical demands. To investigate the morphological diversity of the skulls, we used landmark-based morphometric methods.

Materials and methods

Specimens

This study is based on 150 skulls of 108 species. All skulls are from adult specimens of parrots and belong to the collection of Eötvös Loránd University (Budapest, Hungary), the collection of the Hungarian Natural History Museum (Budapest, Hungary), and the digital archives of Wageningen University (Wageningen, Netherlands). No bird has been killed to obtain its skull; all birds died either of natural causes, whether accidental death or whether it died in captivity.

Groups and diet

This study seeks to test that the different diet and foraging method may have an effect on skull morphology. Before the analyses, we created five groups which represent the following diet categories (Pizo *et al.* 1995, Perrin 2009, Lee *et al.* 2014).

- A: Nectarine, soft food item eaters (Schweizer *et al.* 2014)
- B: Predominantly seed eaters (Boyes & Perrin 2009)
- C: Big and rough food item eaters (Wood 1988, Vaughan *et al.* 2006)
- D: Generalists (McInnes & Carne 1978, Brejaart 1988, Galetti 1993, Wirminghaus *et al.* 2002, Boyes & Perrin 2010)
- E: Other (Diamond & Bond 1991, Schwing 2010).

Landmarks and procedures

The variation of 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). In this case, the meaningful variables are discovered by the analysis that was performed in previous studies (Pecsics *et al.* 2018, 2019).

Table 1. Number and description of landmarks (terminology according to Baumel 1993, Sun *et al.* 2018)

1. táblázat Az egyes landmarkok száma és leírása (terminológia Baumel 1993 és Sun *et al.* 2018 alapján)

Number of landmark	Description of landmark
1	tip of the maxilla
2	the lateral associating point of palatine and maxilla
3	the most anterior-lateral point of *pars lateralis*
4	the most posterior-lateral point of *pars lateralis*
5	*processus pterygoideus* of palatine
6	articulation point of palatine and maxilla
7	articulation point pf pterygoid and quadrate
8	most caudal point of the maxilla
9	articulation of quadrate and jugal
10	most lateral point of opisthotic
11	most caudal point of *condylus occipitalis*
12	most caudal point of *foramen magnum*
13	*prominentia cerebellaris*

We tried to find landmarks for this analysis to cover the geometric form of the skull. The landmarks provide a comprehensive sampling of morphology and the features of biological significance can be explored. Ideal landmarks are discrete and noticeable anatomical features that do not alter their topological positions, providing adequate coverage of the morphology (Zelditch *et al.* 2004). The landmarks were taken from high resolution (1200×1600 pixels) photos. We took 3 photographs from each specimen (lateral, ventral, and dorsal) with closed jaws and without the lower jaw. Images were standardised for the *foramen magnum occipitale* and the tip of the mandible. We investigated the repeatability of the measurements by Spearman's correlation. The test was between two separate digital measures performed on skull photos ($n = 20$). For each specimen, 13 fixed landmarks *(Table 1)* were recorded in ventral view (Guangdi *et al*. 2015, Sun *et al.* 2018). We used 800 sliding landmarks to examine the shape of the whole skull in dorsal and lateral view *(Figure 1)*. These landmarks were allowed to slide along their corresponding curve due to the minimization of the bending energy. The coordinates of the landmarks were digitised using TpsDig 2.16 software (Rohlf 2010) and were transformed using the Procrustes superimposition method. 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 correspond 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) to perform the principal component analysis and extract deformation grids. We only considered those PCs which explain >10% of the variance.

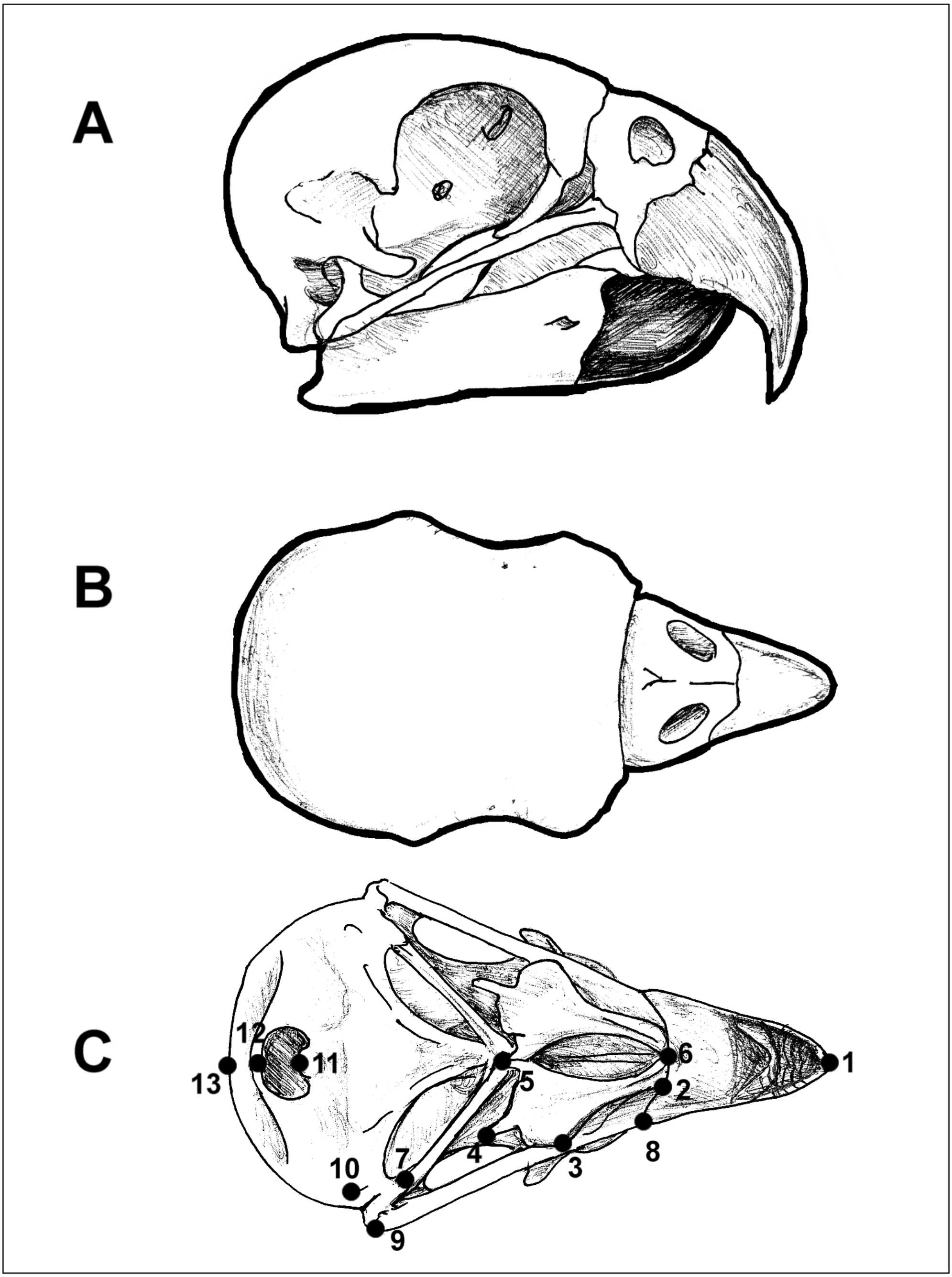


Figure 1. Position and number of landmarks. A: whole skull shape in lateral view, B: whole skull shape in dorsal view, C: the shape fixed landmarks in ventral view (numbers correspond to *Table 1*)

1. ábra A vizsgálatban használt landmarkok száma és pozíciója. A: a teljes koponya oldalnézetből, B: a teljes koponya felülnézetből, C: fix landmarkok alulnézetből (a számok megnevezését lásd a *1. táblázatban*)

Results

Our measures were repeatable, irrespective of measuring mode (all $r > 0.98$, all $P < 0.001$).

The first analysis focused on the whole skull from lateral view *(Figure 2)*. We used sliding landmarks (800) to describe the cranial shape of the parrots. The first three PCs explained 38%, 23% and 14% of the variance in skull shape. The first PC axis described the relative height of the *cranium* (PC1). The macaw species have robust heads with relatively high and massive beaks, while lories and lorikeets have relatively longer and slender skulls with short and delicate beaks. The second and third PC axes described the relative length and curvature of the beak (PC2 and PC3). Species like Barred Parakeet *(Bolborhynchus lineola)*, Turquoise Parrot *(Neophema pulchella)* and Red-headed Lovebird *(Agapornis pullarius)* have very short and curved beaks. The Kea *(Nestor notabilis)* and Slender-billed Parakeet *(Enicognathus leptorhynchus)* are bearing a long, narrow, and slender beak. True parrots and cockatoos share similar morphology *(Figure 3)*.

During the second analysis, we used sliding landmarks (800) to describe the skull in dorsal view. The first two PCs explained 51% and 17% of the variance in shape *(Figure 4)*. The first PC axis described variation in the relative length of the beak (PC1). The Red-shouldered Macaw *(Diopsittaca nobilis)* and Australian King-parrot *(Alisterus scapularis)* have relatively big *neurocranium* and shorter beaks compared with Kea *(Nestor notabilis)* and Slender-billed Parakeet *(Enicognathus leptorhynchus)*. The second PC axis (PC2) described differences in the orientation and curvature of the lacrimal bone and the upper margin of orbits *(Figure 4)*.

For the third analysis, we used fixed landmarks (13) to describe the shape of the *cranium* in dorsal view. The first two PCs explained 48% and 16% of the variance in shape. The first PC axis described the size and position of the palatine bone (PC1). The second PC axis reflected the relative width of the cranium and variation in the relative size of the *neurocranium* compare to the *viscerocranium* (PC2) *(Figure 5)*.

In every case, the generalists are in the middle of the morphospace. We tried to fix the skulls in a standard position to minimize the impact of cranial kinesis (*Figure 6)*.

Except Kea – which is bearing very unique skull attributes – there are no clear differences between taxonomic groups and the species are overlapping in the morphospace.

Discussion

The first analysis resulted differences in the relative height of the *cranium* and the beak in lateral view. Larger species usually have larger beaks compared to the *neurocranium*. The macaw species have robust heads with high and massive beaks. The Hyacinth Macaw *(Anodorhynchus hyacinthinus)* and the Palm Cockatoo *(Probosciger aterrimus)* have strong beaks; these species are able to crack hard food items, like nuts of pods and coconuts. The Alexandrine Parakeet *(Psittacula eupatria)* shares similar morphological attributes to the Scarlet Macaw *(Ara macao)*. The shape of the skull of the macaw species strongly differs from the skull of small lorikeets (e.g. *Charmosyna pulchella*) and small hanging parrots (e.g. *Loriculus vernalis*).

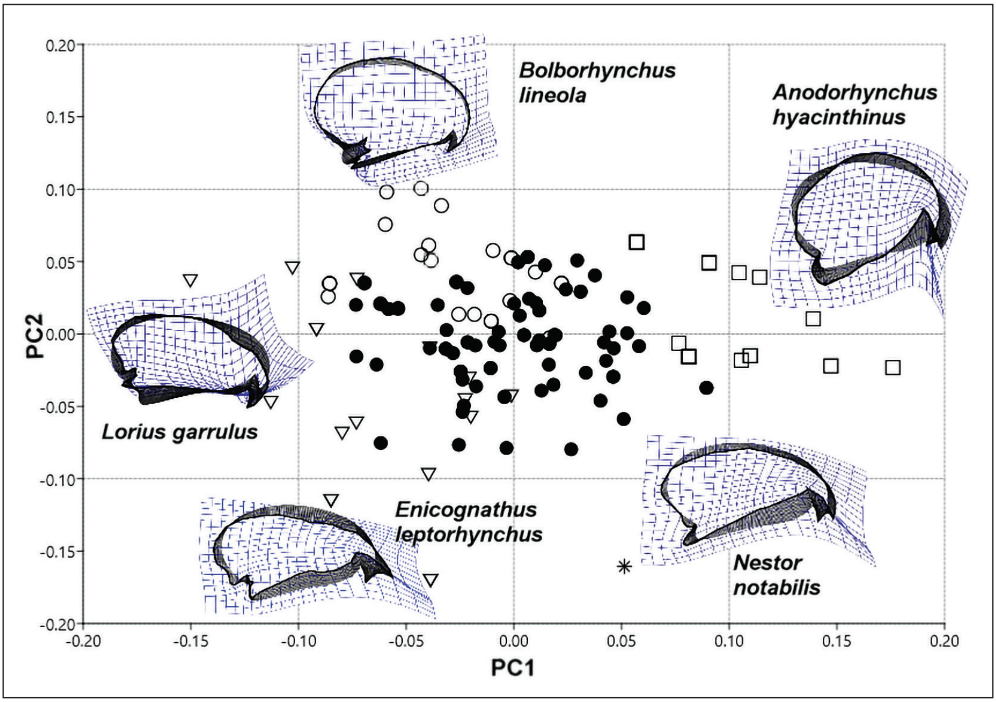


Figure 2. Graphical output of PCA performed on the two-dimensional landmark data (lateral view). PC1–PC2 biplot. The first PC axis described the relative height of the *cranium* (PC1). The second PC axis described the relative length and curvature of the beak (PC2). Thick black areas show the differences compared to the computer generated mean shape

● Generalists, ▿ Nectarine, soft food item eaters, □ Big and rough food item eaters, ○ Predominantly seed eaters, ⁎ Other

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

● Generalisták, ▿ Nektár és lágy táplálékot fogyasztók, □ Nagy és kemény táplálékot fogyasztók, ○ Elsődlegesen magevők, ⁎ Egyéb

Allometry can explain some of the differences between species because the smaller species usually have bigger *neurocranium* and smaller *viscerocranium* (Grant *et al.* 1985). Although Pesquet's Parrot *(Psittrichas fulgidus)* has a large body size, it has a similar skull shape to lories, possibly caused by its highly specialized diet (Pryor *et al.* 2001). Species like Barred Parakeet *(Bolborhynchus lineola)*, Turquoise Parrot *(Neophema pulchella)* and Red-headed Lovebird *(Agapornis pullarius)* have very short and curved beaks for extracting the edible part of the seeds. The strong and tapered beak is in positive correlation with bite performance (Van der Meij & Bout 2004, Herrel *et al.* 2005). With its long, narrow, and slender beak, the Kea *(Nestor notabilis)* digs grubs from rotten logs and roots from the ground (O'Hara *et al.* 2012). This shape has a significant role in the development of extractive foraging techniques. This species has extremely broad diet and there

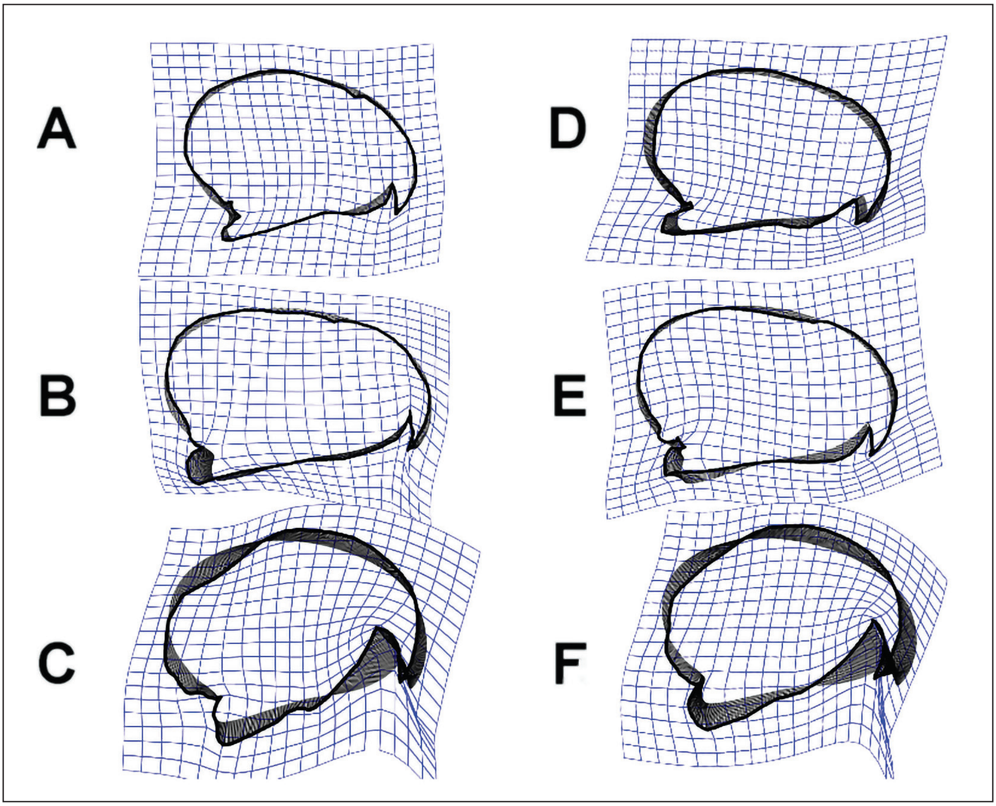


Figure 3. Various cockatoo and parrot species sharing convergent attributes. A: Cockatiel *(Nymphicus hollandicus)*, B: Pale-headed Rosella *(Platycercus adscitus)*, C: Yellow-crested Cockatoo *(Cacatua sulphurea)*, D: Cuban Amazon *(Amazona leucocephala)*, E: Palm Cockatoo *(Probosciger aterrimus)*, F: Hyacinth Macaw *(Anodorhynchus hyacinthinus)*

3. ábra Az egyes kakaduk és papagájok hasonló konvergens bélyegeket hordoznak. A: Nimfapapgáj *(Nymphicus hollandicus)*, B: Sápadtfejű rozella (*Platycercus adscitus)*, C: Aranyosarcú kakadu *(Cacatua sulphurea)*, D: Kubai amazon *(Amazona leucocephala)*, E: Pálmakakadu *(Probosciger aterrimus)*, F: Jácintkék ara *(Anodorhynchus hyacinthinus)*

are relatively subtle morphological differences between individuals and the noticeable intraspecific variation in the foraging ecology. It is clear that bill and head morphology is related to diet in this species (Greer 2015). Slender-billed Parakeet *(Enicognathus leptorhynchus)* – like other parrots – is an intelligent species, which likely promotes its persistence in dynamic landscapes. These characteristics may facilitate the adaptation of foraging behaviour to include most available resources within a given area (Carneiro *et al.* 2012). An overall increased bill length may improve the power or efficiency with which these species can rip off mud and flowers, extract grubs from live wood, or demolish decaying wood. Slender beaks allow the bird to deftly collect small food items from difficult to reach places.

The second analysis showed variety in the relative size of the *neurocranium* and *viscerocranium* like in the first analysis. Seed eaters and the species foraging on rough food

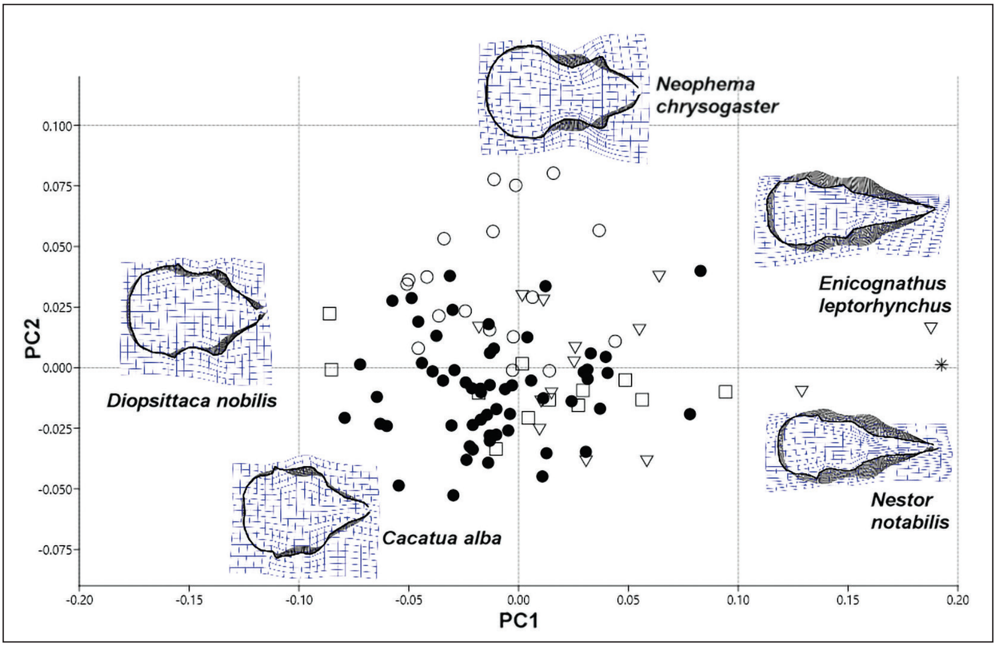


Figure 4. Graphical output of PCA performed on the two-dimensional landmark data (dorsal view). PC1–PC2 biplot. The first PC axis described variation in the relative length of the beak (PC1). The second PC axis (PC2) described differences in the orientation and curvature of the lacrimal bone and the upper margin of orbits. Thick black areas show the differences compared to the computer generated mean shape

● Generalists, ▿ Nectarine, soft food item eaters, ▫ Big and rough food item eaters, ○ Predominantly seed eaters, ∗ Other

4. ábra A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (felülnézet). Az első főtengely (PC1) a csőr relatív hosszúságát, a második főtengely a könnycsont relatív helyzetét és a szemüreg felső részének görbületét magyarázza. A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja

● Generalisták, ▿ Nektár és lágy táplálékot fogyasztók, ▫ Nagy és kemény táplálékot fogyasztók, ○ Elsődlegesen magevők, ∗ Egyéb

material usually have shorter tapered beak. In this analysis, the Kea and the Slender-billed Parakeet showed extreme differences with their elongated beak. The feeding categories are highly overlapping in the morphospace, but in dorsal view the curvature and the height of the beak is non-qualifiable. This analysis also showed differences in the curvature of the upper margin of the orbits. Cockatoo (*Cacatua* sp.) species have broad skulls and the increased distance between the orbits at the line of frontal bone. Australasian cockatoos have pronounced ossified periorbital structures. These birds have a well-developed suborbital arch and *musculus pseudomasseter* (Homberger 2017). At the postorbital region, the *neurocranium* showed a concave surface to the *musculus adductor mandibulae externus*. The amazon parrots (*Amazona* sp.) share similar attributes like cockatoos. Red-rumped Parrot *(Psephotus haematonotus)* and grass parrots (*Neophema* sp.) showed differences in the morphospace. These seed eaters have different skull structures. The frontal region

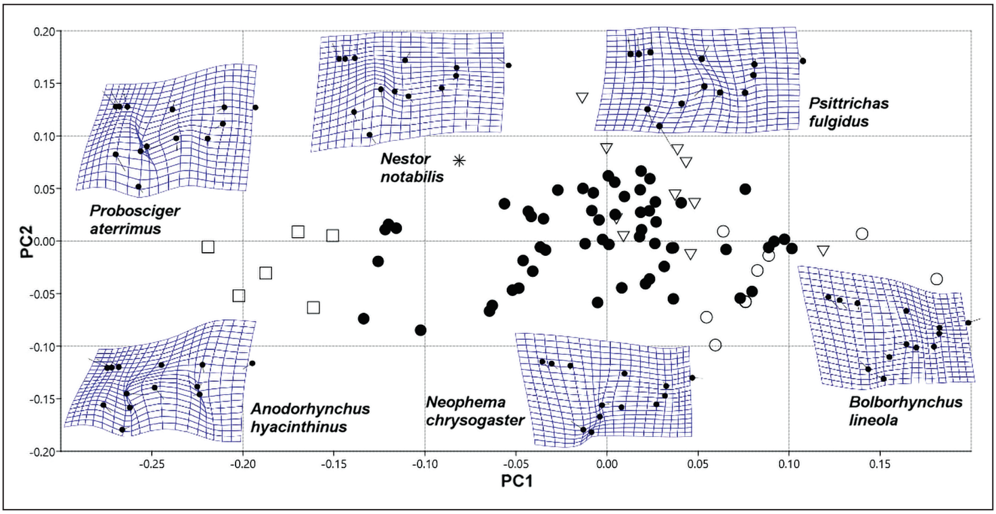


Figure 5. Graphical output of PCA performed on the two-dimensional landmark data (ventral view). PC1–PC2 biplot. The first PC axis described variation the size and position of the palatine bone (PC1). The second PC axis reflected to the relative width of the *cranium* and variation in the relative size of the *neurocranium* compare to the *viscerocranium* (PC2). Thick black areas show the differences compared to the computer generated mean shape

● Generalists, ▿ Nectarine, soft food item eaters, □ Big and rough food item eaters, ○ Predominantly seed eaters, * Other

5. ábra A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (felülnézet). A PC tengelyek a *palatinum* relatív helyzetét és nagyságát (PC1), valamint a *neurocranium* és a *visceroscranium* relatív nagyságát mutatják (PC2). A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja

● Generalisták, ▿ Nektár és lágy táplálékot fogyasztók, □ Nagy és kemény táplálékot fogyasztók, ○ Elsődlegesen magevők, * Egyéb

is narrower at the line of the orbits. The arboreal species have a wider, broad frontal region compared to those species which are mostly foraging on the ground. Arboreal species might use their beak more often as well as their feet to grip branches and haul themselves through the treetops.

The third analysis showed differences in the relative length of the *cranium*. Those species which are foraging on mechanically resistant food (e.g. macaw species and Palm Cockatoo) have a wider and more caudally positioned quadrate bone and *foramen magnum occipitale*. The palatine bone is extremely large with robust pterygoids. These structures support the surface in order to maximize the bite performance and the effectiveness of jaw closure muscles to crash nuts and hard-shelled seeds. These species have high skulls, which also correspond with the size of *musculus ethmomandibularis*. Several features enable parrots to exert strong bite forces during feeding and locomotion, including the strong adductor muscles that are evolutionary novelties in this group. The presence (or absence) and degree of development of these musculoskeletal structures are highly variable among different species (Burton 1974, Tokita 2003). Nectarivore parrots and the Pesquet Parrot generally have narrow skulls with slender quadrate bones and relatively

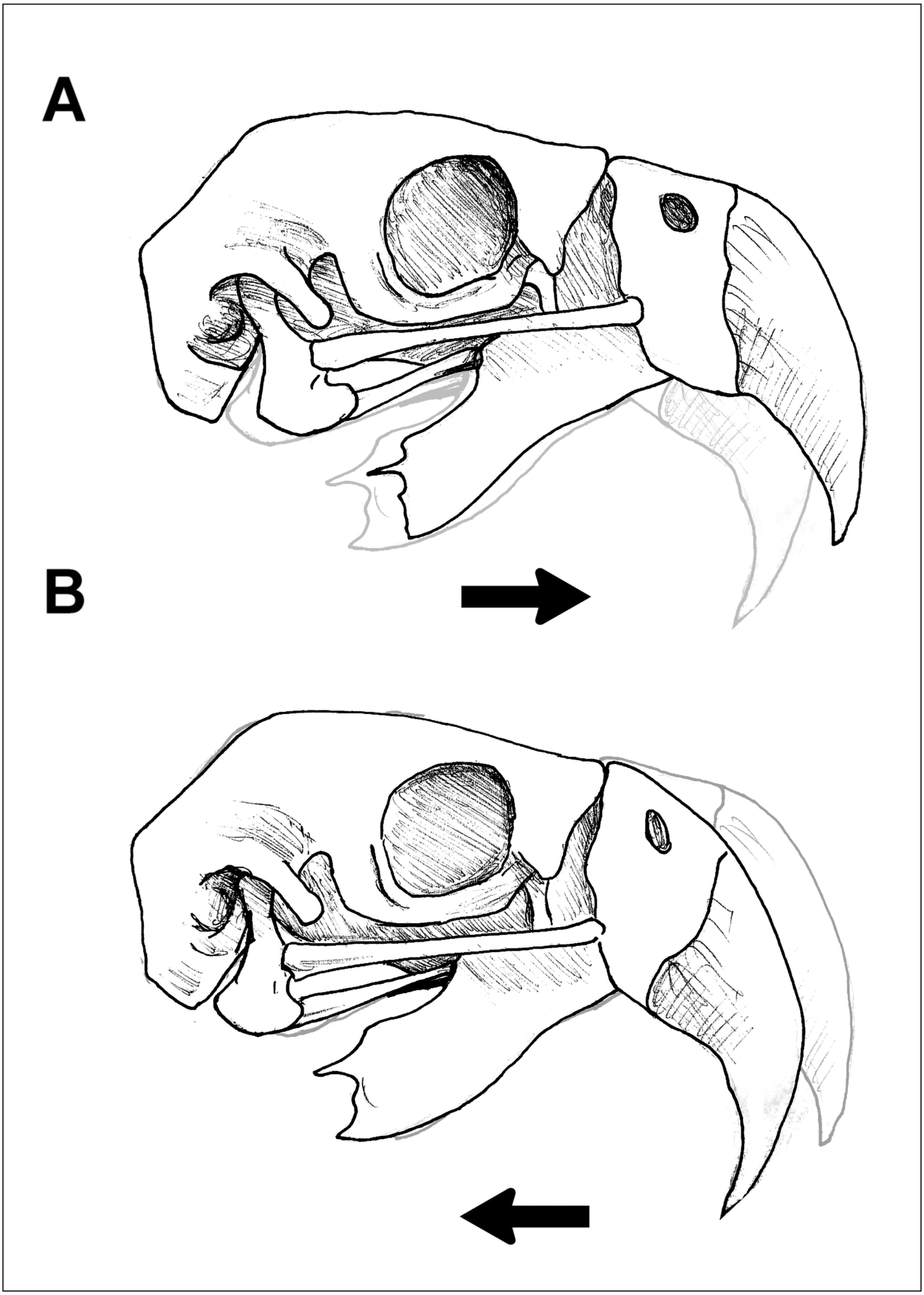


Figure 6. Kinesis of the cranium of a macaw with upper mandible raised (A), with upper mandible lowered (B)

6. ábra Kraniális kinezis egy ara példáján, a felső állkapocscsont felső (A) és alsó pozíciójában (B) gracile palatine and pterygoid bones. This indicates that these species have smaller and weaker pterygoid and adductor muscles. Lories and lorikeets have thinner and structurally weaker beaks than granivorous parrots of a similar size (Holyoak 1973). These lories constitute a highly nectarivorous parrot clade and their diet, associated with morphological innovation, allows them to explore underutilized niches and promote diversification (Schweizer *et al.* 2014). Seed eaters have relatively large *neurocranium*; the maxilla is short and wide. The quadrate bone is wide and positioned anteriorly and pterygoids are longer with broad and divided palatine bones. Bite force and speed of jaw closure perhaps play an important role. Cracking the seeds requires many fast, small, and precise movements in the oral cavity (Homberger 2017). Seed characteristics, size, and shape affected handling time with reference to bill structure (Hrabar & Perrin 2002). Parrots occupy varied dietary niches that require an agile, mobilized feeding apparatus. Cranial kinesis – flexibility among intracranial joints – has a central role in the unique feeding apparatus of this avian order. These birds possess a highly mobile, streptostylic quadrate by moving the rod-like pterygoids. The palatomaxillary system of articulation rotates the rostrum about the synovial craniofacial hinge, providing prokinetic movement between the frontal and nasal bones (Cost *et al.* 2017).

Our results show relationships between cranial attributes and diet preference, but also highlight the morphological complexity and dietary diversity of the feeding apparatus. Future studies reflecting on avian feeding apparatus may increase our knowledge and might be useful to understand the preferences of those species, which are threatened due to habitat loss. It would be interesting to perform combined analyses with cranial shape and attributes of the feet and hypotarsal structures to measure the differences between the arboreal species and those parrots which are conservatively feeding on grasslands. However numerous of species are sexually monomorphic (Miyaki *et al.* 1998), it is possible that there are species – e.g. the Great-billed Parrot *(Tanygnathus megalorynchos)* – where the sexual dimorphism might have role in the cranial shape, as it was observed previously in the case of the Kea (Bond *et al.* 1991). Similarities in the skull shape can reflect also the phylogenetic relation. In this study, we did not investigate the effect of phylogeny. The phylogenetic control would be necessary in a further analysis.

Acknowledgements

We are grateful to Péter Urtz for the technical assistance. The text was supervised by Bridgette Dennett, Emese Bodor and Jenő Nagy.

References

Adams, D. C., Rohlf, F. J. & Slice, D. E. 2004. Geometric morphometrics: ten years of progress following the 'revolution. – Italian Journal of Zoology 71(1): 5–16. DOI: 10.1080/11250000409356545

Anderson, R. A., McBrayer, L. D. & Herrel, A. 2008. Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. – Biological Journal of the Linnean Society 93(4): 709–720. DOI: 10.1111/j.1095-8312.2007.00905.x

Barker, F. K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. 2004. Phylogeny and diversification of the largest avian radiation. – Proceedings of the National Academy of Sciences 101(30): 11040–11045. DOI: 10.1073/pnas.0401892101

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

Beggs, W. & Mankelow, S. 2002. Kea *(Nestor notabilis)* make meals of Mice *(Mus musculus)*. – Notornis 49: 50.

Benavidez, A., Palacio, F. X., Rivera, L. O., Echevarria, A. L. & Politi, N. 2018. Diet of Neotropical parrots is independent of phylogeny but correlates with body size and geographical range. – Ibis 160(4): 742–754. DOI: 10.1111/ibi.12630

Benkman, C. W. 2003. Divergent selection drives the adaptive radiation of Crossbills. – Evolution 57(5): 1176–1181. DOI: 10.1111/j.0014-3820.2003.tb00326.x

Bond, A. B., Wilson, K. J. & Diamond, J. 1991. Sexual dimorphism in the Kea *Nestor notabilis*. – Emu 91(1): 12–19. DOI: 10.1071/MU9910012

Boyes, R. S. & Perrin, M. R. 2009. The feeding ecology of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana. – Ostrich 80(3): 153–164. DOI: 10.2989/OSTRICH.2009.80.3.5.968

Boyes, R. S. & Perrin, M. R. 2010. Aerial surveillance by a generalist seed predator: food resource tracking by Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana. – Journal of Tropical Ecology 26(4): 381–392. DOI: 10.1017/S0266467410000210

Bradbury, J. W. 2003. Vocal communication in wild parrots. – In: de Waal, F. B. M. & Tyack, P. L. (eds.) Animal social complexity: Intelligence, culture, and individualized societies. – Harvard University Press, pp. 293–316.

Brejaart, R. 1988. Diet and feeding behaviour of the Kea *(Nestor notabilis)*. – Unpublished Thesis, Lincoln College, Canterbury, New Zealand

Bright, J. A., Marugán-Lobón, J., Rayfield, E. J. & Cobb, S. N. 2019. The multifactorial nature of beak and skull shape evolution in parrots and cockatoos (Psittaciformes). – BMC Evolutionary Biology 19(1): 104. DOI: 10.1186/s12862-019-1432-1

Bryant, S. L. 1994. Habitat and potential diet of the Ground Parrot in Tasmania. – Emu 94(3): 166–171.

Burton, P. J. K. 1974. Jaw and tongue features in Psittaciformes and other orders with special reference to the anatomy of the Tooth-billed Pigeon *(Didunculus strigirostris)*. – Journal of Zoology 174(2): 255–276. DOI: 10.1111/j.1469-7998.1974.tb03156.x

Carneiro, A. P. B., Jiménez, J. E. & White, Jr, T. H. 2012. Post-fledging habitat selection by the Slender-billed Parakeet *(Enicognathus leptorhynchus)* in a fragmented agricultural landscape of southern Chile. – The Condor 114(1): 166–172. DOI: 10.1525/cond.2011.100127

Carril, J., Tambussi, C. P., Degrange, F. J., Benitez Saldivar, M. J. & Picasso, M. B. J. 2016. Comparative brain morphology of Neotropical parrots (Aves, Psittaciformes) inferred from virtual 3D endocasts. – Journal of Anatomy 229(2): 239–251. DOI: 10.1111/joa.12325

Christidis, L. & Boles, W. 2008. Systematics and taxonomy of Australian birds. – Csiro Publishing

Christidis, L., Schodde, R., Shaw, D. D. & Maynes, S. F. 1991. Relationships among the Australo-Papuan parrots, lorikeets, and cockatoos (Aves: Psittaciformes): protein evidence. – The Condor 93(2): 302–317. DOI: 10.1111/j.1474-919X.1991.tb04570.x

Clarke, C. M. H. 1971. Observations on Population, Movements and Food of the Kea *(Nestor notabilis)*. – NZ Forest Service

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

Cost, I. N., Middleton, K. M., Witmer, L. M., Echols, M. S. & Holliday, C. M. 2017. Comparative anatomy and biomechanics of the feeding apparatus of Parrots (Aves: Psittaciformes). – The FASEB Journal 31(Suppl. 1): pp. 577.

Cracraft, J. 1973. Continental drift, paleoclimatology, and the evolution and biogeography of birds. – Journal of Zoology 169(4): 455–543. DOI: 10.1111/j.1469-7998.1973.tb03122.x

Csermely, D., Bertè, L. & Camoni, R. 1998. Prey killing by Eurasian Kestrels: the role of the foot and the significance of bill and talons. – Journal of Avian Biology 29(1): 10–16. DOI: 10.2307/3677335

Diamond, J. & Bond, A. B. 1991. Social behavior and the ontogeny of foraging in the Kea *(Nestor notabilis)*. – Ethology 88(2): 128–144.

Dumont, E. R. 2003. Bats and fruit: an ecomorphological approach. – In: Kunz, T. H. & Fenton, M. B (eds.) Bat Ecology. – University of Chicago Press, Chicago, pp. 398–429.

Dyke, G. J. & Mayr, G. 1999. Did parrots exist in the Cretaceous period? – Nature 399(6734): 317–318. DOI: 10.1038/20583

Edgar, A. T. (ed.) 1974. Farewell Spit, March 1974. – Notornis 21: 250–259.

Elliott, T. F., Jusino, M. A., Trappe, J. M., Lepp, H., Ballard, G. A., Bruhl, J. J. & Vernes, K. 2019. A global review of the ecological significance of symbiotic associations between birds and fungi. – Fungal Diversity 1–34. DOI: 10.1007/s13225-019-00436-3

Fabbri, M., Koch, N. M., Pritchard, A. C., Hanson, M., Hoffman, E., Bever, G. S., Balanoff, A. M., Morris, Z. S., Field, D. J., Camacho, J., Rowe, T. B., Norell, M. A., Smith, R. M., Abzhanov, A. & Bhullar, B-A. S. 2017. The skull roof tracks the brain during the evolution and development of reptiles including birds. – Nature Ecology & Evolution 1(10): 1543–1550. DOI: 10.1038/s41559-017-0288-2

Forshaw, J. M. 2010. Parrots of the World (Vol. 70). – Princeton University Press

Galetti, M. 1993. Diet of the Scaly-headed Parrot *(Pionus maximiliani)* in a semideciduous forest in southeastern Brazil. – Biotropica 25(4): 419–425. DOI: 10.2307/2388865

Galetti, M. & Rodrigues, M. 1992. Comparative seed predation on pods by parrots in Brazil. – Biotropica 24(2): 222–224. DOI: 10.2307/2388679

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

Greer, A. L. 2015. lntraspecific variation in the foraging ecology and morphology of Kea *Nestor notabilis*. – A thesis submitted in partial fulfilment of the requirement for the Degree of Doctor of Philosophy in Ecology. University of Canterbury, Christchurch, New Zealand

Guangdi, S. I., Dong, Y., Ma, Y. & Zhang, Z. 2015. Shape similarities and differences in the skulls of scavenging raptors. – Zoological Science 32(2): 71–177. DOI: 10.2108/zs130253

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C., Braun, E. L., Braun, M. J. & Huddleston, C. J. 2008. A phylogenomic study of birds reveals their evolutionary history. – Science 320(5884): 1763–1768. DOI: 10.1126/science.1157704

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.

Herrel, A., Podos, J., Huber, S. K. & Hendry, A. P. 2005. Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak shape. – Functional Ecology 19(1): 43–48. DOI: 10.1111/j.0269-8463.2005.00923.x

Holyoak, D. T. 1973. Comments on taxonomy and relationships in the parrot subfamilies Nestorinae, Loriinae and Platycercinae. – Emu 73(4): 157–176. DOI: 10.1071/MU973157

Homberger, D. G. 2006. Classification and status of wild populations of parrots. – Manual of parrot behavior. – Ames (IA): Blackwell Publishing, pp. 3–11.

Homberger, D. G. 2017. The avian lingual and laryngeal apparatus within the context of the head and jaw apparatus, with comparisons to the mammalian condition: functional morphology and biomechanics of evaporative cooling, feeding, drinking, and vocalization. – In: Maina, J. N. (ed.) The biology of the avian respiratory system. – Springer, Cham, pp. 27–97. DOI: 10.1007/978-3-319-44153-5_2

Hrabar, H. D. K. & Perrin, M. 2002. The effect of bill structure on seed selection by granivorous birds. – African Zoology 37(1): 67–80. DOI: 10.1080/15627020.2002.11657157

Iwaniuk, A. N., Dean, K. M. & Nelson, J. E. 2005. Interspecific allometry of the brain and brain regions in parrots (Psittaciformes): comparisons with other birds and primates. – Brain, Behavior and Evolution 65(1): 40–59. DOI: 10.1159/000081110

Janzen, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. – Evolution 23(1): 1–27. DOI: 10.1111/j.1558-5646.1969.tb03489.x

Jarvis, E. D., Mirarab, S., Aberer, A. J., Li, B., Houde, P., Li, C., Ho, S. Y. W., Faircloth, B. C., Nabholz, B., Howard, J. T., Suh, A. *et al.* & Zhang, G. 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. – Science 346(6215): 1320–1331. DOI: 10.1126/science.1253451

Provost, K. L., Joseph, L. & Smith, B. T. 2018. Resolving a phylogenetic hypothesis for parrots: implications from systematics to conservation. – Emu 118(1): 7–21. DOI: 10.1080/01584197.2017.1387030

Kulemeyer, C., Asbahr, K., Gunz, P., Frahnert, F. & Bairlein, F. 2009. Functional morphology and integration of corvid skulls-a 3D geometric morphometric approach. – Frontiers of Zoology 6(1): 2. DOI: 10.1186/1742-9994-6-2

Lee, A. T., Brightsmith, D. J., Vargas, M. P., Leon, K. Q., Mejia, A. J. & Marsden, S. J. 2014. Diet and geophagy across a western Amazonian parrot assemblage. – Biotropica 46(3): 322–330. DOI: 10.1111/btp.12099

Lill, A. 2009. Food resources and urban colonisation by lorikeets and parrots. – Victorian Naturalist 126(3): 70–72.

Marriner, G. R. 1908. The Kea: A New Zealand Problem: Including a Full Description of this Very Interesting Bird, Its Habitat and Ways, Together with a Discussion of the Theories Advanced to Explain Its Sheep-killing Propensities. – Marriner Bros

Marugán-Lobón, J. & Buscalioni, Á. D. 2006. Avian skull morphological evolution: exploring exo- and endocranial covariation with two-block partial least squares. – Zoology 109(3): 217–230. DOI: 10.1016/j.zool.2006.03.005

Mayr, G. 2010. Parrot interrelationships–morphology and the new molecular phylogenies. – Emu 110(4): 348–357. DOI: 10.1071/MU10035

Mayr, G., Rana, R. S., Rose, K. D., Sahni, A., Kumar, K. & Smith, T. 2013. New specimens of the early Eocene bird *Vastanavis* and the interrelationships of stem group Psittaciformes. – Paleontological Journal 47(11): 1308–1314.

McBrayer, L. D. 2004. The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards. – Zoological Journal of the Linnean Society 140(3): 403–416. DOI: 10.1111/j.1096-3642.2003.00106.x

McCormack, J. E., Harvey, M. G., Faircloth, B. C., Crawford, N. G., Glenn, T. C. & Brumfield, R. T. 2013. A phylogeny of birds based on over 1,500 loci collected by target enrichment and high-throughput sequencing. – PLoS One 8(1): e54848. DOI: 10.1371/journal.pone.0054848

McInnes, R. S. & Carne, P. B. 1978. Predation of cossid moth larvae by Yellow-tailed Black Cockatoos causing losses in plantations of *Eucalyptus grandis* in north coastal New South Wales. – Wildlife Research 5(1): 101–121.

Miyaki, C. Y., Griffiths, R., Orr, K., Nahum, L. A., Pereira, S. L., & Wajntal, A. 1998. Sex identification of parrots, toucans, and curassows by PCR: perspectives for wild and captive population studies. Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association 17(5): 415–423.

O'Hara, M., Gajdon, G. K. & Huber, L. 2012. Kea logics: how these birds solve difficult problems and outsmart researchers. – Logic and Sensibility 5: 23–38.

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

Pecsics, T., Laczi, M., Nagy, G., Kondor, T. & Csörgő, T. 2018. Analysis of skull morphometric characters in Owls (Strigiformes). – Ornis Hungarica 26(1): 41–53. DOI: 10.1515/orhu-2018-0003

Pecsics, T., Laczi, M., Nagy, G., Kondor, T. & Csörgő, T. 2019. Analysis of skull morphometric characters in diurnal raptors (Accipitriformes and Falconiformes). – Ornis Hungarica 27(1): 117–131. DOI: 10.2478/orhu-2019-0008

Pizo, M. A., Simáo, I. & Galetti, M. 1995. Diet and flock size of sympatric parrots in the Atlantic forest of Brazil. – Ornitologia Neotropical 6: 87–95.

Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Lemmon, E. M. & Lemmon, A. R. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. – Nature 526(7574): 569–573. DOI: 10.1038/nature15697

Pryor, G. S., Levey, D. J., Dierenfeld, E. S. & Bosque, C. 2001. Protein requirements of a specialized frugivore, Pesquet's Parrot *(Psittrichas fulgidus)*. – The Auk 118(4): 1080–1088. DOI: 10.1093/auk/118.4.1080

Ragusa-Netto, J. & Fecchio, A. 2006. Plant food resources and the diet of a parrot community in a gallery forest of the southern Pantanal (Brazil). – Brazilian Journal of Biology 66(4): 1021–1032. DOI: 10.1590/S1519-69842006000600008

Rand, A. L. 1942. Results of the Archbold Expeditions, No. 43. Birds of the 1938–1939 New Guinea expedition. – Bulletin of the American Museum of Natural History 79: 425–516.

Renton, K. 2001. Lilac-crowned Parrot diet and food resource availability: resource tracking by a parrot seed predator. – The Condor 103(1): 62–69. DOI: 10.1093/condor/103.1.62

Renton, K., Salinas-Melgoza, A., De Labra-Hernández, M. Á. & de la Parra-Martínez, S. M. 2015. Resource requirements of parrots: nest site selectivity and dietary plasticity of Psittaciformes. – Journal of Ornithology 156(1): 73–90. DOI: 10.1007/s10336-015-1255-9

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

Schweizer, M., Güntert, M., Seehausen, O., Leuenberger, C. & Hertwig, S. T. 2014. Parallel adaptations to nectarivory in parrots, key innovations and the diversification of the *Loriinae*. – Ecology and Evolution 4(14): 2867–2883. DOI: 10.1002/ece3.1131

Schwing, R. 2010. Scavenging behaviour of Kea *(Nestor notabilis)*. – Notornis 57(2): 98–99.

Sun, Y., Si, G., Wang, X., Wang, K. & Zhang, Z. 2018. Geometric morphometric analysis of skull shape in the Accipitridae. – Zoomorphology 137: 445–456. DOI: 10.1007/s00435-018-0406-y

Sustaita, D. & Hertel, F. 2010. In vivo bite and grip forces, morphology and prey-killing behavior of North American accipiters (Accipitridae) and falcons (Falconidae). – Journal of Experimental Biology 213(15): 2617–2628. DOI: 10.1242/jeb.041731

Temple, P. 1996. The book of the Kea. – Auckland: Hodder Moa Becket

Terborgh, J., Robinson, S. K., Parker III., T. A., Munn, C. A. & Pierpont, N. 1990. Structure and organization of an Amazonian forest bird community. – Ecological Monographs 60(2): 213–238. DOI: 10.2307/1943045

Tokita, M. 2003. The skull development of parrots with special reference to the emergence of a morphologically unique cranio-facial hinge. – Zoological Science 20(6): 749–758. DOI: 10.2108/zsj.20.749

Tokita, M. 2006. Cranial neural crest cell migration in Cockatiel *Nymphicus hollandicus* (Aves: Psittaciformes). – Journal of Morphology 267(3): 333–340. DOI: 10.1002/jmor.10408

Tokita, M. & Nakayama, T. 2014. Development of the trigeminal motor neurons in parrots: Implications for the role of nervous tissue in the evolution of jaw muscle morphology. – Journal of Morphology 275(2): 191–205. DOI: 10.1002/jmor.20208

Tokita, M., Kiyoshi, T. & Armstrong, K. N. 2007. Evolution of craniofacial novelty in parrots through developmental modularity and heterochrony. – Evolution & Development 9(6): 590–601. DOI: 10.1111/j.1525-142X.2007.00199.x

Van der Meij, M. A. A. & Bout, R. G. 2004. Scaling of jaw muscle size and maximal bite force in finches. – Journal of Experimental Biology 207(16): 2745–2753. DOI: 10.1242/jeb.01091

Vaughan, C., Nemeth, N. & Marineros, L. 2006. Scarlet Macaw, *Ara macao* (Psittaciformes: Psittacidae) diet in Central Pacific Costa Rica. – Revista de Biología Tropical 54(3): 919–926.

Ward, A. B., Weigl, P. D. & Conroy, R. M. 2002. Functional morphology of raptor hindlimbs: implications for resource partitioning. – The Auk 119(4): 1052–1063.

Waterhouse, D. M. 2006. Parrots in a nutshell: the fossil record of Psittaciformes (Aves). – Historical Biology 18(2): 227–238. DOI: 10.1080/08912960600641224

Wirminghaus, J. O., Downs, C. T., Symes, C. T. & Perrin, M. R. 2002. Diet of the Cape Parrot, *Poicephalus robustus*, in afromontane forests in Kwazulu-Natal, South Africa. – Ostrich 73(1–2): 20–25. DOI: 10.2989/00306520209485347

Wood, G. A. 1988. Further field observations of the Palm Cockatoo *Probosciger aterrimus* in the Cape York Peninsula, Queensland. – Corella 12: 48–52.

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

Zusi, R. L. 1993. Patterns of diversity in the avian skull. – In: Hanken, J. & Hall, B. K. (eds.) The Skull, Vol. 2. Patterns of Structural and Systematic Diversity. – University of Chicago Press, Chicago, pp. 391–437.

Zweers, G. A., Berkhoudt, H. & Berge, J. V. 1994. Behavioral mechanisms of avian feeding. – In: Bels, V. L., Chardon, M. & Vandewalle, P. (eds.) Biomechanics of feeding in vertebrates. – Springer, Berlin, Heidelberg, pp. 241–279.

Ornis Hungarica 2020. 28(1): 121–168.
DOI: 10.2478/orhu-2020-0009

Evolution of Corvids and their Presence in the Neogene and the Quaternary in the Carpathian Basin

Jenő (Eugen) Kessler

Received: September 09, 2019 – Revised: February 12, 2020 – Accepted: February 18, 2020

Kessler, J. (E.) 2020. Evolution of Corvids and their Presence in the Neogene and the Quaternary in the Carpathian Basin. – Ornis Hungarica 28(1): 121–168. DOI: 10.2478/orhu-2020-0009

Abstract: Corvids are the largest songbirds in Europe. They are known in the avian fauna of Europe from the Miocene, the beginning of the Neogene, and are currently represented by 11 species. Due to their size, they occur more frequently among fossilized material than other types of songbirds, and thus have been examined to the largest extent. In the current article, we present their known evolution and their fossilized taxa in Europe and examine the osteology of extant species.

Keywords: Corvidae, Neogene, Quaternary, Europe, Carpathian Basin, osteology

Összefoglalás: A varjúfélék a legnagyobb termetű, Európában is elterjedt énekesmadarak. A kontinens madárfaunájában a neogén elejétől, a miocénből ismertek, és jelenleg 11 fajjal vannak képviselve. Termetük következtében gyakrabban előfordulnak a fosszilis anyagban, mint a többi énekesmadár típus, és ennek következtében nagyobb mértékben is tanulmányozták őket. Jelen tanulmányban bemutatjuk az ismert európai evolúciójukat és fosszilis taxonjaikat, és foglalkozunk a recens fajok csonttanával is.

Kulcsszavak: Corvidae, neogén, negyedidőszak, Európa, Kárpát-medence, csonttan

Department of Paleontology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c, Hungary, e-mail: kessler_jeno@yahoo.com

Introduction

About half of the current avian species – if not more – consists of songbirds, which are distributed all around the world apart from Antarctica with a large number of specimens. Despite this fact, we know little of their origins and evolution. They supposedly formed in the ancient continent of Gondwana, but their fossilized remains in the Palearctic and Nearctic are only known from the Neogene, and even those only in small numbers. Recently, however, their research received a boost, and thus the number of identified and described taxa and new fossil species increased (Kessler 2013a, 2013b, 2015).

The families of the order Corvidae are an exception to this, and due to their larger size, they were always in the focus of interest of paleornithologists. Most songbird species had been described during the past two centuries from this family. During their classification, we follow the Brodkorb type of systematics, since those that are based on DNA data (Sibley & Ahlquits 1990, Monroe & Sibley 1993, Jarvis *et al.* 2014) cannot be used in case of fossils in the absence of comparative molecular material, and other types of systematics classify solely based on appearance and feathers, excluding skeletons that can be examined within the framework of paleontology (e.g. Clements 1974, Cramp 1998, Dickinson & Christidis 2014).

Brodkorb (1978) distinguishes two subfamilies within the family:

- Garbulinae (Bole, 1825) to which he only classifies Nearctic taxa *(Miocitta, Protocitta, Hetocitta)* from the Neogene and Quaternary of North America. Examples of this are †*Miocitta galbreathy* (Brodkorb 1972) (from the Miocene of Colorado), †*Protocitta ayax* Brodkorb, 1972 (from the Pliocene of Kansas and Texas), †*P. dixi* (Brodkorb 1957) (from the Pleistocene of Florida and Texas), †*Henocitta brodkorbi* Holman 1959 (from the Pleistocene of Florida);
- *Corvinae* (Bonaparte 1831), where the Palearctic species belong. Brodcorb mentions the following species from outside Europe: *Corvus* †*wetmorei* (Brodkorb, 1959) (from the Pleistocene of Bahama), *C.* †*pumilis* (Wetmore, 1920) (from the Quaternary of Puerto Rico and the Virgin Islands), *C.* †*moriorum* (Forbes, 1892) (from the Quaternary of the Chatham Islands). Apart from the Corvidae finds, crow remains were recently described from the Miocene of North America (Olson & Rasmussen 2001) report the taxon *Corvus* aff *ossifragus* (Wilson, 1812) from the site at Lee Creek Mine, based on a *tibiotarsus* find.

We discuss fossil corvids of the western Palearctic and the Carpathian Basin in the systematic section after the osteology chapter.

Abbreviations: Q1-Q2 – Lower Pleistocene; **Q3 (Q3/I-Q3/II)** – Middle Pleistocene; **Q4/I** – Upper Pleistocene; **Q4/II** – Holocene; † – extinct/fossil species – subspecies.
A – total lengths; B – partial lengths; C – breadth of proximal epiphysis; C1 – partial breadth of proximal epiphysis; D – thickness of proximal epiphysis; E – breadth of diaphysis; E1 – partial breadth of diaphysis; F – breadth of distal epiphysis; G – thickness of distal epiphysis; H – height of distal epiphysis.

Osteology of Corvids

Anatomical terminology (after: Milne-Edwards 1868, Fürbringer 1888, Lambrecht 1933, Ballmann 1966, Mourer-Chauviré 1975, Baumel *et al.* 1979, Gilbert *et al.* 1981, Cheneval 1983, Jánossy 1985, Solti 1996, Tomek & Bochenski 2000, Kessler 2013a) *(Figure 1).*

Method of measurement: (after: von den Driesch 1976, Gál 2002, Kessler 2013b) *(Figure 2).*
A = TL – total length;
B = PL – partial length;
C = Bp – breadth of the proximal end;
C1 = partial breadth of the proximal end;
D = partial length of the proximal end;
E = Sc – breadth of the corpus;
E1 = partial breadth of the corpus;
F = Bd – breadth of the distal end;
G = thickness of the distal end;
H = height of the distal end.

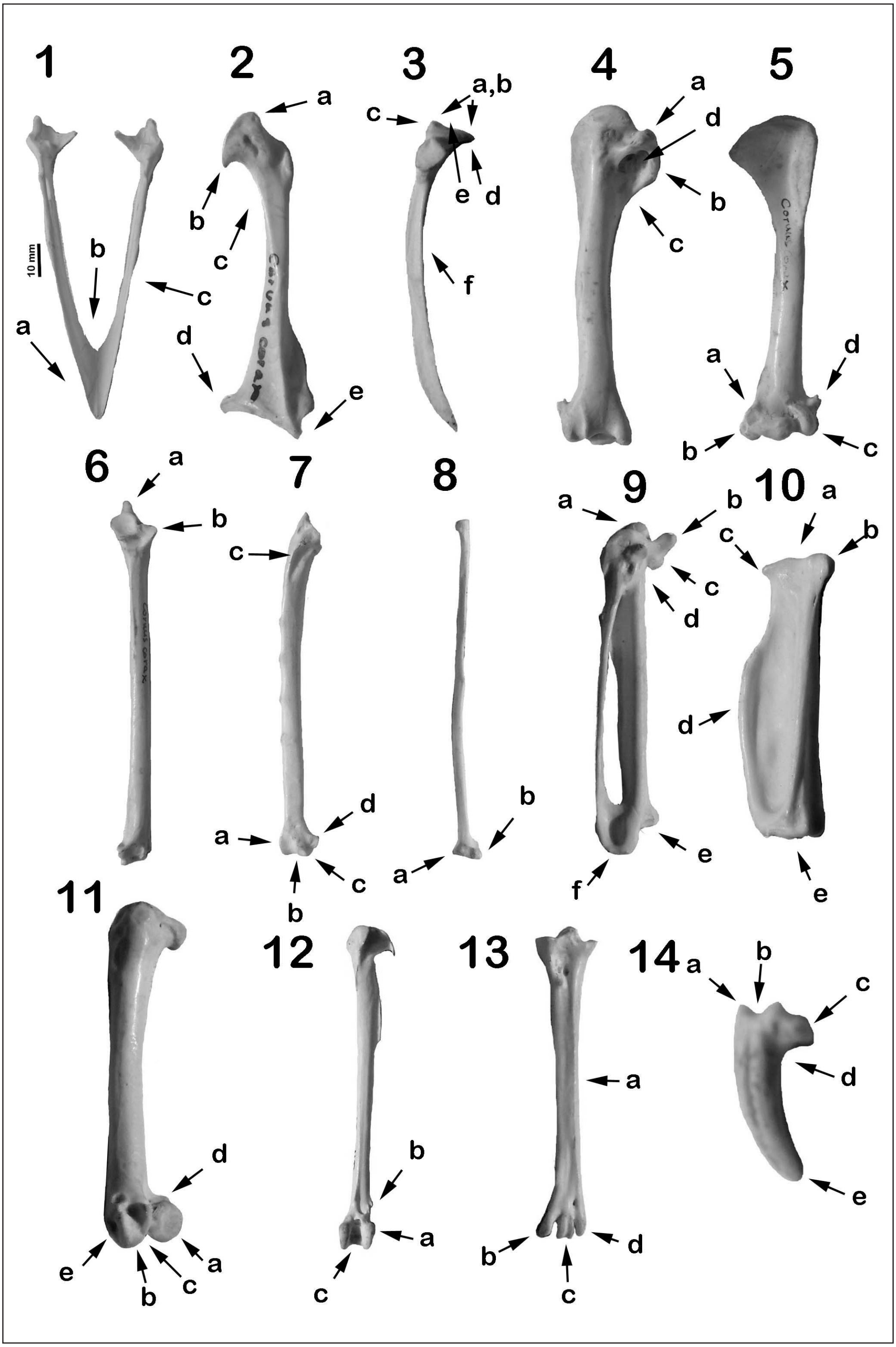

1
b
10 mm
c
a
2
a
b
c
d
e
Corvus corax
3
a,b
c
e
d
f
4
a
d
b
c
5
Corvus corax
a
d
b
c
6
a
b
Corvus corax
7
c
d
a
c
b
8
b
a
9
a
b
c
d
e
f
10
a
c
b
d
e
11
d
e
b
c
a
12
b
a
c
13
a
b
d
c
14
a
b
c
d
e

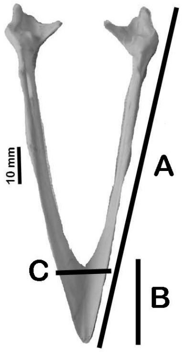
Figure 1. Corvus corax Linnaeus, 1758 osteology characters:

1. *Mandibula*: a. the pointed end of the *rostrum mandibulae;* b. the immersed part of the *rostrum*; c. the *ramus mandibulae, pars symphysialis;*
2. *Coracoideum*: a. the *processus acrocoracoidalis*; b. the *processus procoracoidalis*; c. the *sulcus musculi supracoracoideus*; d. the *angulus medialis*; e. the *processus lateralis*;
3. *Scapula*: a. the dorsal branch of the *acromion*; b. the lateral branch of the *acromion;* c. the pit between the branches of the *acromion*; d. the *corpus scapulae;*
4. *Humerus*, epiphysis proximalis: a. the *tuberculum ventrale*; b. the *crista bicipitalis*; c. the edge between *crista bicipitalis* and *corpus humeri;* d. the *fossa pneumotricipitalis*;
5. *Humerus*, epiphysis distalis: a. the *tuberculum supracondylare ventrale;* b. the *processus flexorius;* c. the *condylus dorsalis*; d. the *processus supracondylaris dorsalis;*
6. *Ulna*, epiphysis proximalis: a. the *olecranon*; b. the *cotyla dorsalis*; c. the *impressio brachialis*;
7. *Ulna*, epiphysis distalis: a. the *condylus dorsalis ulnaris*; b. the *sulcus intercondylaris;* c. the *condylus ventralis ulnaris*; d. the *tuberculum carpale;*
8. *Radius*: a. the *tuberculum aponeurosis ventrale*; b. the *tuberculum aponeurosis dorsale;*
9. *Carpometacarpus*: a. the *trochlea carpalis;* b. the *processus extensorius;* c. the *processus alularis;* d. the *fovea subalularis;* e. the *protuberantia metacarpale majus;* f. the *facies articularis digitale minor;*
10. *Phalanx proximalis digiti majoris*: a. the *margo proximalis;* b. the *tuberculum ventralis;* c. the *tuberculum dorsalis;* d. the *margo dorsalis;* e. the *margo distalis;*
11. *Femur*, epiphysis distalis: a. the *condylus medialis;* b. the *condylus lateralis*; c. the *sulcus intercondylaris;* d. the *epicondylus medialis;* e. the *epicondylus lateralis;*
12. *Tibiotarsus*, epiphysis distalis: a. the *epicondylus lateralis*; b. the *tuberculum retinaculum musculi fibularis*; c. the *incisura intercondylaris*;
13. *Tarsometatarsus*, epiphysis distalis: a. the *margo medialis;* b. the *troclea metatarsi* II.: c. the *trochlea metatarsi* III.; d. the *trochlea metatarsi* IV.;
14. *Phalanx ungularis*: a. the *tuberculum extensorium*; b. the *cotyla articularis*; c. the *tuberculum flexorium;* d. the curvature of the *margo plantaris*; e. the *apex phalangis*

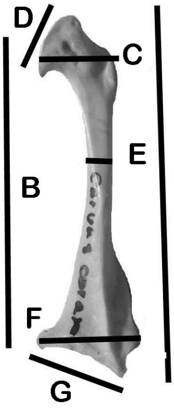
1. ábra Corvus corax Linnaeus, 1758 csonttani jellegek:

1. Alsó állkapocs: a. a *rostrum mandibulae* hegye*;* b. bemélyedés a *rostrum*-on; c. *ramus mandibulae, pars symphysialis;*
2. Hollócsőrcsont: a. *processus acrocoracoidalis*; b. *processus procoracoidalis*; c. *sulcus musculi supracoracoideus*; d. *angulus medialis*; e. *processus lateralis*;
3. Lapocka: a. az *acromion* dorzális ága; b. az *acromion* oldalsó ága*;* c. az *acromion* ágai közti bemélyedés alakja; d. *corpus scapulae;*
4. Felkarcsont, proximális vég: a. *tuberculum ventrale*; b. *crista bicipitalis*; c. a *crista bicipitalis* és a *corpus humeri* közti él jellege*;* d. *fossa pneumotricipitalis*;
5. Felkarcsont, disztális vég: a. *tuberculum supracondylare ventrale;* b. *processus flexorius;* c. *condylus dorsalis*; d. *processus supracondylaris dorsalis;*
6. Singcsont proximális vég: a. *olecranon*; b. *cotyla dorsalis*; c. *impressio brachialis*;
7. Singcsont disztális vég: a. *condylus dorsalis ulnaris*; b. *sulcus intercondylaris;* c. *condylus ventralis ulnaris*; d. *tuberculum carpale;*
8. Orsócsont: a. *tuberculum aponeurosis ventrale*; b. *tuberculum aponeurosis dorsale;*
9. Kézközépcsont: a. *trochlea carpalis;* b. *processus extensorius;* c. *processus alularis;* d. *fovea subalularis;* e. *protuberantia metacarpale majus;* f. *facies articularis digitale minor;*
10. A nagy kézujj első ujjperce: a. *margo proximalis;* b. *tuberculum ventralis;* c. *tuberculum dorsalis;* d. *margo dorsalis;* e. *margo distalis;*
11. Combcsont, disztális vég: a. *condylus medialis;* b. *condylus lateralis*; c. *sulcus intercondylaris;* d. *epicondylus medialis;* e. *epicondylus lateralis;*
12. Lábszárcsont, disztális vég: a. *epicondylus lateralis*; b. *tuberculum retinaculum musculi fibularis*; c. *incisura intercondylaris*;
13. Csüd, disztális vég: a. *margo medialis;* b. *troclea metatarsi* II.: c. *trochlea metatarsi* III.; d. *trochlea metatarsi* IV.;
14. Karomcsont: a. *tuberculum extensorium*; b. *cotyla articularis*; c. *tuberculum flexorium;* d. a *margo plantaris* íve; e. *apex phalangis*

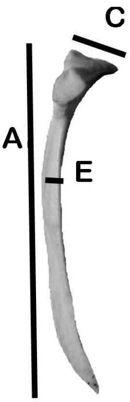
1



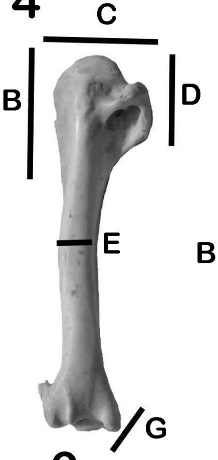
2



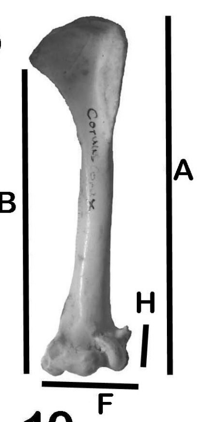
3



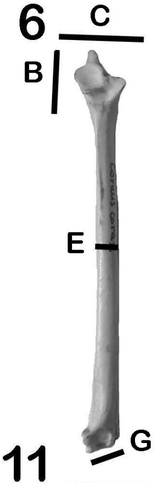
4



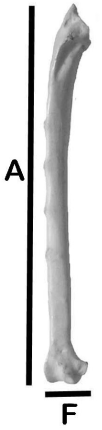
5



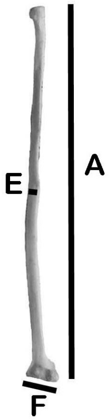
6



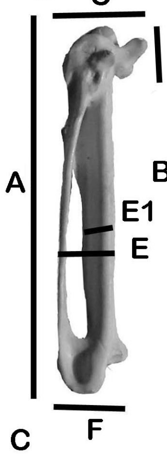
7



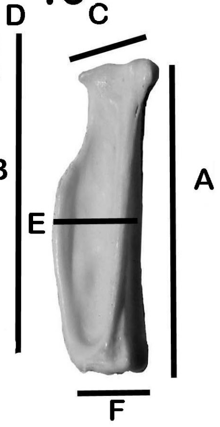
8



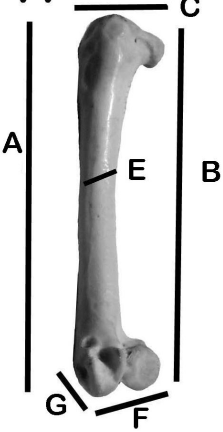
9



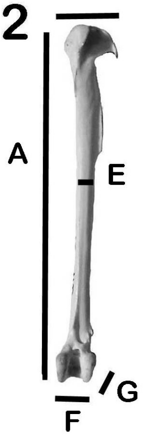
10



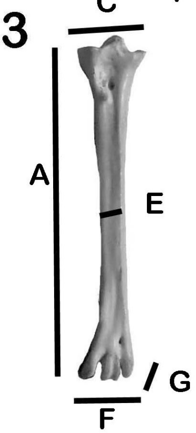
11



12



13



14

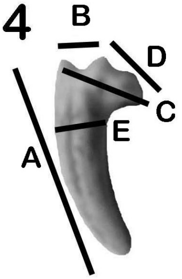


Figure 2. Measurements methods of bones:

1. *Mandibula*: A. total length; B. length of the *rostrum*; C. breadth of the *rostrum*;
2. *Coracoideum*: A. total length; B. partial length; C. length of the *processus procoracoidalis*; D. breadth of the corpus and *processus procoracoidalis*; E. breadth of the corpus; F. total breadth of the distal end; G. partial breadth of the distal end.
3. *Scapula*: A. total length; C. breadth of the proximal end; E. breadth of the corpus;
4-5. *Humerus*: A. total length; B. partial length 1; C. breadth of the proximal end; D. partial length 2; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end; H. height of the distal end;
6-7. *Ulna*: A. total length; B. length of the proximal epiphysis; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
8. *Radius*: A. total length; F. breadth of the distal end;
9. *Carpometacarpus*: A. total length; B. partial length; C. breadth of the proximal end; D. length of the processus extensorius; E. breadth of the corpus; E1: breadth of the metacarpus majus; F. breadth of the distal end;
10. *Phalanx proximalis digiti majoris*: A. total length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end;
11. *Femur*: A. total length; B. partial length 1.; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
12. *Tibiotarsus*: A. total length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
13. *Tarsometatarsus*: A. total length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
14. *Phalanx ungularis*: A. total length; B. length of the *cotyla articularis*; C. breadth of the proximal end; D. length of the *tuberculum flexorium;* E. breadth of the *corpus*

2. ábra A csontok mérési mintái:

1. Alsó állkapocs: A. teljes hossz; B. a csőr vég hossza; C. a csőrvég szélessége;
2. Hollócsőrcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég részleges szélessége;
3. Lapockacsont: A. teljes hossz; C. proximális vég szélessége; E. a test szélessége;
4-5. Felkarcsont: A. teljes hossz; B. részleges hossz 1.; C. proximális vég szélessége; D. részleges hossz 2.; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága; disztális vég magassága;
6-7. Singcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
8. Orsócsont: A. teljes hossz; F. a disztális vég szélessége;
9. Kézközépcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; D. a *processus flexorius* hossza; E. a test szélessége; E1: a *metacarpus majus* vastagsága; F. a disztális vég szélessége;
10. Kézujjperc (II. ujj, 1. perc): A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége;
11. Combcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
12. Lábszárcsont: A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
13. Csüd: A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
14. karomcsont: A. teljes hossz; B. izületi vápa hossza; C. proximális vég szélessége; D. a *processus flexorius* szélessége; E. a test szélessége

1. *Mandibula* *(Figure 3)*
1.a the pointed end of the *rostrum mandibulae*:
– medium long and medium width: *Corvus, Garrulus, Pica*;
– long and narrow: *Pyrrhocorax*;
– long and medium width: *Nucifraga*;
1.b the immersed part of the *rostrum*:
– narrow semicircular: *Pyrrhocorax*;
– pointed: *Corvus frugilegus*;
– ovoid: *Corvus corax, C. corone, C. monedula, Pica*;
– semi-circle with small recess: *Garrulus*;
– wide semi-circle: *Nucifraga*;
1.c the form of the *ramus mandibulae*:
– short: *Nucifraga*;
– long and medium wide: *Corvus, Garrulus, Pica*;
– long and narrow: *Pyrrhocorax*;

2. *Coracoideum* *(Figure 4)*
2.a the *processus acrocoracoideus (tuberculum brachiale)*:
– curved and pointed: *Corvus corax, C. monedula, Garrulus, Pica, Pyrrhocorax*;
– narrow and pointed: *Nucifraga*;
– strongly curved and pointed: *Corvus corone, C. frugilegus*;
2.b the *acrocoracoideum:*
– semicircular: *Corvus corone, Pyrrhocorax graculus*;
– wide cone-shaped: *Corvus moinedula, Pica, Pyrrhocorax pyrrhocorax*;
– assymmetric cone-shaped: *Corvus corax, C. frugilegus*;
– small pointed cone-shaped: *Garrulus*;
– small bunted cone-shaped: *Nucifraga*;
2.c the *sulcus musculi supracoracoidei*:
– symmetrically semicircular: *Corvus, Garrulus, Pyrrhocorax*;
– flattened: *Nucifraga, Pica*;
2.d the *angulus medialis:*
– pointed: *Garrulus, Nucifraga*;
– pointed and curved: *Pyrrhocorax graculus*;
– protruding: *Corvus monedula, Pyrrhocorax pyrrhocorax*;
– truncated: *Corvus corax, C. corone, C. frugilegus, Pica*;
2.e the *processus lateralis*:
– semicircular-shaped: *Corvus frugilegus, Garralus, Nucifraga, Pica*;
– symmetric truncated: *Corvus corone, Pyrrhocorax graculus*;
– asymmetric truncated: *Corvus corax, C. monedula, Pyrrhocorax pyrrhocorax*;

3. *Scapula* *(Figure 5)*
3.a the length of the branches of *acromion*:
– symmetrically (equal): *Nucifraga, Pica*;
– asymmetrically (unequal): *Corvus, Garrulus, Pyrrhocorax*;

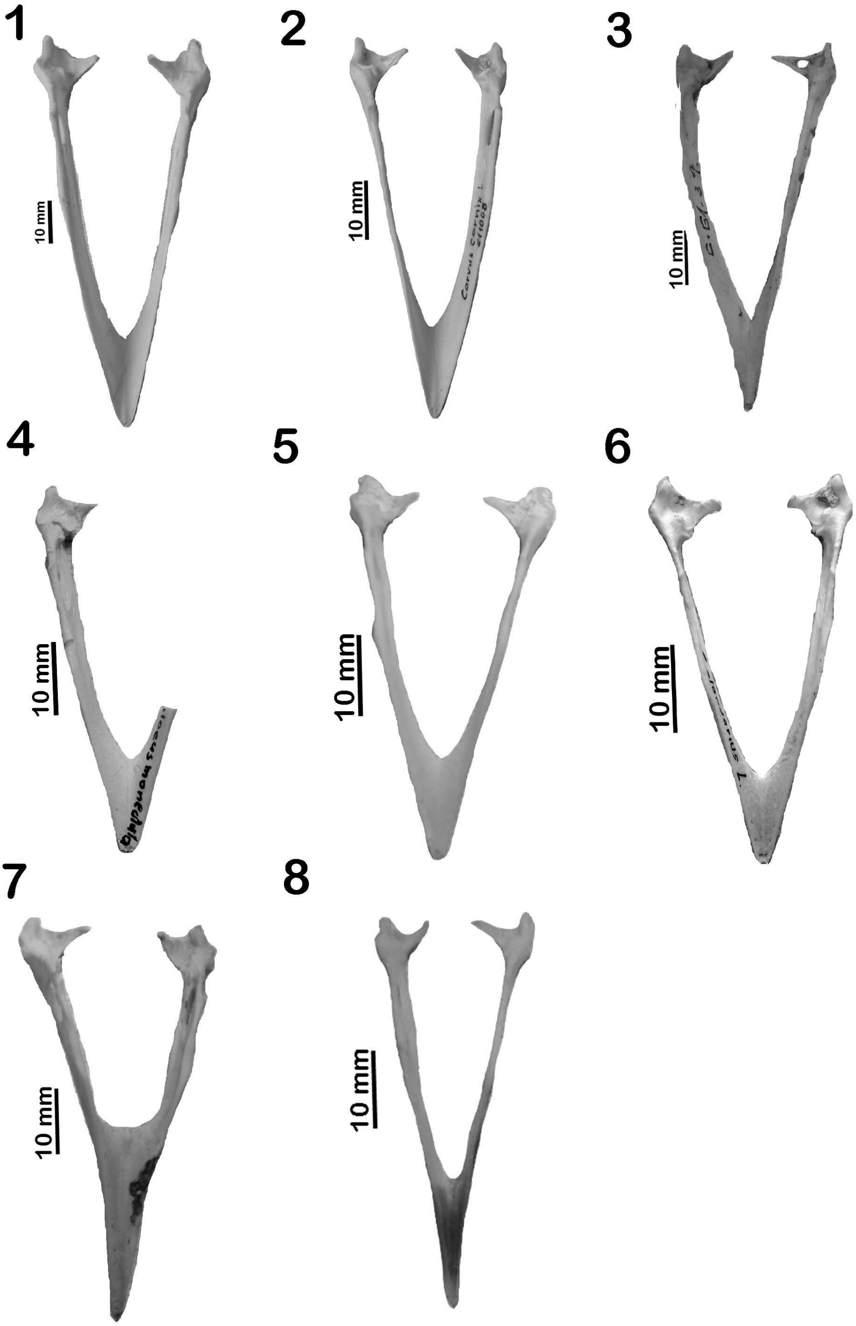


Figure 3. *Mandibula* (dorsal surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*

3. ábra Alsó állkapocs (háti nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*

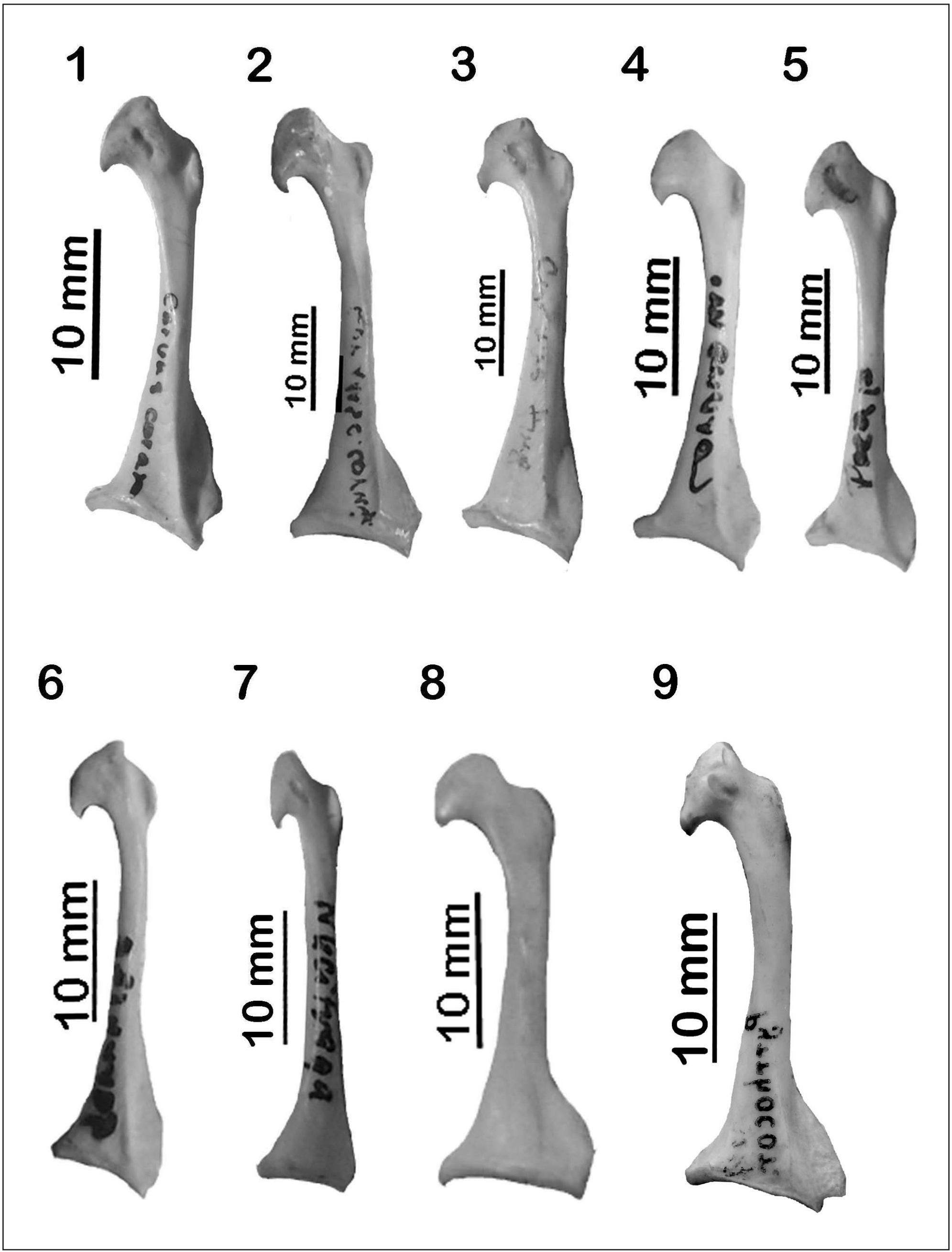


Figure 4. Left *coracoideum* (ventral surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

4. ábra Bal oldali hollócsőrcsont (hasi oldal): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

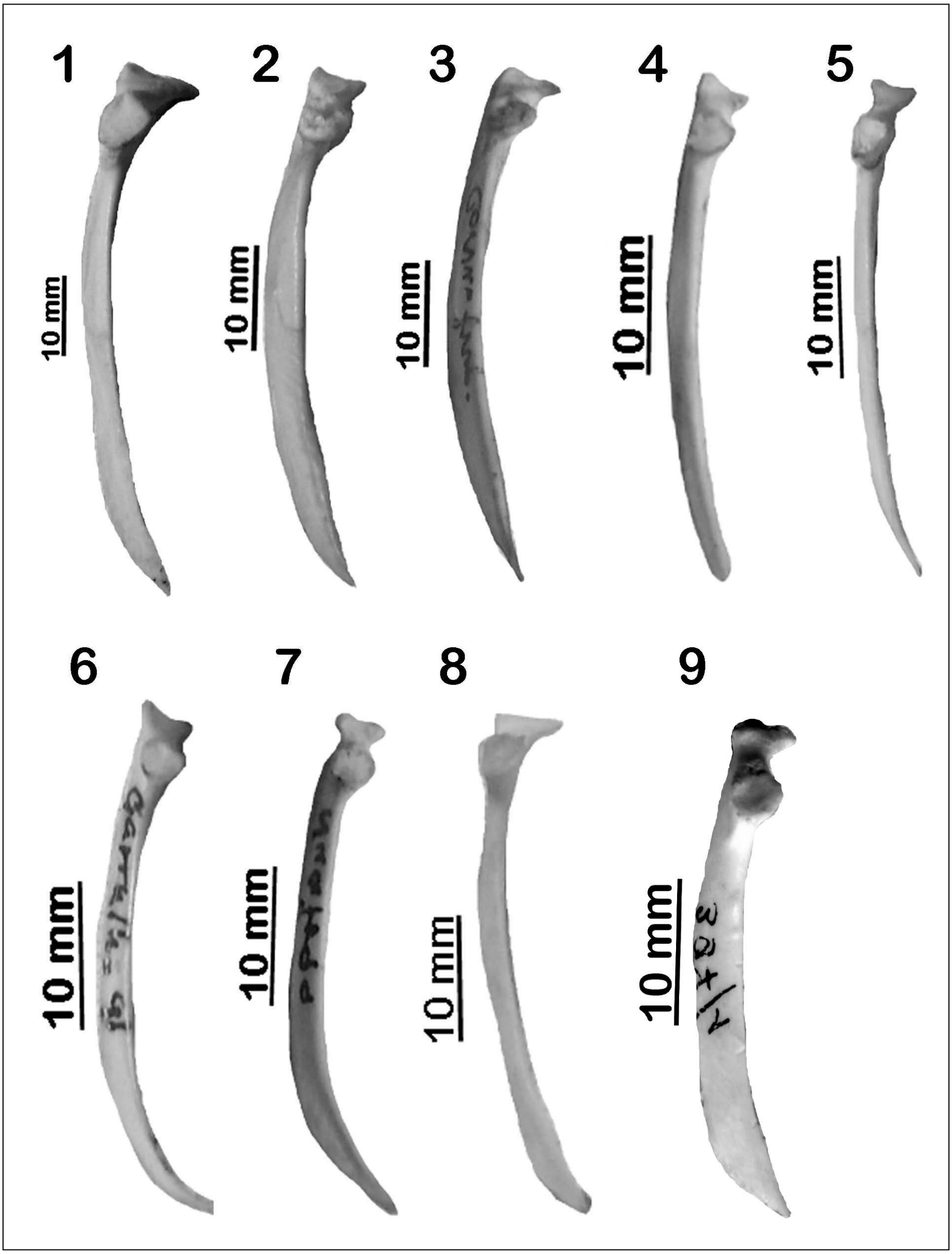


Figure 5. Right *scapula* (medial surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

5. ábra Jobb oldali lapocka csont (mediális oldal): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

3.b the shape of the branches of *acromion*:
– symmetrically (equal): *Nucifraga, Pica, Pyrrhocorax graculus*;
– asymmetrically (unequal): *Corvus, Garrulus, Pyrrhocorax pyrrhocorax*;
3.c the *apex dorsalis* (dorsal branch):
– short and blunted: *Corvus frugilegus, Pyrrhocorax pyrrhocorax*;
– short and pointed: *Corvus corax, C. corone, Pyrrhocorax graculus*;
– long and blunted: *Corvus monedula, Nucifraga, Pica*;
– long and pointed: *Garrulus*;
3.d the *apex lateralis* (lateral branch):
– short and blunted: *Garrulus*;
– short and pointed: *Corvus corone, C. monedula*;
– long and blunted: *Nucifraga, Pica, Pyrrhocorax pyrrhocorax*;
– long and pointed: *Corvus corax, C. frugilegus, Pyrrhocorax graculus*;
3.e the pit between the branches:
– shallow and symmetrical: *Corvus corone, C. monedula, Nucifraga, Pica, Pyrrhocorax pyrrhocorax*;
– shallow and unsymmetrical: *Corvus corax, C. frugilegus, Garrulus*;
– straight: *Pyrrhocorax graculus*;
3.f the shape of corpus:
– curved: *Garrulus, Nucifraga*;
– very wide: *Pyrrhocorax pyrrhocorax*;
– wide: *Corvus cornix; C. frugilegus*;
– moderately wide: *Corvus corax, C. monedula, Garrulus, Nucifraga, Pyrrhocorax graculus*;
– narrow: *Pica*;

4. *Humerus* (proximal *epiphysis*) *(Figure 6)*
4.a the *tuberculum ventrale*:
– strongly protruding: *Corvus, Pyrrhocorax graculus*;
– poorly protruding: *Garrulus, Nucifraga, Pica, Pyrrhocorax pyrrhocorax*;
4.b the projection of the *crista bicipitalis*:
– prominent and rounded: *Garrulus*;
– truncated: *Pica, Pyrrhocorax graculus*;
– rounded and not prominent: *Corvus, Nucifraga, Pyrrhocorax pyrrhocorax*;
4.c the distal edge of the *crista bicipitalis*:
– flatly curved: *Corvus corone, C. frugilegus, C. monedula, Nucifraga*;
– strongly curved: *Corvus corax, Garrulus, Pica, Pyrrhocorax pyrrhocorax*;
– straight: Pyrrhocorax graculus;
4.d the *fossa pneumotricipitalis*:
– split: *Corvus, Garrulus, Nucifraga, Pica, Pyrrhocorax*;

5. *Humerus* (distal *epiphysis*) *(Figure 7)*
5.a the *tuberculum supracondylare ventrale*:
– protuberant: *Corvus corax*;

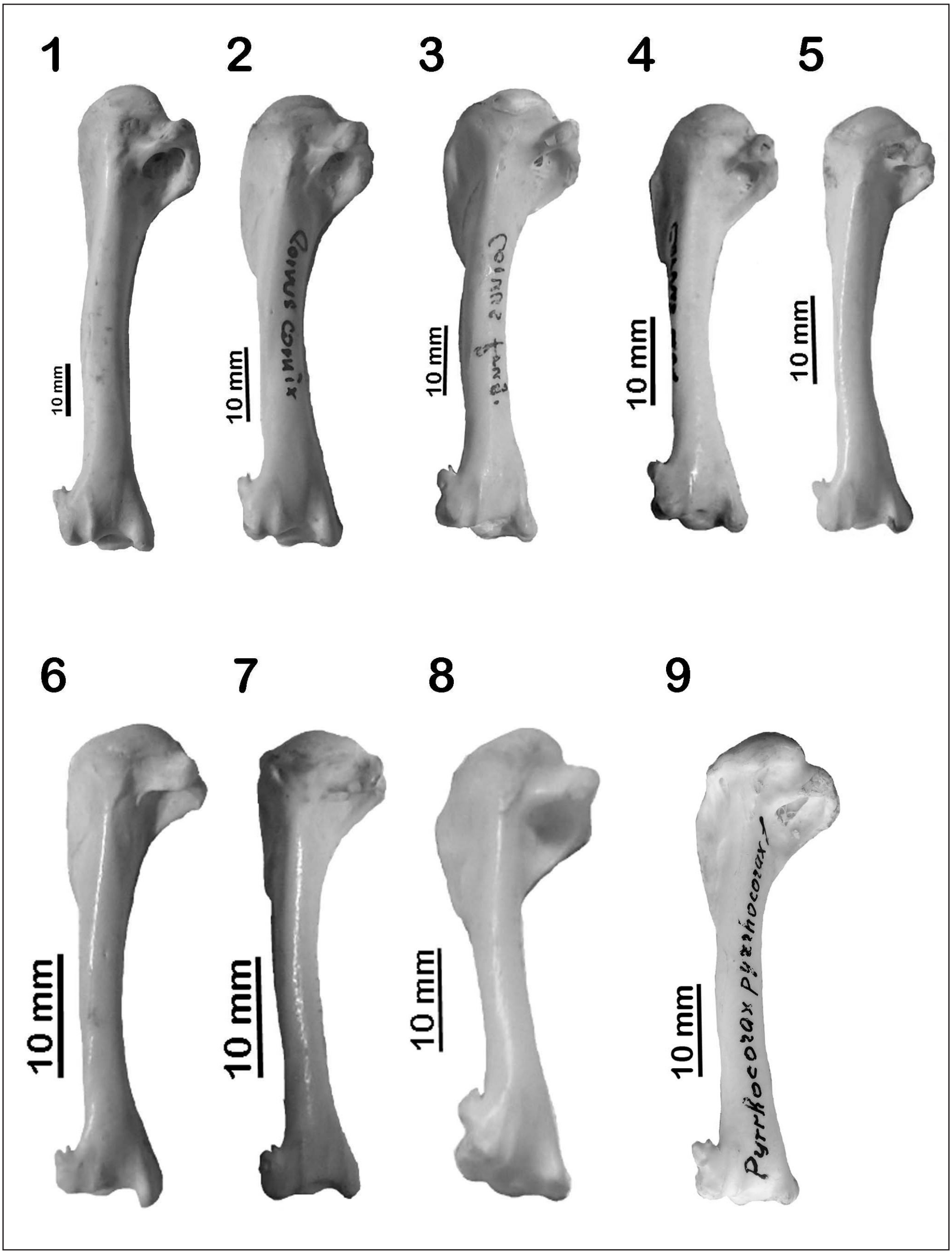


Figure 6. Left *humerus* (caudal surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

6. ábra Bal oldali felkarcsont (palmáris oldal): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

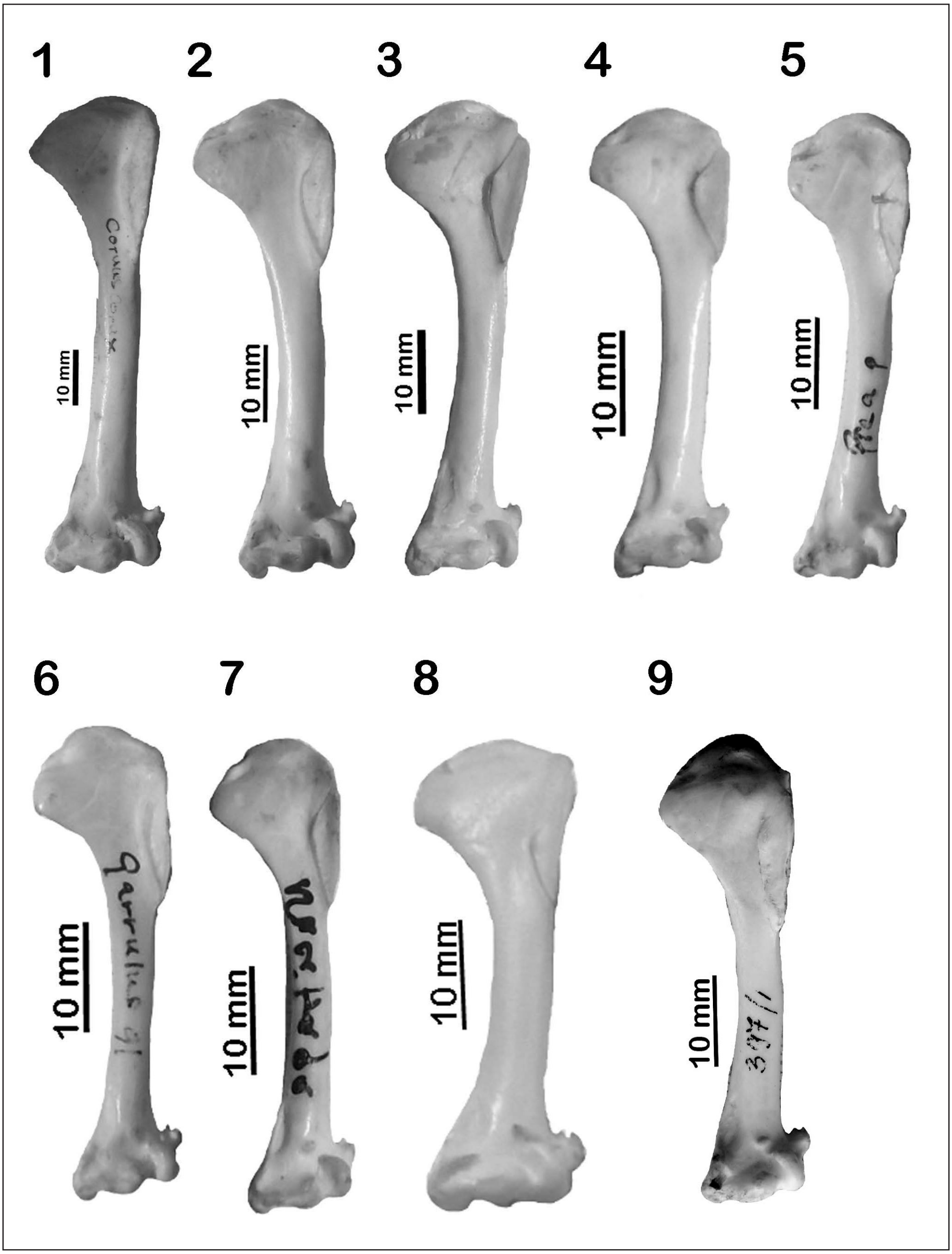


Figure 7. Left *humerus* (cranial surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

7. ábra Bal oldali felkarcsont (dorzális oldal): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

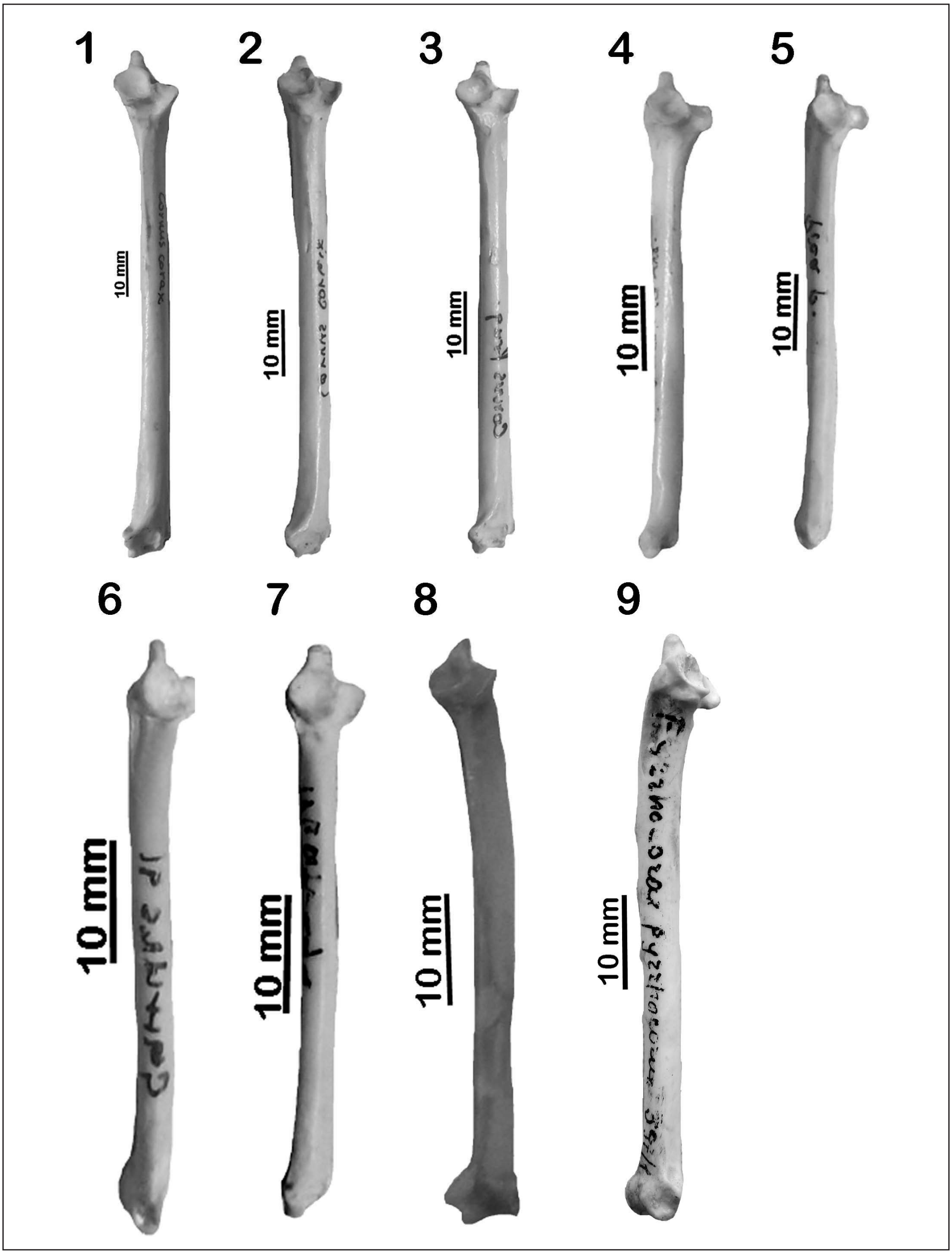


Figure 8. Left *ulna* (ventral aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

8. ábra Bal oldali singcsont (hasi nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

– not prominent: *Corvus corone, C. frugilegus, C. monedula, Garrulus, Nucifraga, Pica, Pyrrhocorax*;

5.b the *processus flexorius*:

– with rounded end: *Corvus frugilegus, Garrulus, Nucifraga, Pica, Pyrrhocorax graculus*;

– with truncated end: *Corvus corax, C. monedula, Pyrrhocorax pyrrhocorax*;

– with asymmetrical cone end: *Corvus corone*;

5.c the *condylus dorsalis*:

– rounded: *Corvus corax, C. corone, C. frugilegus, C. monedula, Garrulus, Nucifraga, Pica, Pyrrhocorax*;

5.d the *processus supracondylaris dorsalis*:

– two-pronged unequal: *Corvus corax, C. corone, C. frugilegus, C. monedula, Garrulus, Nucifraga, Pica, Pyrrhocorax*;

6. *Ulna* (proximal *epiphysis*) *(Figure 8)*

6.a the *olecranon*:

– short and blunt: *Corvus*;

– long and blunt: *Garrulus, Nucifraga, Pica, Pyrrhocorax pyrrhocorax*;

– asymmetrical and pointed: *Pyrrhocorax graculus*;

6.b the *cotyla dorsalis*:

– semicircular: *Garrulus*;

– conical asymmetrical: *Corvus corax, C. corone, C. frugilegus*;

– conical: *Nucifraga*;

– pointed conical: *Pyrrhocorax*;

– truncated: *Corvus monedula*;

– long and blunt: *Pica*;

6.c. the *tuberculum ligamentum collateralis ventralis*:

– developed: *Garrulus*;

– undeveloped: *Corvus, Nucifraga, Pica, Pyrrhocorax*;

7. *Ulna* (distal *epiphysis*) *(Figure 9)*

7.a the shape of the *condylus dorsalis*:

– pointed cone: *Corvus corone, Nucifraga*;

– blunted cone: *Corvus corax, C. frugilegus, Pica, Pyrrhocorax*;

– rounded: *Corvus monedula, Garrulus*;

7.b the shape of the *sulcus intercondylaris*:

– curved: *Corvus corax, C. corone, Garrulus*;

– asymmetrically curved: *Corvus frugilegus*;

– pointed: *Corvus monedula, Nucifraga, Pica, Pyrrhocorax*;

7.d the shape of the *condylus ventralis*:

– conical: *Corvus corone, C. frugilegus, Nucifraga, Pyrrhocorax graculus*;

– blunt cone: *Corvus corax, Garrulus*;

– rounded: *Corvus monedula, Pica*;

– semicircle: *Pyrrhocorax pyrrhocorax*;

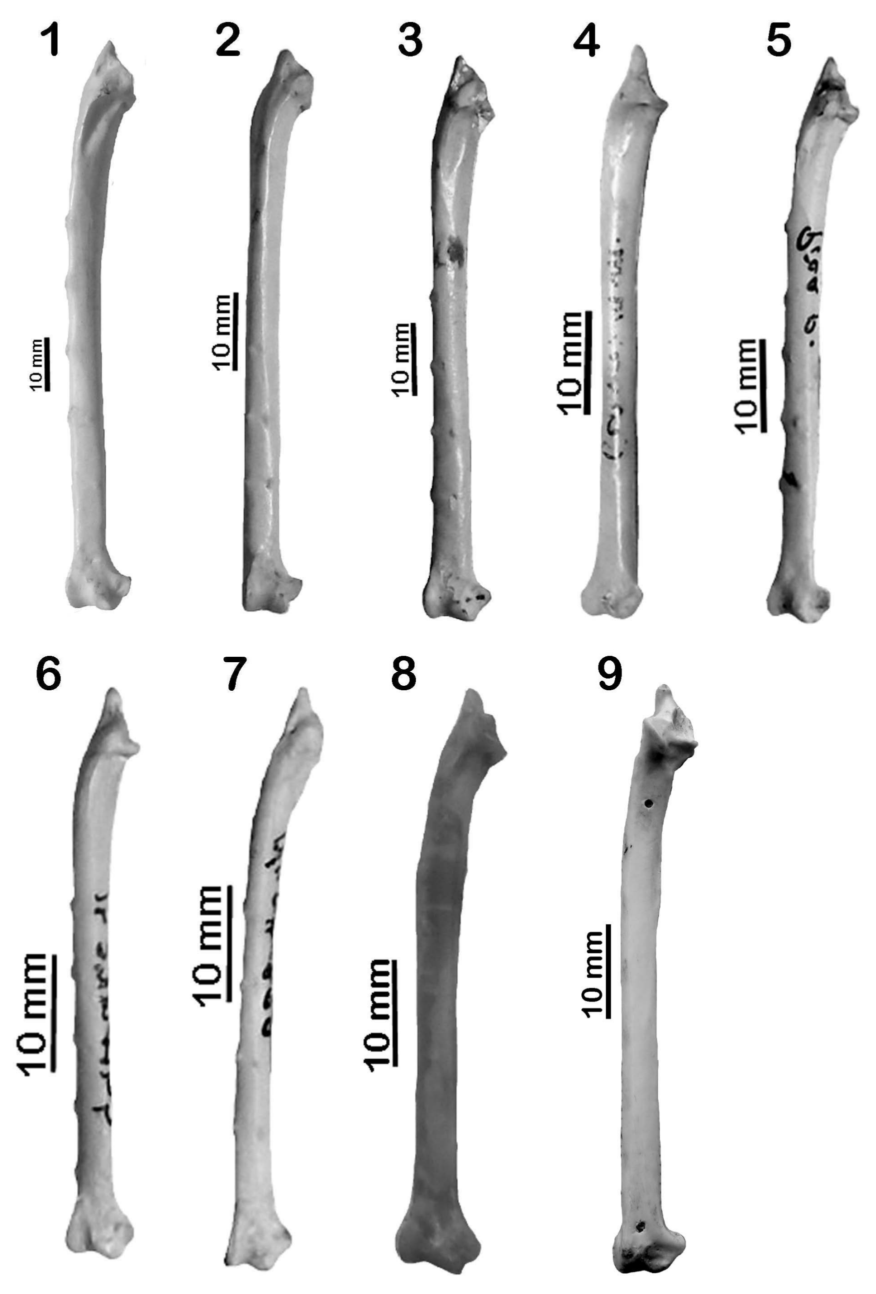


Figure 9. Left *ulna* (dorsal aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

9. ábra Bal oldali singcsont (háti nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

7.e the shape of the *tuberculum carpale*:
– semicircular: *Corvus modeula, Garrulus, Pyrrhocorax*;
– conical: *Corvus frugilegus, Nucifraga*;
– asymmetrical: *Corvus corax, C. corone*;
– truncated: *Pica*;

8. *Radius* *(Figure 10)*
8.a the shape of the *tuberculum aponeurosis ventralis:*
– conical: *Corvus corax; Garrulus glandarius, Nucifraga caryocatactes*;
– blunted cone: *Corvus corone, C. frugilegus, Pyrrhocorax pyrrhocorax*;
– rounded: *Pica, Pyrrhocorax graculus*;
– oblique rectangle: *Corvus monedula*;
8.b the shape of the *tuberculum aponeurosis dorsalis:*
– blunted cone: *Corvus corone, C. frugilegus, Garrulus, Pyrrhocorax pyrrhocorax*;
– symmetrical blunted cone: *Corvus corax, Nucifraga*;
– rounded: *Corvus monedula, Pyrrhocorax graculus*;
– semicircular: *Pica*;

8. *Carpometacarpus* *(Figure 11)*
8.a the shape of the a *trochlea carpalis*:
– semicircle: *Corvus frugilegus*;
– asymmetrically semicircle: *Corvus corax*;
– symmetrically cone: *Corvus corone, C. monedula*;
– symmetrically blunt cone: *Pyrrhocorax*;
– asymmetrically blunt cone: *Garrulus, Nucifraga, Pica*;
8.b the form of the *processus extensorius*:
– pointed cone: *Pyrrhocorax graculus*;
– slanting pointy cone: *Corvus corone, C. frugilegus*;
– leaning blunt cone: *Corvus monedula, Garrulus*;
– extension with rounded end: *Corvus corax, Nucifraga*;
– asymmetrically: *Pica, Pyrrhocorax pyrrhocorax*;
8.c the shape of the *processus alularis*:
– rectangular: *Corvus corone, C. frugilegus, C. monedula, Garrulus, Nucifraga, Pica, Pyrrhocorax*;
– rounded: *Corvus corax*;
8.d the form of the *fovea subalularis*:
– conical groove: *Corvus corax, Pica*;
– irregular conical groove: *Corvus mondedula, Nucifraga*;
– missed: *Corvus corone, C. frugilegus; Garrulus, Pyrrhocorax*;
8.e the shape of the *facies articularis digitale major*:
– rounded: *Corvus monedula, Garrulus, Pica, Pyrrhocorax*;
– straight: *Corvus frugilegus, Nucifraga*;
– oblique: *Corvus corax, C. corone*;

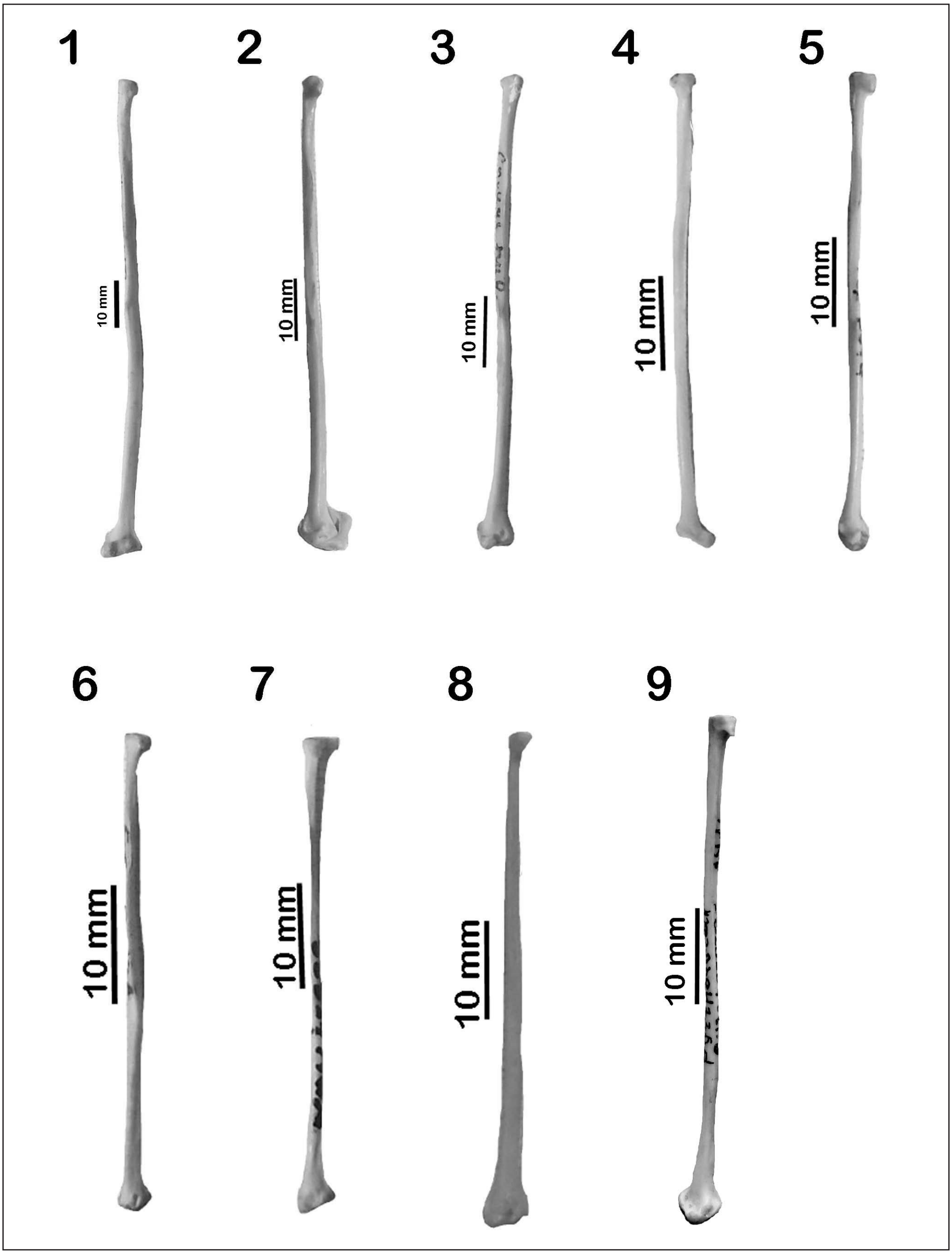


Figure 10. Left *radius* (dorsal aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

10. ábra Bal oldali orsócsont (háti nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

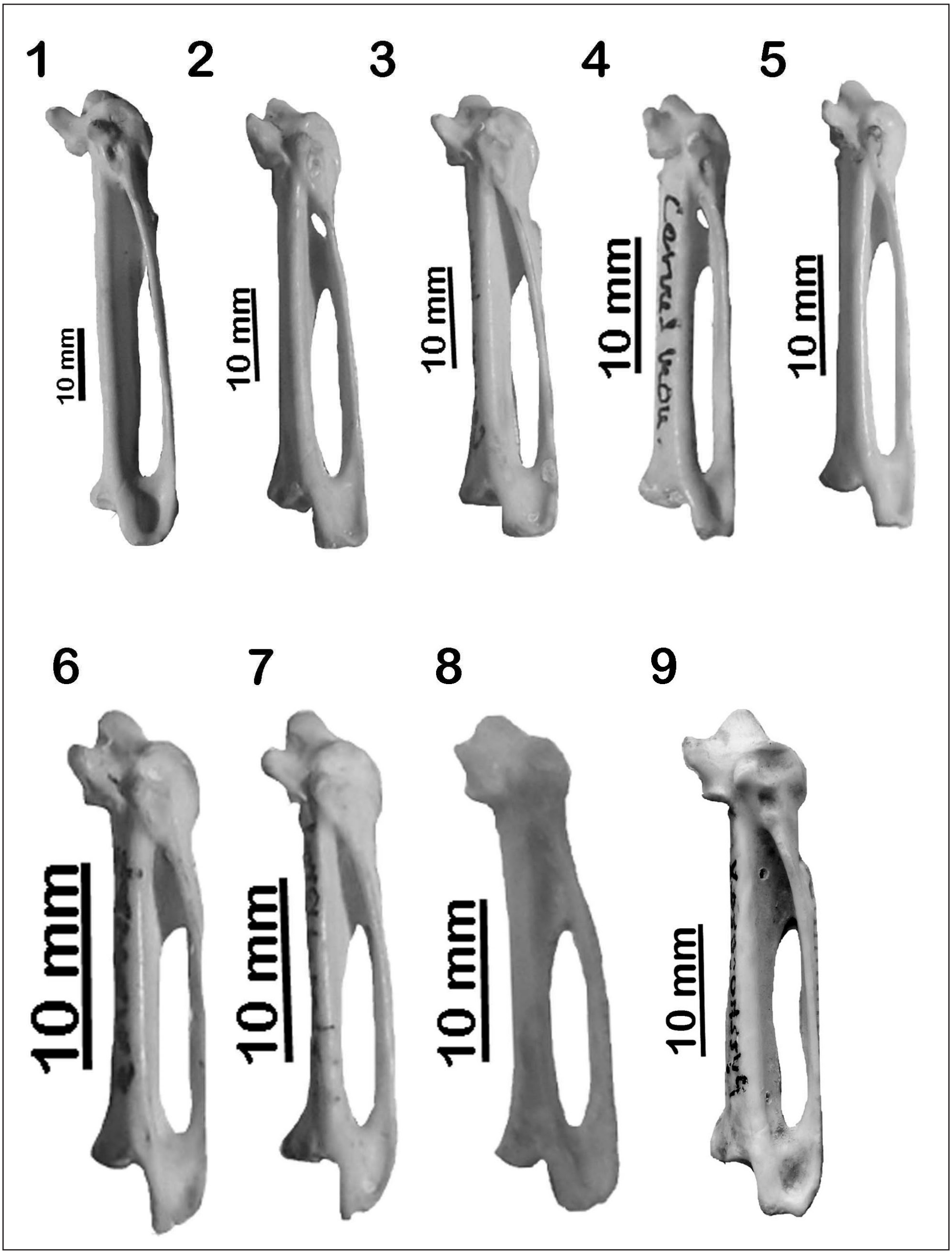


Figure 11. Left *carpometacarpus* (ventral aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

11. ábra Bal oldali kézközépcsont (hasi nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

8.f the shape of the *facies articularis digitale minor*:
– rounded: *Corvus corax, Pyrrhocorax graculus*;
– with cut-off end: *Corvus corone, C. frugilegus, Pica, Pyrrhocorax pyrrhocorax*;
– asymmetricall cone: *Garrulus, Nucifraga*;
– concave: *Corvus monedula*;

9. *Phalanx proximalis digiti majoris* *(Figure 12)*
9.a the form of the *margo proximalis*:
– strongly bulging: *Nucifraga*;
– weakly bulging: *Corvus corax, C. corone, Garrulus*;
– with a little protrusion: *Corvus frugilegus, Pyrrhocorax graculus*;
– flattened: *Corvus monedula, Pica, Pyrrhocorax pyrrhocorax*;
9.b the form of the *tuberculum ventralis*:
– rounded: *Corvus corax, C. corone, Pyrrhocorax graculus*;
– symmetrical blunt cone: *Corvus frugilegus, C. monedula, Pica, Pyrrhocorax pyrrhocorax*;
– asymmetrical blunt cone: *Nucifraga*;
9.c the form of the *tuberculum dorsalis*:
– pointed cone: *Pyrrhocorax*;
– symmetrical bunt cone: *Corvus corax, C. monedula, Nucifraga, Pica*;
– asymmetrical bunt cone: *Corvus corone, C. frugilegus*;
– semicircle: *Garrulus*;
9.d the character of the *margo dorsalis*:
– rounded: *Corvus corax, Pyrrhocorax pyrrhocorax*;
– straight: *Corvus corone, C. frugilegus, Pica, Garrulus*;
– wavy: *Corvus monedula, Nucifraga, Pyrrhocorax graculus*;
9.e the character of the *margo distalis*:
– rounded: *Garrulus*, *Pica*;
– wavy: *Corvus, Nucifraga, Pyrrhocorax*;

10. *Femur* (distal *epiphysis*) *(Figure 13)*
10.a the shape of the *condylus medialis*:
– semicircle: *Corvus*;
– blunt cone: *Garrulus, Pica, Pyrrhocorax*;
– pointed cone: *Nucifraga*;
10.b the character of the *sulcus intercondylaris*:
– deeply concave: *Corvus moedula, C. frugilegus, Pica, Pyrrhocorax*;
– weakly concave: *Garrulus, Nucifraga*;
– cone shaped: *Corvus corax, C. corone*;
10.c the shape of the *condylus lateralis*:
– broadly rounded: *Nucifraga*;
– rounded: *Corvus, Pyrrhocorax*;
– conical: *Garrulus, Pica*;

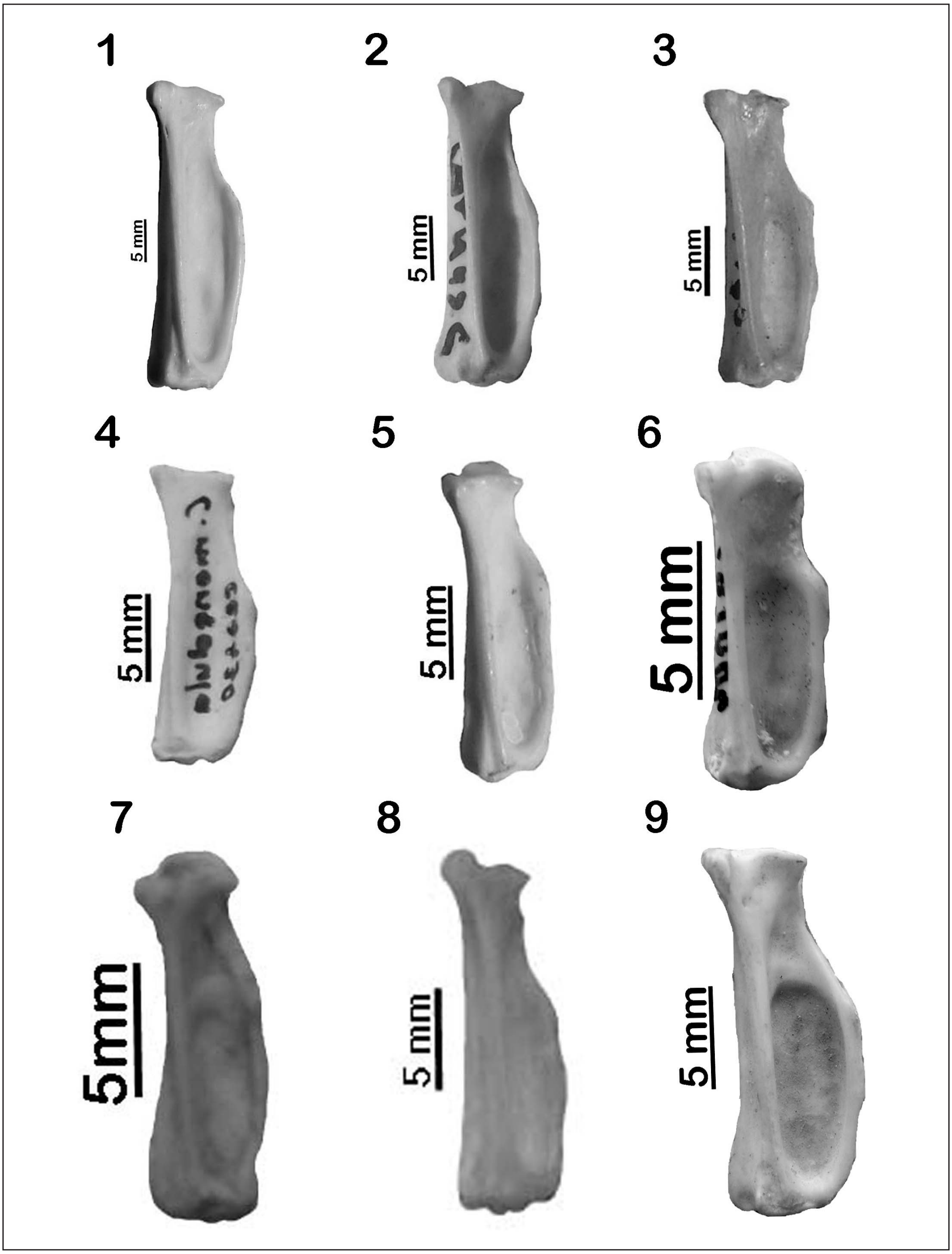


Figure 12. Left *phalanx proximalis digiti majoris* (ventral aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

12. ábra Bal oldali kézujjperc (I. ujjperc, 2. ujj, hasi nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

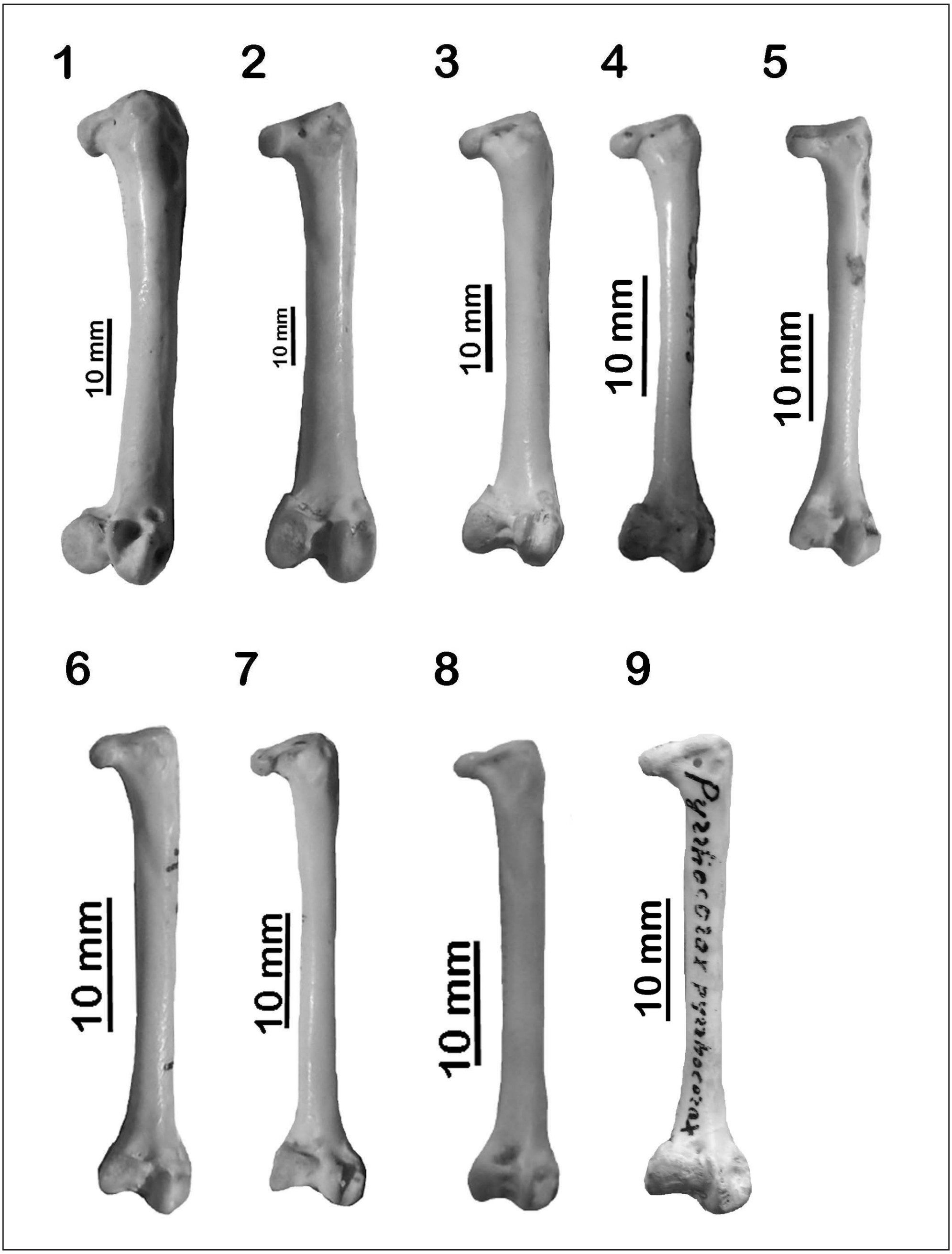


Figure 13. Right *femur* (caudal aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

13. ábra Jobb oldali combcsont (palmáris nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

10.d the form of the *epicondylus medialis*:
– pointedly protruding: *Corvus*;
– rounded protruding: *Nucifraga*;
– not arching: *Garrulus, Pica, Pyrrhocorax*;
10.e the form of the *epicondylus lateralis*:
– rounded protruding: *Nucifraga*;
– bulging: *Corvus, Garrulus, Pyrrhocorax*;
– not arching: *Pica*;

11. *Tibiotarsus* (distal *epiphysis*) *(Figure 14)*
11.a the shape of the *epicondylus lateralis*:
– rounded: *Corvus corone, G. frugilegus, Garrulus, Nucifraga, Pyrrhocorax*;
– semicircular: *Pica*;
– asymmetrical: *Corvus corax, C. monedula*;
11.b the form of the *incisura intercondylaris*:
– wavy: *Corvus corone, C. frugilegus, C. monedula*;
– asymmetrically arched: *Corvus corax, Pyrrhocorax*;
– asymmetrically wavy: *Garrulus*;
– flattened: *Nucifraga, Pica*;
11.c the character of the *tuberculum retinaculi musculi fibularis*:
– weakly protruding*: Corvus frugilegus, Pyrrhocorax*;
– strongly protruding: *Corvus corax, C. corone, C. monedula, Garrulus, Nucifraga, Pica*;

12. *Tarsometatarsus* (distal *epiphysis*) *(Figure 15)*
12.a the character of the *margo medialis*:
– straight: *Corvus corax, C. corone, C. monedula, Garrulus, Nucifraga, Pica, Pyrrhocorax*;
– concave: *Corvus frugilegus*;
12.b the shape of the *troclea metatarsi* II.:
– with cut-off end: *Corvus frugilegus, Pica*;
– with rounded end: *Corvus corax, C. monedula, Garrulus, Nucifraga*;
– conical: *Corvus corone, Pyrrhocorax*;
12.c the shape of the *trochlea metatarsi* III.:
– symmetrical shaped: *Corvus, Garrulus, Pica, Pyrrhocorax*;
– asymmetrical shaped: *Nucifraga*;
12.d the shape of the *trochlea metatarsi* IV.:
– conical: *Corvus frugilegus, Nucifraga*;
– blunt cone: *Corvus corone, Corvus monedula, Garrulus, Pyrrhocorax pyrrhocorax*;
– asymmetrically: *Corvus corax, Pica, Pyrrhocorax graculus*;

13. *Phalanx ungularis* *(Figure 16)*
Knowing that there are four claws on one leg and they are different, I do not give a detailed description.

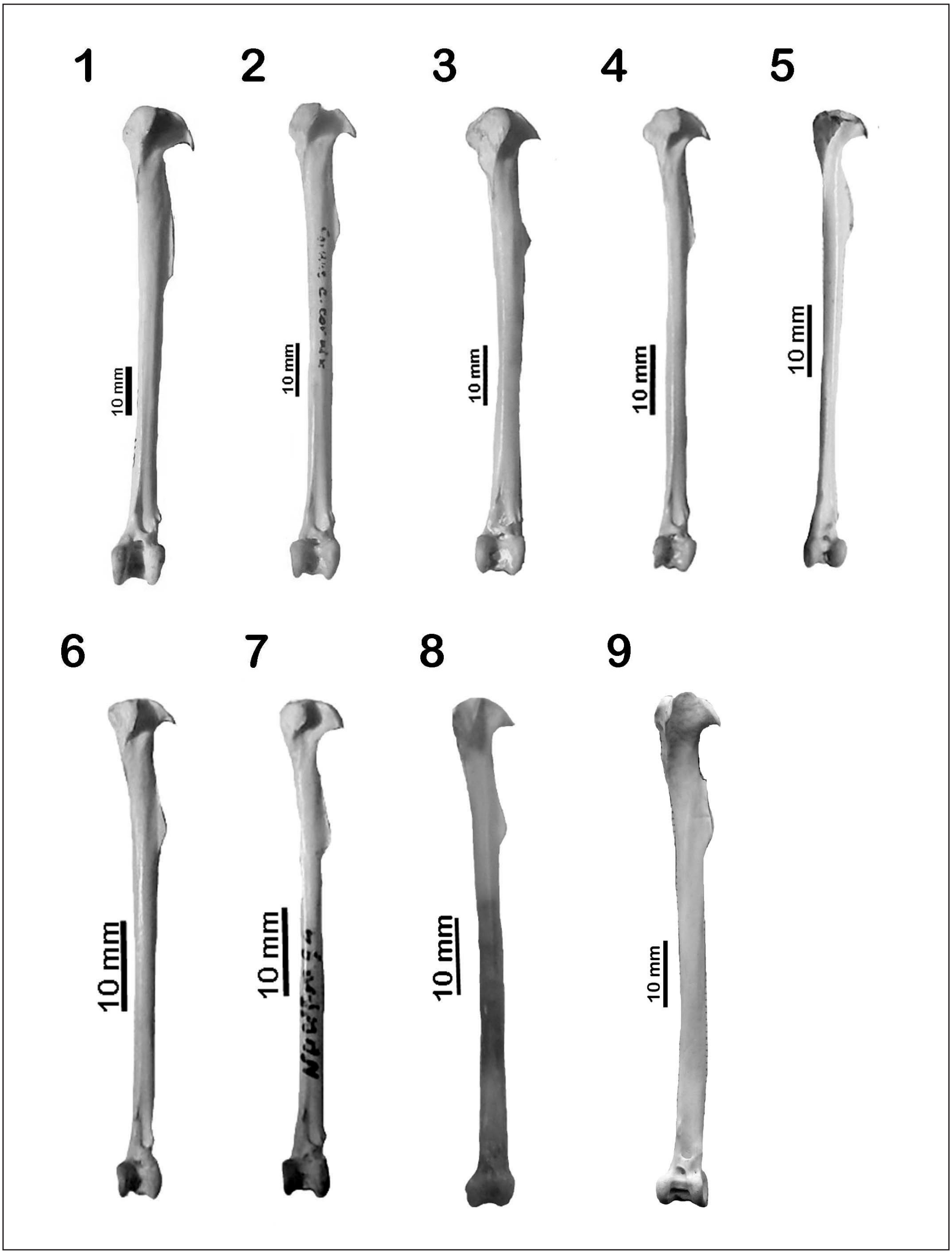


Figure 14. Left *tibiotarsus* (cranial aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

14. ábra Bal oldali lábszárcsont (dorzális nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

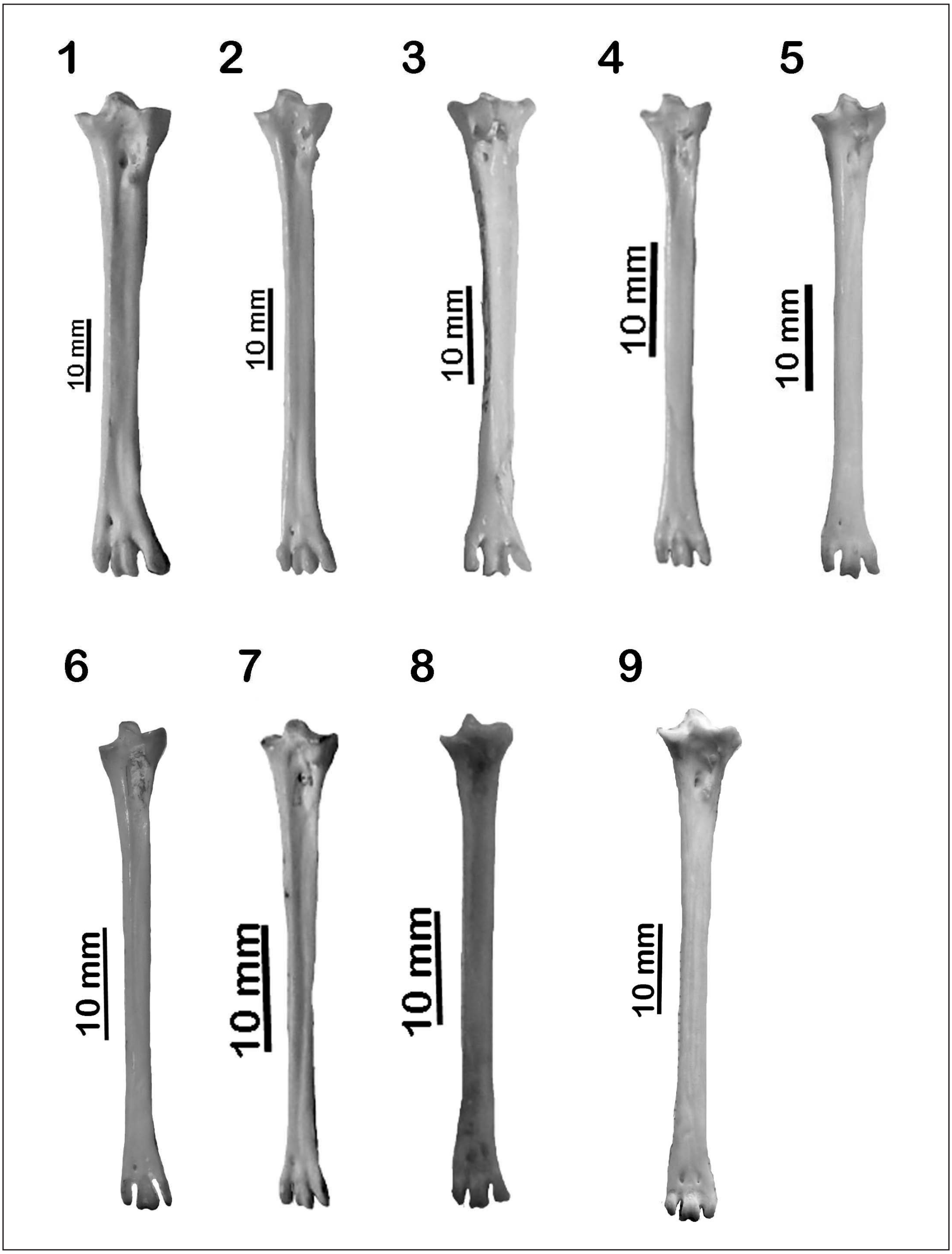


Figure 15. Right *tarsometatarsus* (dorsal aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

15. ábra Jobb oldali csüd (háti nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

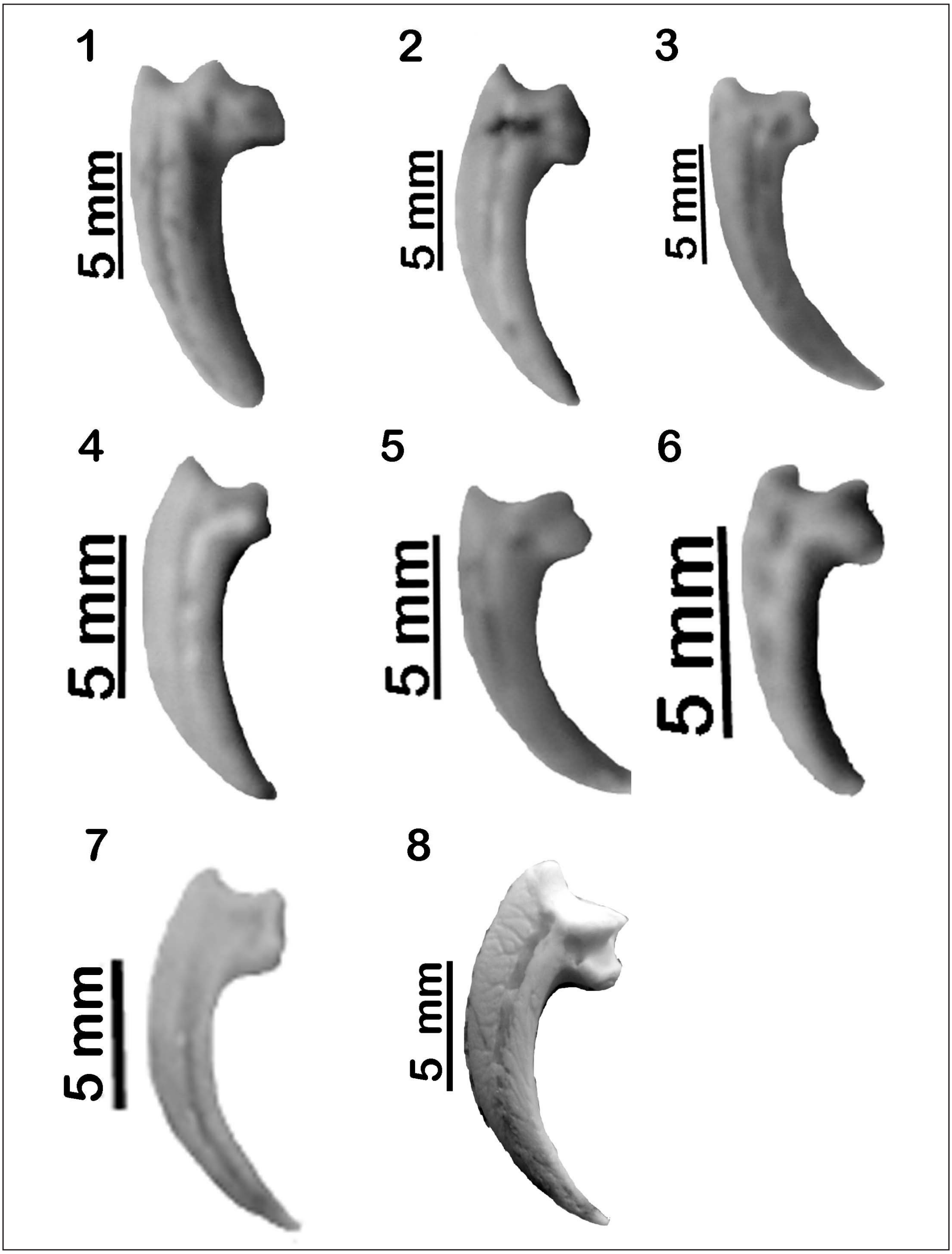


Figure 16. Phalanx ungualis (lateral aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Nucifraga caryocatactes*; 7. *Pyrrhocorax graculus*; 8. *Pyrrhocorax pyrrhocorax*

16. ábra Karomcsont (oldalsó nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Nucifraga caryocatactes*; 7. *Pyrrhocorax graculus*; 8. *Pyrrhocorax pyrrhocorax*

Systematics

Fam. Corvidae (Vigors, 1825) *(Table 1–6)*
Corvids are the largest songbirds in Europe, hence they are unmistakable with any other members of songbird families. They live from plains to snowy mountains. They have sedentary, as well as migratory, species. They nest in crevices of rocks or on trees. They are omnivores. Their species shift occurred mainly in the Pleistocene. They are well represented in fossilized materials both in species and in numbers. This is not only due to their large population, seasonal constancy and relatively slower flight, but mostly due to their remains that are large enough to be detected via traditional collection methods.

– *Corvus* Linnaeus, 1758
– *Corvus † pliocaenus* (Portis, 1889) / syn. *C. †betfianus* Kretzoi, 1962; *(Table 1)*

Site and era: Polgárdi, Upper Miocene (MN 13) (Hungary) (Kessler 2010); Beremend 26, Lower Pliocene (MN 15) (Kessler 2010); Beremend 15, 18, Upper Pliocene (MN 16) (Jánossy 1992, 1996); **Q1**: Beremend 16, 17 (Jánossy 1992, 1996) (all in Hungary); Betfia 9 (Gál 2002) (Romania); **Q2:** Betfia „Aven" (Kessler 1975, Jánossy 1979, Gál 2002), Betfia 5 (Kretzoi 1962, Kessler 1975, Jánossy 1979, Gál 2002) (all in Romania); **Q3**: Tarkő 2 (Jánossy 1979) (Hungary). From sites in Europe outside the Carpathian Basin **Q1-2:** Czech Republic, France, Germany, Spain; **Q3:** France (Tyrberg 1998).

We described a similar species, *Corvus simionescui* (Kessler, 1979) (Măluşteni-Bereşti, Romania, Lower Pliocene, MN 15) next to the Carpathian Basin, Mlíkovskỳ (2002) classified it to the recent *Corvus corone* species as well.

A common characteristic of taxa described with different names is that they range in size between crows and ravens. Mlikovskỳ (2002) classifies certain taxa *(C. antecorax, C. pliocaenus janossyi)* to ravens, while others *(Corvus pliocaenus, C. betfianus)* to the recent Hooded Crow *(C. corone)*. In our opinion, it is a transitional species that had gone extinct in the Middle Pleistocene. Due to the age and dimensions of the finds, we deem the species *Corvus pliocaenus* as valid. This is the oldest corvid of this size in Europe.

– *Corvus † hungaricus* Lambrecht, 1916 /syn. *C. antecorax* Mourer-Chauviré, 1975; *C. pliocaenus janossyi* Mourer-Chauviré, 1975

Site and era: **Q1:** Beremend 17 (Kessler 2010), Nagyharsányhegy 2 (all in Hungary) (Lambrecht 1916, Kessler 2010).

Material: distal end of right *humerus*, right *tarsometatarsus* (as holotype) (Nagyharsányhegy); distal end of *humerus*, 2 proximal end of *carpometacarpus*, proximal end of *femur*, 3 fragments of *tarsometatarsus* (1 proximale, 2 distale), (Beremend 17).

Dimensions: *tarsometarsus* A = 67 mm, C = 10 and 11.29 mm, E = 4.0 and 4.51, 4.27 mm, F = 8.67 and 7.94 mm, G = 5.26 and 4.56 mm; humerus C = 18.69 mm, D = 10.08 mm, F = 13.5 mm; *carpometacarpus* C = 12.68 and 12.36 mm, D = 6.91 and 6.94 mm.

It is a corvid with a lean skeleton and a size between crows and ravens. Mlikovskỳ (2002) suggests reevaluation of the taxon, which we conducted, and the results confirmed the original diagnosis. In addition, we found the proximal fragment of a humerus as well at the site of Nagyharsány mountain. Its identification from Beremend also confirms the reality of the taxon, and since other raven-sized species known from the fossilized and recent avian fauna of Europe were described later, we suggest keeping the taxon based on the principal of priority as well.

From Late Pliocene – Early Pleistocene and Middle Pleistocene of France (Senéze, Saint-Estéve-Janson, Lunel Viel, MN 17-18, **Q2** and **Q3**) the *Corvus antecorax* (Mourer-Chauviré, 1975) and *Corvus pliocaenus janossyi* (Mourer-Chauviré, 1975) finds of similar sizes are known (Mourer-Chauviré 1975).

– *Corvus* † *harkanyensis* Kessler, 2010

Site and era: Csarnóta 2, Upper Pliocene (MN 15-16) (Hungary) (Kessler 2010).

Material: distal end of right *humeus* – as holotype; distal end of left *tibiotarsus* – as paratype.

Dimensions: *humerus*: E = 4.90 mm; F = 11.53 mm; G = 5.89 mm; H = 6.20 mm; *tibiotarsus* E= 3.10 mm; F = 5.60 mm; G = 5.71 mm;

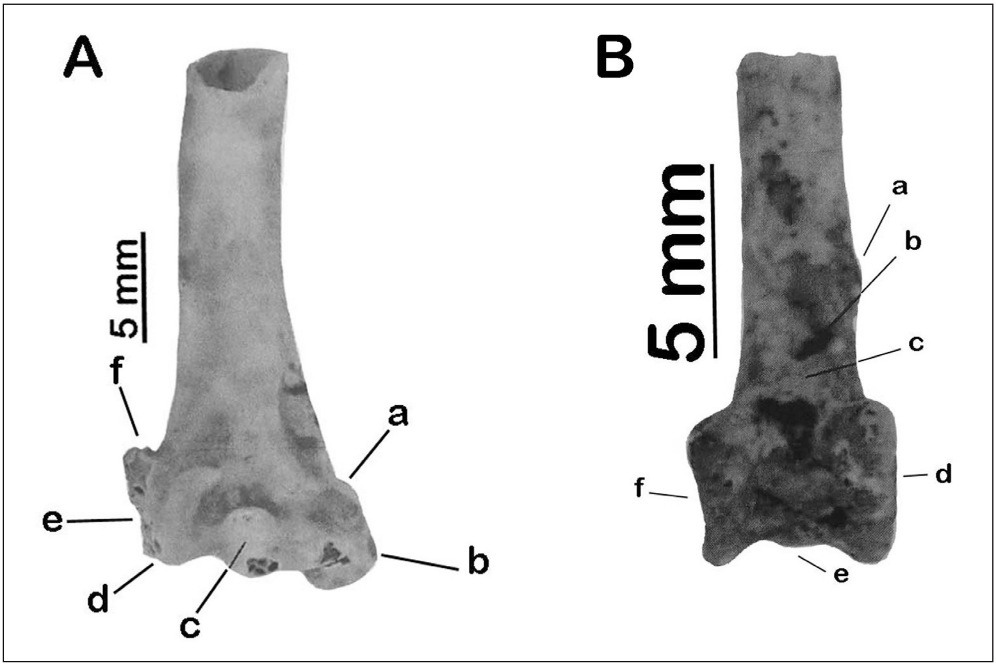


Figure 17. Corvus harkanyensis Kessler, 2010 – A. distal end of right humerus (holotype): a. *tuberculum supracondylare ventrale;* b. *processus flexorius;* c. *condylus dorsalis*; d. *condylus ventralis*; e. *epicondylus ventralis*; f. *processus supracondylaris dorsalis*; B. distal end of left *tibiotarsus* (paratype): a. *tuberculum retinaculum musculi fibularis*; b. sulcus extensorius; c. pons tendineus; d. *epicondylus lateralis*; e. *incisura intercondylaris*; f. *epicondylus medialis*

17. ábra *Corvus harkanyensis* Kessler, 2010 – A jobb oldali felkarcsont disztális vége (holotípus): a. *tuberculum supracondylare ventrale;* b. *processus flexorius;* c. *condylus dorsalis*; d. *condylus ventralis*; e. *epicondylus ventralis*; f. *processus supracondylaris dorsalis*; B. bal oldali lábszárcsont disztális vége (paratípus): a. *tuberculum retinaculum musculi fibularis*; b. sulcus extensorius; c. pons tendineus; d. *epicondylus lateralis*; e. *incisura intercondylaris*; f. *epicondylus medialis*

A corvid with the size of a Jackdaw, at the distal epiphysis of which in cranial view *(Figure 17A)* the tuberculum supracondylare ventrale (a) is more prominent than the present *Corvus* species, the *condylus ventralis* (c) is not ovoid but round in shape, the *epicondylus ventralis* (e), though damaged, is much wider and stouter, the *processus flexorius* (b) is curled up. On the distal end of the tibiotarsus *(Figure 17B),* in cranial view the end of the *sulcus extensorius* (c) above the *pons supratendineus* (b) is not rounded but has a pointed end (Kessler 2010).

Its name stems from the nearby town of Harkány. The fossilized species bearing characteristics and dimensions of the recent jackdaw was probably the ancestor of the form we see today in the Carpathian Basin.

Smaller *Corvus* species are only known from the Upper Pliocene (*C. cf. monedula*: Văršec Bulgária, MN 17; Boev 1995, 2000) among the avian fauna of Europe. From the Carpathian Basin and its immediate vicinity from the early Pleistocene of Stránská skála, Czech Republic, from where the *Corvus moravicus* (Mlikovskỳ 1995) extinct species was described, but the person describing it subsequently revoked it and reclassified the material as *C. monedula* (Mlikovskỳ 2002). The latter had been identified from several Middle and Upper Pleistocene sites (Jánossy 1979, Gál 2002).

– ***Corvus monedula*** **Linnaeus, 1758** / syn. *Corvus* cf. † *moravicus* Mlíkovskỳ, 1996

Q1: Betfia 2, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002); **Q1-2:** Betfia „Aven” (Kessler 1975, Jánossy 1979, Gál 2002) (all in Romania); **Q2:** Nagyharsányhegy 1-4 (Lambrecht 1916, 1933, Jánossy 1979) (Hungary); **Q3:** Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988) (Croatia); **Q4/I:** Merkenstein (Wettstein & Mühlhofer 1938), Mixnitz – Drachenhöhle (Lambrecht 1933) (all in Austria); Velika Pecina (V. Malez 1984, 1986, 1988) (Croatia); Bajót-Baits Cave, Bajót-Hóman Cave (Jánossy 1979), Csákvár-Eszterházy Cave (Lambrecht 1933, Kretzoi 1954, Jánossy 1979), Felsőtárkány-Peskő Cave (Lambrecht 1912, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986), Szilvásvárad-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986), Tata-Kálváriahegy no. 4. Cave (Gál 2004, 2005b), Tokod-Nagyberek (Jánossy 1979) (all in Hungary); Homoródalmási-Orbán Balázs Cave (Vîrghiş-Peştera Mare) (Kessler 1977, Gál 2002), Körösmart (Rîpa), (Jánossy in Hamar & Csák 1969, Kessler 1974b, Gál 2002), Nándor-Nándori Cave (Nandru-Peştera Curata) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II:** Bodajk-Rigólyuk (Kordos 1984), Budapest-Sas György Place, Csepel Vízművek (Gál 2015), Csákvár-Esterházy Cave (Kretzoi 1954), Felsőtárkány-Petényi Cave (Jánossy 1979), Legény-Cave (Lambrecht 1914), Szendrő-Felsővár (Gál 2015), Széchény (Gál 2015), Székesfehérvár-Sziget (Gál 2015) (all in Hungary); Bégakalodva (Cladova) (Gál 2004), Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Kisbács-Bácsitorok (Baciu, Gura Baciului) (Kessler 2013a), Körösbánlaki Cave (Peştera din Bălnaca) (Kessler 1982), Peterd-Tordai-Hasadék-Magyar Cave

(Petreşti, Cheile Turzii-Peştera Ungurească) (Kessler & Gál 1998, Gál 2004), Remetelórév-Bólyikői Cave (Lorău-Peştera din Piatra Boiului) (Kessler 1982); Révi caves (Peşterile din Vadu Crişului) (Kessler 1982), Székelykeresztúr (Cristuru-Secuiesc) (Gál 2008, 2015), Szkerisoara-Sasok Cave (Scărişoara, Peştera Vulturilor) (Kessler 1982, Jurcsák & Kessler 1986, 1988), Vársonkolyos-Izbîndiş Cave, Vársonkolyos-Kis Magyar Cave (Şuncuiuş, Peştera Izbîndiş; Peştera Napiştileu) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** Bulgaria, Czech Republic, France, Ukraine; **Q3:** Czech Republic, France, Germany, Spain, Ukraine; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, France, Germay, Greece, Ireland, Italy, Montenegro, Moldova, Poland, Portugalia, Russia, Schwitzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

[Note: Gál (2002) identifies the species as *C. † moravicus* from the Betfia 9 site, but Mlikovskỳ (2002) reclassifies the fossil taxon as *C. monedula* based on the Corvidae size database published by Kessler and Moldvai (1993). We find it necessary to distinguish between present jackdaws from the Upper Pliocene-Lower Pleistocene and Upper Pleistocene at least on a subspecies level, named *C. monedula † moravicus.*]

– *Corvus corax* Linnaeus, 1758

Q3/I: Hundsheim (Mlikovskỳ 2009) (Austria); **Q3/II:** Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I:** Velika Pecina (M. Malez & Rukavina 1975, V. Malez 1984, 1986, 1988) (Croatia); Bajót-Baits Cave, Bajót-Jankovich Cave (Jánossy 1979a, 1979b); Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Felsőtárkány-Peskő-Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Kesztölc-Bivak Cave (Jánossy 1979), Pilisszántói I. Cave Lambrecht 1915, 1933, Jánossy 1979, 1986), Répáshuta-Balla Cave (Lambrecht 1912a, 1912b, 1933), Tatabánya-Szelim Cave (Jánossy 1979a, 1979b) (all in Hungary); Nándor-Nándori Cave (Nandru-Peştera Curata) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II:** Felsőnyék-Várhegy (Gál 2004, 2015), Felsőtárkány-Petényi Cave (Jánossy 1979), Mélyvölgy (Jánossy 1979), Pilisszentkereszt, Szendrő-Felsővár (Gál 2015) (all in Hungary), Kazánszoros-Climente Cave (Cazanele Mari-Peştera Climente I) (Kessler 1981, Gál 2002); Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Kazánszoros-Icoana Cave (Cazanele Mari, Peştera Icoana) (Kessler 1985, Jurcsák & Kessler 1986, 1988), Kovászna (Covasna) (Bindea 2008), Körösbánlaki Cave (Peştera din Bălnaca) (Kessler 1982) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** Greece; **Q3:** Azerbaijan, Croatia, Czech Republic, France, Ukraine; **Q4:** Armenia, Austria, Belgium, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Italy, Montenegro, Moldova, Norway, Poland, Portugalia, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Corvus corone* Linnaeus, 1758

Q3: Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I:** Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Szilvásvárad-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986), Varbó-Lambrecht Kálmán Cave (Jánossy 1964, 1979) (all in Hungary); Körösmart (Rîpa) (Jánossy in Hamar & Csák 1969, Kessler 1974b, Gál 2002), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Rév-Pince Cave (Vadu Crişului, Peştera Pincelului) (Gál 2002) (all in Romania); **Q4/II:** Teufelslucke (Söergel 1966) (Austria); Bajcsa-Castle (Gál 2015), Balatonlelle-Kenderföldek (Gál 2005b), Felsővadász-Várdomb, Hajdúnánás (Gál 2015), Nagysomlyói Fosse (Kessler 2010) (all in Hungary); Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Körösbánlaki-Cave (Peştera din Bălnaca) (Kessler 1982), Peterd-Tordai-hasadék – Magyar Cave (Petreşti, Cheile Turzii-Peştera Ungurească) (Kessler & Gál 1998, Gál 2005a), Remetelórév-Bólyikői Cave (Lorău-Peştera din Piatra Boiului) (Kessler 1982), Révi caves (Peşterile din Vadu Crişului) (Kessler 1982), Szkerisoara-Sasok Cave (Scărişoara, Peştera Vulturilor) (Kessler 1982, Jurcsák & Kessler 1986, 1988), Vársonkolyos-Kis Magyar Cave, Vársonkolyosi caves (Şuncuiuş-Peştera Napisteleu-Peşterile din Şuncuiuş) (Kessler 1977, Gál 2002) (all in Romania); Padina (Classon 1980, Gál 2004) (Serbia). From sites in Europe outside the Carpathian Basin **Q3:** Azerbaijan, Croatia, Czech Republic, France, Germany, Greece, Spain; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Croatia, Czech Republic, France, Georgia, Germany, Italy, Malta, Portugalia, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Corvus frugilegus* Linnaeus, 1758

Q4/I: Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986) (all in Hungary); **Q4/II:** Bajcsa-Castle (Gál 2002, 2015), Balatonkeresztúr-Réti dűlő (Gál 2004), Bodajk-Rigólyuk (Kordos 1984), Endrőd 39 (Gál 2005a), Pilismarót-Malompatak (Jánossy 1985), Széchény (Gál 2015), Szendrő (Gál 2005b, Tassi 2006), Tác-Gorsium (Bökönyi 1984, Jánossy 1985), Visegrád-Palace (Gál 2015) (all in Hungary); Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Körösbánlaki Cave (Peştera din Bălnaca) (Kessler 1982), Vársonkolyosi caves (Kessler 1977, Gál 2002) (Şuncuiuş-Peşterile din Şuncuiuş) (all in Romania); Padina (Classon 1980, Gál 2004) (Serbia). **Q3:** Azerbaijan, Germany, Greece; **Q4:** Belgium, Bosnia-Herzegovina, Croatia, France, Germany, Greece, Ireland, Italy, Netherlands, Ukraine, United Kingdom (Tyrberg 1998).

– Corvus corone/frugilegus

Q4/II: Kaposújlak-Várdomb, Paks-Gyapa, Dombóvár-Tesco (Gál 2017);

[Note: there are only very small morphological differences between the skeletal parts of the Hooded Crow *(Corvus corone cornix)* and the Rook *(C. frugilegus)*, but the bones of the former species are slightly more robust. Incidentally, the subspecies – Carrion Crow, which is widespread in the western and southern parts of Europe, is also pure black, like the juvenile crow. The latter is rarely reported from fossil finds, probably because of the great similarity. Presumably, it occurs in many materials because the two species could not be separated. All indications are that a separation of the two species may have occurred recently, probably in the Holocene.]

– *Corvus* sp. foss. indet.

Site and era: Litke 2 (MN 5) (Kessler & Hír 2011), Polgárdi 4 (MN 13) (Jánossy 1991, 1995), Beremend 26 (MN 15) (Kessler 2010), Villány 3 (MN 16) (Kessler 2010) (all in Hungary).

[Note: material from the Neogene mostly consists of claws. Claws of corvids have a typical shape, but since there is a size difference between the four claws, and those belonging to species of more or less similar sizes cannot be reliably distinguished, we can only classify them to the genus level.]

– ***Corvus* sp. indet.**

Q1: Villány 5 (Kessler 2010), Beremend 17 (Jánossy 1991, 1992) (all in Hungary); **Q4/I:** Szárazgerence (Jánossy 1979, 1986), Varbó-Lambrecht Kálmán Cave (Jánossy 1964, 1979) (all in Hungary), Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas) (Lambrecht 1913, 1933) (Slovakia); **Q4/II:** Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Tatabánya-alsó – Törekvés Cave (Kessler 2010), Maroslele-Pana (Bökönyi 1964, Jánossy 1979, 1985, Gál 2005a, 2005b), Szolnok-Szanda (Jánossy 1985, Gál 2005a, 2005b) (all in Hungary).

Spread: From the Late Pliocene of Spain and Bulgaria (Puebla de Valverde, as well as Slivnica, MN 17-18) *Corvus* finds described to the genus level are known from the Neogene of Europe (Mlíkovskỳ 2002).

– **† *Miocorvus* Lambrecht 1933**

– *Miocorvus* † *larteti* (Milne-Edwards, 1871)

Site and era: Tasádfő (Tăşad, Romania), Middle Miocene (MN 7) (Gál & Kessler 2006, Kessler 2010); Mátraszőlős 3, Middle Miocene (MN 7/8); Rudabánya, Upper Miocene (MN 9) (Kessler 2010, Kessler & Hír 2012); Polgárdi 4, Upper Miocene (MN 13); Csarnóta 2, Beremend 26, Lower Pliocene (MN 15) (Kessler 2010) (all in Hungary).

Material: distal end of *humerus* (Mátraszőlős 3), distal end of *carpometacarpus*, *phalanx 1. digiti II. alae* (Csarnóta 2), 4 distal fragments of *tibiotarsus* (Rudabánya 3, Polgárdi 4, Beremend 26), 4 *phal. pedis* (Tasádfő).

Dimensions: *humerus* F = 10.11 mm; *carpometacarpus* F = 5.6 mm, G = 3.3 mm; *phal. alae* C = 3.36 mm, E = 4.69 mm, F = 3.43 mm; *tibiotarsus* E=2.49, 2.80 and 2.92 mm, F=5.44, 5.51, 5.65 and 5.78 mm, G=5.72 and 6.89 mm; *tarsometatarsus* F = 5.6 mm, G = 3.3 mm.

The small (jay-sized) crow described by Milne-Edwards (*Corvus larteti* Milne-Edwards, 1871) was renamed by Lambrecht (1933). We classified the material described by Jánossy (1979, 1997) from the Csarnóta 2 site here as well, but this is highly questionable due to the age difference.

Outside of the typical site (the Middle Miocene of France) (Sansan, MN 6) (Milne-Edwards 1871), it was also reported in 2006 from the Middle Miocene of Tășad, Romania (MN 7) (Kessler & Venczel 2009) and the Middle Miocene of Dobrogea as well, also in Romania (Credinţa, MN 8) (Gál & Kessler 2006).

– *Garrulus* Vieillot, 1816
– *Garrulus glandarius* (Linnaeus, 1758)

Q1: Németóvár 4B (Deutsch-Altenburg, Austria) (Jánossy 1981), Beremend 17 (Q1) (Jánossy 1992) (Hungary); Betfia 2, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002) (Romania); **Q1-2:** Betfia „Aven" (Kessler 1975, Jánossy 1979, Gál 2002), Kiskóh-Medvék Cave (Chişcău-Peştera Urşilor) (Kessler 1982) (all in Romania); **Q3/I:** Hundsheim (Mlíkovskỳ 1998, 2002) (Austria); Vindija (M. Malez 1961, V. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I:** Mixnitz-Drachenhöhle (Lambrecht 1933) (Austria); Krapina, Velika Pecina, Veternica (V. Malez 1973, 1984, 1986, 1988, V. Malez-Bačić 1979) (all in Croatia); Bajót-Baits Cave, Bajót-Hóman Cave (Jánossy 1979), Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Pilisszántói I. Cave **(**Lambrecht 1915, 1933, Jánossy 1979, 1986), Szilvásvárad-Istállóskői Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1952, 1955, 1979, 1986), Varbó-Lambrecht Kálmán-Cave (Jánossy 1964, 1979) (all in Hungary); Hidegszamos-Csont Cave (Someşul Rece) (Lambrecht 1915), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II:** Balatonkeresztúr-Réti dűlő **(**Gál 2004, 2015), Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Felsőtárkány-Petényi Cave (Jánossy 1979), Legény Cave (Kormos 1914), Miskolc-Felső-forrás, Anonym Cave (Kessler 2010), Rezi (Kessler 2009), Tatabánya-alsó – Törekvés Cave (Kessler 2010), Vác-Széchenyi street, Visegrád-Várkert (Gál 2015) (all in Hungary); Remetelórév-Bólyikői Cave (Lorău-Peştera din Piatra Boiului) (Kessler 1982), Révi caves (Peşterile din Vadu Crișului) (Kessler 1982), Szegyestel-Drăcoiaia Cave (Sighiştel, Peştera Drăcoaia) (Kessler 1982); Székelykeresztúr (Cristuru-Secuiesc) (Gál 2008, 2015), Vársonkolyos-Kis Magyar Cave (Şuncuiuş, Peştera Napiştileu) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** France, Germany; **Q3:** Czech Republic, France, Germany, Italy, Ukraine, United Kingdom; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Ireland, Italy, Luxemburg, Moldova, Poland, Portugalia, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Nucifraga* Vieillot, 1816
– *Nucifraga caryocatactes* Linnaeus, 1758

Q1: Betfia 9 (Gál 2002) (Romania); **Q3:** Vindija (M. Malez 1961, M. Malez & Rukavina 1979, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I:** Merkenstein (Wettstein & Mühlhofer 1938), Mixnitz-Drachenhöhle (Lambrecht 1933) (Austria); Bajót-Öregkő (Kormos 1914), Balla-Cave, Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Galgóc (Lambrecht 1915, 1933), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986) (all in Hungary); Barcarozsnyó (Peștera Gura Cheii-Râşnov) (Gál 1998, 2002), Szegyestel-Măgura Cave (Sighiştel, Peştera Măgura) (Kessler 1982, 1985, Gál 2002) (all in Romania); Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas) (Lambrecht 1913, 1933) (Slovakia); **Q4/II:** Teufelslucke (Soergel 1966) (Austria); Felsőtárkány-Petényi Cave (Jánossy 1979) (Hungary); Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a Fischer & Stephan 1977), Révi caves (Peşterile din Vadu Crişului) (Kessler 1982), Szkerisoara-Coiba Mare Cave (Scărişoara, Peştera Coiba Mare) (Kessler 1982), Jurcsák & Kessler 1986, 1988), Vársonkolyos-Izbîndiş Cave, Vársonkolyos-Kis Magyar Cave (Şuncuiuş, Peştera Izbîndiş, Peştera Napiştileu) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** Spain; **Q3:** Czech Republic, France, Germany, Italy, Ukraine; **Q4:** Austria, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Italy, Poland, Portugalia, Russia, Switzerland, Spain (Tyrberg 1998).

– *Pica* (Linnaeus, 1758)

– *Pica pica † major* Jánossy, 1979 *(Table 2)*

Site and era: **MN 15:** Beremend 26 (Kessler 2010), Csarnóta 2 (Jánossy 1979, Kessler 2010) (all in Hungary); **Q1:** Beremend 16, 17 (Jánossy 1992) (Hungary); Betfia 2, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002) (all in Romania); **Q2:** Betfia „Aven" (Kessler 1975, Jánossy 1977, 1979, Gál 2002) (Romania); **Q2:** Nagyharsányhegy 1-4 (Lambrecht 1916, 1933, Jánossy 1979) (Hungary); **Q3/I:** Hundsheim (Lambrecht 1933, Jánossy 1979) (Austria); Dorog-Hungáriahegy (Jánossy 1953, 1986, Jánossy & Vörös 1987), Vértesszőlős 2 (Jánossy 1979, 1990) (all in Hungary).

Mlikovskỳ (2002) classifies the fossil magpie species to the recent Western Jackdaw *(Corvus monedula)* based on the material from Stránská Skála classified by Jánossy (1972). When examining the fossilized material, we determined that this does not apply to the material from the Carpathian Basin, as the dimensional and morphological characteristics both refute this. Based on examination of the Csarnóta 2, Beremend 26 and numerous Lower Pleistocene materials, the validity of the fossilized subspecies is evident. The magpie characteristics, as well as the larger sizes than that of the present species, can be clearly shown. The present species is only known from the Middle Pleistocene of Europe, and is probably the direct descendant of the fossil subspecies.

Mourer-Chauviré (1975) also describes the fossil subspecies *(Pica pica major)* from the Middle Pleistocene (Saint-Estéve Janson, Lunel Viel, **Q3**), while the present species is only known from the Upper Pleistocene. Another magpie find described to the genus level (*Pica* sp.) is known from the late Pliocene of Bulgaria (Vāršec MN 17) (Mlikovskỳ 2002).

– *Pica pica* (Linnaeus, 1758)

Q3/II: Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I:** Mixnitz-Drachenhöhle (Lambrecht 1933) (Austria);

Bajót-Öregkő (Lambrecht 1914), Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Cserépfalu-Subalyuk Cave (Jánossy 1979); Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979a, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Kesztölc-Bivak Cave (Jánossy 1979), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986), Répáshuta-Balla Cave (Lambrecht 1912a, 1912b, 1933), Szilvásvárad-Istállóskői Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1952, 1955, 1979, 1986), Tatabánya-Kálváriahegy Cave no. 4. (Gál 2004, 2005b), Varbó-Lambrecht Kálmán Cave (Jánossy 1964, 1979) (all in Hungary); Körösmart (Rîpa) (Jánossy in Hamar & Csák 1969, Kessler 1974b, Gál 2002), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II:** Teufelslucke (Soergel 1966) (Austria); Budapest-Sas György square – Teleki Palace (Gál 2015), Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Felsőtárkány-Petényi Cave (Jánossy 1979), Ludas-Budzsák (Bökönyi 1974, Gál 2005a), Pilismarót-Malompatak (Jánossy 1985) (all in Hungary); Bégakalodva (Cladova) (Gál 2005a), Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Körösbánlaki Cave (Peştera din Bălnaca) (Kessler 1982), Remetelórév-Bólyikői Cave (Lorău-Peştera din Piatra Boiului) (Kessler 1982), Révi Cave (Peşterile din Vadu Crişului) (Kessler 1982), Vársonkolyosi caves (Peşterile din Şuncuiuş) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** Spain; **Q3:** Azerbaijan, Croatia, Czech Republic, France, Germany, Italy, Spain, Ukraine; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Croatia, Czech Republic, France, Georgia, Germany, Ireland, Italy, Montenegro, Moldova, Poland, Portugalia, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Pyrrhocorax* Vieillot, 1816

– *Pyrrhocorax graculus* † *vetus* Kretzoi, 1962 *(Table 3)*

Site and era: **MN 15:** Beremend 26 (Kessler 2010), Csarnóta 2 (Jánossy 1972) (all in Hungary); **MN 16:** Villány 3 (Kessler 2010 as *Pyrrhocorax pyrrhocorax*) (Hungary); **Q1:** Beremend 17 (Jánossy 1991, 1992) (Hungary); Betfia 2, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002) (Romania); **Q1-2**: Betfia „Aven" (Kessler 1975, Jánossy 1979, Gál 2002) (Romania); **Q2:** Betfia 5 (Kretzoi 1962, Kessler 1975, Jánossy 1979, Gál 2002), Kiskóh-Medvék-Cave 2 (Chişcău-Peştera Urşilor) (Kessler 1982, Jurcsák & Kessler 1988, Gál 2002) (all in Romania); Méhész (Vcelare) (Jánossy 1979) (Slovakia); **Q3/I:** Hundsheim (Lambrecht 1933, Jánossy 1979, Mlikovskỳ 1998, 2002) (Austria); Tarkő 3, 4 (Jánossy 1979) (Hungary); Gombaszög (Gombasek) (Kessler 2009) (Slovakia).

Mlikovskỳ (2002) classified the subspecies with different sizes and especially ratios to those of the present alpine chough. This is countered by the facts that on the one hand, the differences indicated by the diagnosis are clearly visible, and on the other hand, its subsequent characteristics can be associated with much earlier materials (Csarnóta 2, Beremend 17, and numerous other Lower and Middle Pleistocene sites). All this supports our opinion that this is a fossil subspecies, as well as the direct ancestor, of the present species.

– *Pyrrhocorax graculus* (Linnaeus, 1766)

Q3/II: Vindija (M. Malez 1961, V. Malez 1973, 1986, 1988, M. Malez & Rukavina 1979, Musil 1980) (Croatia); **Q4/I:** Merkenstein (Wettstein & Mühlhofer 1938), Mixnitz-Drachenhöhle (Lambrecht 1933) (all in Austria); Velika Pecina (M. Malez & Rukavina 1975, V. Malez 1984, 1988) (Croatia); Bajót-Öregkő (Kormos 1914), Bajót-Hóman Cave (Jánossy 1979), Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Cserépfalu-Subalyuk Cave (Jánossy 1979); Csobánka-Kiskevélyi Cave (Lambrecht 1912a, 1912b, 1915, 1933, Jánossy 1979), Kesztölc-Bivak Cave (Jánossy 1979), Pilisszántói I. Cave **(**Lambrecht 1915, 1933, Jánossy 1979, 1986), Szilvásvárad-Istállóskői Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1952, 1955, 1979, 1986), Vaskapu Cave (Mottl 1941) (all in Hungary); Barcarozsnyó (Gura Cheii-Cave, Râşnov) (Gál 1998, 2002), Hidegszamos-Csont Cave (Peştera cu Oase, Someşul Rece) (Lambrecht 1915), Măgura-Valea Coacazei Cave (Măgura-Peştera din Valea Coacăzei) (Gál 2002), Nándor-Nándori Cave (Nandru-Peştera Curata) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Peterd-Tordai-hasadék – Binder Cave (Cheile Turzii-Peștera Binder) (Kessler 1985, Gál 2002) (all in Romania); **Q4/II:** Knochenhöhle (Bocheński & Tomek 1994), Grosse Offenbergerhöhle (Bocheński & Tomek 1994), Hohlensteinhöhle (Bocheński & Tomek 1994), Tropfsteinhöhle, Tunnelhöhle (Fladerer 1993) (all in Austria); Felsőtárkány-Petényi Cave (Jánossy 1979), Hosszúhegyi Cave (Jánossy 1979b) (all in Hungary); Herkulesfürdő-Rablók Cave (Băile Herculane, Peştera Hoţilor) (Kessler 1981, Gál 2002), Kazánszoros-Climente Cave (Cazanele Mari, Peştera Climente I) (Kessler 1981, Gál 2002), Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** Bulgaria, Spain, Ukraine; **Q3:** Azerbaijan, Czech Republic, France, Georgia, Germany, Spain, Ukraine; **Q4:** Austria, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Italy, Montenegro, Poland, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

The present species is also known from the Late Pliocene of Bulgaria and Spain (Văršec and Meda Gran, MN 17) – these, however, supposedly belong to the fossil subspecies above – as well as from numerous sites in France and a few in Greece from the Lower and Middle Pleistocene. It can nowadays be found in the Alps, Pyrenees and the Balkan Peninsula (as well as the Upper Pleistocene and Holocene sediments of the caves located there) (Mlikovskỳ 2002).

– *Pyrrhocorax pyrrhocorax* (Linnaeus, 1758)

Q2: Nagyharsányhegy 1-4 (Kessler 2010) (Hungary); **Q3/I:** Hundsheim (Mlikovskỳ 2009) (Austria); **Q3/II:** Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); Solymár-Ördöglyuk (Jánossy 1979) (Hungary); **Q4/I:** Luegloch (Mottl 1953) (Austria); Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Répáshuta-Balla Cave (Lambrecht 1912a, 1912b, 1933) (all in Hungary); Körösmart (Rîpa) (Jánossy in Hamar & Csák 1969, Kessler 1974b, Gál

2002), Rév-Pince Cave (Vadu Crişului, Peştera Pincelului) (Gál 2002) (all in Romania); **Q4/II:** Grosse Offenbergerhöhle (Bocheński & Tomek 1994) (Austria); Kazánszoros-Törökiik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977) (Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** Spain, Ukraine; **Q3:** Azerbaijan, Czech Republic, France, Georgia, Spain, Ukraine; **Q4:** Austria, Bosnia-Herzegovina, Bulgaria, Croatia, France, Georgia, Greece, Italy, Luxemburg, Portugalia, Romania, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Perisorius* Bonaparte, 1831
– *Perisorius infaustus* Bonaparte, 1831
Q4/I: Répáshuta-Balla-Cave (Lambrecht 1912, 1933) (Hungary);

– **Corvidae gen. et sp. foss. indet.**
MN 15: Beremend 26 (Kessler 2010: as *Nucifraga caryocatactes*) (Hungary);

– **Corvidae gen. et sp. indet.**
Q2: Ürömhegy (Jánossy 1961, 1986); **Q4/I:** Tatabánya-Kálvária no. 4. Cave (Gál 2004, 2005b) (all in Hungary);

Conclusions

From the introduction of Corvids and by listing their finds from the Neogene and the Quaternary, it became evident that although their fossil and subfossil remains are frequent at several sites, the number of species is relatively low, both regarding extinct and present taxa.

Their classification is made harder – as it became evident when discussing osteology – by the fact that there is a large amount of morphological homogeneity, and identifying them is often only aided by size differences. It is no coincidence that on this basis, Mlíkovsky (2002) classified numerous known extinct species to present taxa or synonymizes.

Acknowledgements

The author wishes to express his deep gratitude to Mihály Gasparik for access in recent bird bone collection in the Natural History Museum of Hungary, to referees for their help in the revision of the text and to József Vuts and Lóránd Abos for the language revision.

Table 1. *Corvus* † *pliocaenus* (Portis), 1889
(Abbreviations: cor=*coracoideum*; scap=*scapula*; hum=*humerus*; rad=*radius*; cmcp=*carpometacarpus*; fem=*femur*; tib=*tibiotarsus*; tmt=*tarsometatarsus*; ph.a=*phalanga* 1. *digiti* II; ph. p.=*phalanga pedis*; ph.u.=*phalanga unguis*; x, xd=number of copies; A-G=see bone sizes)

1. táblázat *Corvus* † *pliocaenus* (Portis), 1889
(Rövidítések: cor=*coracoideum*; scap=*scapula*; hum=*humerus*; rad=*radius*; cmcp=*carpometacarpus*; fem=*femur*; tib=*tibiotarsus*; tmt=*tarsometatarsus*; ph.a=*phalanga* 1. *digiti* II; ph. p.=*phalanga pedis*; ph.u.=*phalanga unguis*; x, xd=példányszám; A-G=lásd: csontméretek)

Bones	**Total length**	**Partial length**	**Breadth prox.end**	**Thicknes prox.end**	**Breadth of corpus**	**Breadth distal end**	**Thickness dist.end**	**Other sizes**	**Localities**	**Source**
coracoideum	44.00								Beremend 17	Jánossy 1992
"	50.00								"	"
carpometacarpus	61.00								"	"
femur-exemplare	54.60–655.00								"	"
scapula		12.06	6.33	6.65	5.37				Betfia 5	Gál 2002
carpometacarpus						10.08			Betfia "Aven"	"
"								E1=4.00	Betfia 5	"
"			6.30						"	"
tarsometatarsus					4.90				"	"
coracoideum					4.65		11.38		Polgárdi 5	Kessler 2010
femur			11.26		5.11				"	"
coracoideum					4.49				Beremend 17	"
humerus					8.20	18.69	10.08		"	"
carpometacarpus			12.36	6.94					"	"
"			12.68	6.91					"	"
femur			12.00	7.98					"	"
ulna						11.42	8.01		Beremend 26	"
femur					4.75	11.05	8.88		"	"

Table 2. *Pica pica* † *major* Jánossy, 1979
(Abbreviations: cor=*coracoideum*; scap=*scapula*; hum=*humerus*; rad=*radius*; cmcp=*carpometacarpus*; fem=*femur*; tib=*tibiotarsus*; tmt=*tarsometatarsus*; ph.a=*phalanga* 1. *digiti* II; ph. p.=*phalanga pedis*; ph.u.=*phalanga unguis*; x, xd=number of copies; A-G=see bone sizes)

2. táblázat *Pica pica* † *major* Jánossy, 1979
(Rövidítések: cor=*coracoideum*; scap=*scapula*; hum=*humerus*; rad=*radius*; cmcp=*carpometacarpus*; fem=*femur*; tib=*tibiotarsus*; tmt=*tarsometatarsus*; ph.a=*phalanga* 1. *digiti* II; ph. p.=*phalanga pedis*; ph.u.=*phalanga unguis*; x, xd=példányszám; A-G=lásd: csontméretek)

Bones	**Total length**	**Partial length**	**Breadth prox.end**	**Thicknes prox.end**	**Breadth of corpus**	**Breadth distal end**	**Thickness dist.end**	**Other sizes**	**Localities**	**Source**
humerus			13.40						Hundsheim	Jánossy 1979
coracoideum				cca.7.50					Csarnóta 2	Kessler 2010
〃					2.13				〃	〃
〃					2.35				〃	〃
scapula		6.26	3.47	4.44	3.04				〃	〃
ulna			6.65		3.21				〃	〃
radius					1.81	4.48	2.51		〃	〃
phalanga 1. digiti II.	3.43		4.39						〃	〃
femur		7.54	4.03	3.51					〃	〃
tibiotarsus					3.50	5.52	5.76		〃	〃
phalanga pedis	6.70	2.55	1.24	1.71					〃	〃
〃	9.00								〃	〃
coracoideum			5.80						Beremend 17	〃
carpometacarpus	34.22	29.69	8.47	4.27		5.47	3.01		Baremend 26	〃
〃					cca. 7.00			E1=3.10	〃	〃
phalanga pedis	12.50	3.78	1.85	3.10					〃	〃

Table 3. *Pyrrhocorax graculus* †*vetus* Kretzoi, 1962
(Abbreviations: cor=*coracoideum*; scap=*scapula*; hum=*humerus*; rad=*radius*; cmcp=*carpometacarpus*; fem=*femur*; tib=*tibiotarsus*; tmt=*tarsometatarsus*; ph.a=*phalanga* 1. *digiti* II; ph. p.=*phalanga pedis*; ph.u.=*phalanga unguis*; x, xd=number of copies; A-G=see bone sizes)

3. táblázat *Pyrrhocorax graculus* †*vetus* Kretzoi, 1962
(Rövidítések: cor=*coracoideum*; scap=*scapula*; hum=*humerus*; rad=*radius*; cmcp=*carpometacarpus*; fem=*femur*; tib=*tibiotarsus*; tmt=*tarsometatarsus*; ph.a=*phalanga* 1. *digiti* II; ph. p.=*phalanga pedis*; ph.u.=*phalanga unguis*; x, xd=példányszám; A-G=lásd: csontméretek)

Bones	**Total length**	**Partial length**	**Breadth prox.end**	**Thicknes prox.end**	**Breadth of corpus**	**Breadth distal end**	**Thickness dist.end**	**Other sizes**	**Localities**	**Source**
carpometacarpus	36.20	33.20				8.20		E1=3.00	Betfia “Aven”	Kretzoi 1862
tibiotarsus					3.15	5.43	6.12		“	“
“					3.28	6.44	5.85		“	“
coracoideum	31.45	29.19	6.60	3.31	2.90				“	Gál 2002
humerus		20.64	12.82		4.70				“	“
ulna					4.16	7.73	5.57		“	“
“					3.65	7.60	4.82		“	“
radius			3.32	3.03					“	“
femur	37.81	35.95	7.15	4.08	3.20	7.24	5.41		“	“
“					3.40	7.89	5.74		“	“
“					3.30				“	“
tibiotarsus	65.20		7.53	6.74	3.45	5.84	5.64		“	“
“				6.76	3.00				“	“
tarsometatarsus					2.53				“	“
coracoideum					2.75		8.50		Betfia 2	“
ulna					3.87	7.00	4.70		“	“
tibiotarsus					3.00				“	“
“						6.22	5.05		“	“
tarsometatarsus					2.80				“	“
phalanga pedis	10.00	3.19	1.81	3.15					Betfia 9	“
“	9.50	3.65	2.00	3.29					“	“
humerus						10.84	5.78		Kiskóh 1	“
ulna	59.85	7.70	8.32	9.22	4.27	7.96	5.41		Gombaszög	Kessler 2010
femur			8.10	5.44	3.65				“	“
“						6.61	5.04		“	“
tibiotarsus						6.19	5.70		“	“

Table 4. Corvidae – *mandibula, coracoideum, scapula, humerus* dimensions
4. táblázat Varjúfélék – alsó állkapocs, hollócsőrcsont, lapocka, felkarcsont méretek

Bone (Figure 3–6)	***Corvus corax***	***C. corone***	***C. frugilegus***	***C. monedula***	***Pica pica***	***Garrulus gland.***	***Nucifraga caryoc.***	***Pyrrhocorax gr.***	***P. pyrrhocorax***
mandibula – A	96.00	70.00	72.00	51.00	49.00	49.00	65.00	53.00	
" – B	22.00	17.00	17.00	13.00	13.00	11.00	30.00	15.00	
" – C	14.00	11.00	10.00	11.00	9.00	8.00	13.00	10.00	
coracoideum – A	58.80	41.40–44.40	39.20–43.00	32.00–33.10	29.60–35.90	29.00–30.70	32.90	31,50–32.72	33.00–35.87
" – B	53.50	38.30–41.20	36.20–39.40	30.30–31.00	28.00–33.40	27.10–28.90	30.10	28.80–28.90	28.80–32.71
" – C	12.10	9.00–9.20	8.10–8.90	5.90–7.00	5.80–7.10	5.20	5.30	7.50	7.50
" – D	12.50	9.30–10.40	8.40–9.70	6.60–6.70	5.90–7.30	5.30–6.30	5.40	6.55–7.30	6.85–7.50
" – E	5.00	2.70–3.40	3.00–3.20	2.30–2.40	2.00–2.40	1.90–2.00	2.10–3.00	2.50	3.00
" – F	16.90	11.70–12.60	9.80–11.80	8.50–8.90	7.00–9.40	6.90–7.30	8.00	9.50–10.92	10.00–11.11
" – G	14.50	12.00	10.00	8.70	8.00	6.50	7.00	9.52	9.62
scapula – A	64.80	47.20–50.00	43.40–48.40	34.90–35.50	35.80–40.60	34.00–36.00	36.00	38.00–40.36	42.00–42.17
" – B	16.10	10.60–11.80	10.20–11.30	7.70–8.30	6.50–9.00	6.80–7.20	7.00	9.00–9.23	9.50–10.00
" – C	8.20	5.20–5.30	4.40–5.40	3.70–4.00	3.40–4.30	3.20–3.30	3.90	3.70	3.70
" – D	9.30	5.90–6.60	5.20–6.30	3.90–4.30	4.30–4.80	4.60–4.70	4.40	5.51	5.21
" – E	6.10	4.00–4.50	3.70–4.00	2.70–2.90	2.60–3.60	2.50	2.40	3.50–4.00	3.63–4.00
humerus – A	93.00	60.20–67.00	60.50–64.60	41.40–48.80	40.60–49.20	39.00–42.10	40.20–42.40	41.60–45.60	53.44–54.30
" – B	37.00	25.20–26.00	23.50–25.40	17.70–18.80	16.60–20.00	15.40–17.10	17.00	19.00–21.33	21.97–22.00
" – C	26.40	18.00–18.40	16.20–19.00	12.80–15.40	12.20–14.00	11.3–13.2	12.20–12.80	12.50–14.07	14.74–16.00
" – D	25.50	17.40–17.70	16.00–18.80	12.40–13.20	12.20–14.00	10.40–12.20	12.00	14.16	15.34
" – E	8.50	6.00–6.30	5.30–6.00	4.10–4.60	3.80–4.90	3.40–4.10	3.50–3.80	4.60–5.18	5.205.50
" – F	19.30	14.10–15.00	13.00–14.20	9.40–11.10	10.00–11.00	9.30–11.00	9.80–10.00	11.78–13.00	11.86–14.50
" – G	11.30	7.80–8.60	7.80–8.20	5.4–6.10	5.40–6.80	4.40–5.00	4.80	6.17	6.22
" – H	7.80	5.00	4.90	3.50	3.90	3.20	3.10	6.90	6.80

Table 5. Corvidae – *ulna, radius, carpometacarpus, phalanga* 1. *digiti* II. dimensions
5. táblázat Varjúfélék – singcsont, orsócsont, kézközépcsont, szárny 1. ujjperc, II. ujj méretek

Bone (Figure 7–10)	***Corvus corax***	***C. corone***	***C. frugilegus***	***C. monedula***	***Pica pica***	***Garrulus gland.***	***Nucifraga caryoc.***	***Pyrrhocorax gr.***	***P. pyrrhocorax***
ulna – A	112.40	76.50–81.40	73.00–79.80	56.70–58.20	51.00–61.30	48.00–50.30	49.80	57.00–59.09	66.67–68.00
" – B	13.80	9.20–9.80	8.40–9.90	6.80–7.10	6.40–7.40	6.20–6.30	6.20	7.87–8.00	8.30–9.00
" – C	15.80	10.00	9.10–10.70	6.80–8.20	6.80–8.90	6.70–7.10	7.00	8.20–8.47	8.69–9.50
" – E	6.70	4.80–5.00	4.40–5.00	3.20–3.50	3.00–3.70	3.00–3.40	3.10	4.00	4.29–4.50
" – F	12.80	9.10–9.40	8.30–9.50	6.40–6.60	6.90–7.20	5.70–6.00	6.20	7.00–7.82	8.129.00
" – G	9.30	6.40–6.90	6.20–6.60	4.60–5.20	4.30–5.20	4.20–4.40	4.30	5.00–5.41	5.81
radius – A	102.00	69.40–73.80	67.30–73.00	51.00–54.00	45.40–55.00	42.80–44.40	44.70	51.00–53.70	60.26–62.00
" – C	5.80	3.90–4.70	3.40–4.10	3.00–3.10	2.80–3.70	2.80–3.10	3.00	3.50–4.08	3.89–5.00
" – D	4.40	3.20–3.70	3.00–3.40	2.30–2.40	2.20–2.80	2.20–2.30	2.60	2.81–2.90	2.81–3.50
" – E	3.40	2.00–2.40	1.80–2.00	1.40–1.50	1.30–1.60	1.30–1.50	1.50	1.60–1.90	1.58–2.00
" – F	8.50	5.70–6.00	5.50–6.00	4.00–4.10	3.50–4.00	2.90–3.50	3.70	4.80–5.48	5.02
carpometacarpus – A	70.00	46.60–49.80	44.60–48.10	34.80–35.20	30.10–37.70	25.60–28.00	29.20	35.00–36.49	38.00–39.75
" – B	60.50	40.00–42.50	38.50–42.30	30.40–31.00	25.00–34.20	21.30–22.80	24.30	29.00–31.22	33.15–34.00
" – C	15.00	10.30–11.00	9.70–10.60	7.30–7.70	7.00–8.70	7.00–7.20	7.20	7.60–9.10	8.30–9.39
" – D	7.40	5.30–5.80	4.90–5.30	3.60–3.90	3.20–4.40	3.00–3.50	3.40	4.57	4.31
" – E	11.20	7.80–8.20	7.80–8.40	5.40–6.20	5.40–6.20	5.00–5.20	5.00	6.00–6.98	6.00–6.68
" – E1	5.80	3.90–4.00	3.50–4.20	2.70–3.00	2.40–3.10	2.40–2.60	2.50	3.35–3.50	3.30–4.00
" – F	15.30	10.00–10.50	9.80–11.00	7.10–7.70	6.40–8.00	6.00–6.30	6.30	8.50–8.81	9.22–9.50
" – G	7.00	4.50–4.60	4.00–5.00	3.10–3.20	2.80–3.70	2.50–2.80	3.10	3.65	3.90
phalanga 1. digiti II. – A	35.00	21.00	22.00	17.00	18.00	11.00	13.00	15.00	18.00
" – C	8.50	6.00	6.50	5.00	4.00	3.50	3.50	5.00	5.50
" – E	9.50	7.00	7.00	5.50	4.50	4.00	4.00	6.00	6.50
" – F	8.00	6.00	6.00	4.50	4.00	3.00	3.00	4.50	5.00

Table 6. Corvidae – *femur, tibiotarsus, tarsometatarsus* dimensions
6. táblázat Varjúfélék – combcsont, lábszárcsont, csüd méretek

Bone (Figure 11–13)	***Corvus corax***	***C. corone***	***C. frugilegus***	***C. monedula***	***Pica pica***	***Garrulus gland.***	***Nucifraga caryoc.***	***Pyrrhocorax gr.***	***P. pyrrhocorax***
femur – A	67.70	45.80–53.50	45.50–47.90	36.40–38.60	36.20–42.20	36.60–37.90	38.70	40.00–41.10	40.90–42.50
" – B	64.00	42.50–50.00	42.80–45.00	34.20–36.20	34.00–40.00	34.40–35.70	36.70	38.50–39.1	38.50–40.50
" – C	15.30	9.60–10.30	9.00–10.00	6.90–7.70	7.00–8.00	6.90–7.20	7.00	7.30–8.00	8.30–9.00
" – D	9.10	6.20–6.50	5.80–6.80	4.00–4.40	4.20–5.30	4.30–4.70	4.20	4.64–50	5.20–5.60
" – E	6.50	4.30–4.80	4.00–4.30	3.00–3.10	3.20–3.60	3.00–3.20	3.00	3.49–3.60	4.03
" – F	14.70	10.00–10.60	9.20–10.00	6.90–7.80	7.00–7.90	6.80–7.00	7.70	7.60–8.25	9.23–9.60
" – G	11.60	8.00–8.80	7.50–8.20	5.80–6.20	5.40–6.20	5.20–5.80	5.80	6.71–6.90	7.67–8.00
tibiotarsus – A	112.00	81.30–89.20	79.00–84.00	63.10–64.80	58.40–70.60	58.30–61.40	59.30	71.95–77.50	69.00–75.38
" – B	18.20	12.40–13.80	13.00	8.90–9.60	8.70–10.20	8.70–9.20	8.10	10.69–12.30	10.00–12.19
" – C	12.80	8.90–9.20	7.50–8.80	5.80–6.90	6.00–7.40	6.30–7.00	6.10	7.25–10.00	8.22–8.80
" – D	6.00	4.10–4.80	3.80–4.60	2.80–3.10	2.80–3.50	2.70–2.90	3.00	3.20	4.45–5.00
" – E	5.00	3.60	3.70	2.40	2.70	2.50	2.40	4.00	3.20
" – F	12.00	8.10–8.80	7.50–8.60	5.70–6.00	5.40–6.70	5.40–6.20	5.90	7.32–7.50	6.50–7.08
" – G	10.70	8.00–8.20	7.1–8.00	5.80–6.20	5.30–6.30	5.30–5.50	5.40	6.57–7.00	6.10–6.92
tarsometatarsus – A	66.00–69.00	51.40–60.00	51.20–55.00	41.20–44.10	40.80–50.20	40.50–43.50	40.70	44.80–47.65	51.00–56.50
" – C	12.00–13.20	8.80–10.00	8.30–9.30	6.10–6.90	6.50–7.10	5.90–6.20	6.20	7.04–7.50	8.48–9.50
" – D	12.20–14.00	8.60–9.30	8.60–9.60	6.20–7.50	6.90–7.50	6.60–7.20	6.00	6.70–7.88	8.00–8.45
" – E	4.80–5.00	3.40–3.80	3.00–3.40	2.30–2.70	2.30–2.70	2.10–2.40	2.30	2.80	3.02
" – F	9.20–9.50	6.80	6.00–7.00	5.10–5.20	4.20–4.70	4.20–4.70	4.60	5.51–5.66	5.90–6.00
" – G	5.50–6.00	4.00–4.40	3.50–4.20	2.80–3.10	2.80–2.90	2.80–2.90	3.00	2.89–3.00	3.35–3.50

References

Ballmann, P. 1966. Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt [The birds of the altburdigalen fissure filling of Wintershof (West) in Eichstaett]. – Inaugural Dissertation zur erlangung der Doktorwürde der nHohe Naturwissenschaftlichen Fakultät der Ludwig Maximiliane, Universität zu München, München (in German)

Baumel, J. J., King, A. S., Lucas, A. M., Breazile, J. E. & Evans, H. E. 1979. Nomina anatomica avium. – Academical Press, London

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

Bocheński, Z. M. & Tomek, T. 1994. Fossil and subfossil bird remains from five Austrian caves. – Acta Zoologica Cracoviensia 37: 347–358.

Boev, Z. N. 1995. Middle Villafranchian birds from Varshets (western Balkan range – Bulgaria). – In: Peters, D. S. (ed.) Acta palaeornithologica Courier Forschungsinstitut Senckenberg 181: 259–269.

Boev, Z. N. 2000. Neogene avifaunas of Bulgaria. – Vertebrata Palasiatica 38(Suppl.): 2–3.

Bökönyi, S. 1964. A maroslele-panai neolithikus telep gerinces faunája [The vertebrate fauna of the neolithic site of Maroslele-Pana]. – Archeológiai Értesitő 91: 87–93.

Bökönyi, S. 1984. Animal husbandry and hunting in Tác-Gorsium [The vertebrate fauna of the Roman town in Pannonia]. – Akadémiai Kiadó, Budapest

Brodkorb, P. 1978. Catalogue of fossil birds, Part 5. (Passeriformes). – Bulletin of the Florida State Museum, Biological Sciences 23(3): 139–228.

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

Cheneval, J. 1983. Révision de l'avifaune du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France) (Gaviiformes à Anseriformes) [Review of the avifauna of aquitanien deposit of Saint-Gérand-le-Puy (Allier, France) (Gaviiformes to Anseriformes)]. – Unpublished Thesis (Nr. 1380), Université Claude-Bernard, Lyon (in French)

Clements, J. 1974. The Clements Checklist of the Birds of the World. – Cornell University Press

Classon, A. T. 1980. Padina and Starcevo: game, fish and eattle. – Palaeohistoria 22: 142–173.

Cramp, S. (ed.) 1998. The Complete Birds of the Western Palearctic on CD rom. – Oxford University Press

Dickinson, E. C. & Christidis, L. (eds.) 2014. The Howard and Moore Complete Checklist of the Birds of the World, 4th ed., Vol. 2. Passerines. – Aves Press, Eastbourne, UK.

Driesch, A. von den 1976. A guide to the measurements of animal bones from archaeological sites. – Peabody Museum Bulletin 1: 148.

Fischer, K. & Stephan, B. 1977. Vogelknochenfunde aus Quartären Ablagerungen Südwestrumaniens [Bird bones from Quaternary deposits in South-west Romania]. – Annalen für Ornithologie 1: 79–90. (in German)

Fladerer, F. A. 1993. Neue Daten aus jung- und mittelpleistozänen Höhlensedimenten im Raum Peggau-Deutschfeistritz, Steiermark [New data from young and middle Pleistocene cave sediments in the area Peggau-Deutschfeistritz, Styria]. – Fundberichte aus Österreich 31: 369–374. (in German)

Fürbringer, M. 1888. Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stutz- und Bewegungeorgane [Studies on the morphology and systematics of birds, also contribute to the anatomy of the mounting socket and locomotor organe]. – Amsterdam, Jena (in German)

Gál, E. 1998. Avifauna fosila a pesterii Gura Cheii de la Râsnov (Jud Brasov) [Fossil avifauna of Gura Cheii cave in Râsnov (Jud Brasov)]. – Studia Universitatis Babes-Bolyai, Biologia 43 (1–2):88–93 (in Romanian)

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

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

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

Gál, E. 2005a. New evidence of fowling and poultry keeping in Pannonia, Dacia and Moesia during the period of the Roman Empire. – In: Gruppe, G. & Peters, J. (eds.) Feathers, grit and symbolism. Birds and humans in the Ancient Old and New Worlds. – Proceedings of the 5th Meeting of the ICAZ Bord Working Group, Munich, Germany, 26-30 July 2004. – Documenta Archaeobiologiae 3. Verlag Marie Leidorf GmbH.Rahden/Westf., 301–316.

Gál, E. 2005b. Animal remains from archaeological excavations in North-Eastern Hungary. – In: Gál, E., Juhász, I. & Sümegi, P. (eds.) Environmental archaeology in North-Eastern Hungary. – Varia Archaeologica Hungarica 19: 139–174.

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

Gál, E. 2008. A székelykeresztúri késő középkori udvarház állatcsontleletei [Animal bone remains from the late medieval manor house at Székelykeresztúr]. – In: Benkő, E. & Székely, A. (eds.) Középkori udvarház és nemesség a Székelyföldön [Medieval Manor House and Nobility in Székelyland]. pp. 301–355. Nap Kiadó, Budapest, Hungary (in Hungarian)

Gál, E. 2010. Animal remains from the multi-period site of Hasjdúnánás – Fürjhalom-dűlő. Part II. Finds from the Árpád Period (10TH–13TH Centuries) – Acta Archaeologica Academiae Scientiarum Hungaricae 61(2010): 425–444. DOI: 10.1556/AArch.61.2010.2.4

Gál, E. 2013. Bird bone remains from Bronz Age settlements in the Carpathian Basin. – In: Vicze, M, Poroszlai, I. & Sümegi, P. (eds.) Koszider: Hoard, Phase, Period? – Round table conference in the Koszider problem, „Matrica" Museum, Százhalombatta 2006, 193–205.

Gál, E. 2015. „Fine feathers make fine birds": the exploitaion of wild birds in medieval of Hungary. – Antaeus 33: 345–368.

Gál, E. 2017. Animals at the awn of metallurgy in south-western Hungary. Relationships between people and animals in southern Transdanubia during the Late Copper to Middle Bronze Ages. – Budapest: Institute of Archaeology, Research Centre forthe Humanities, Hungarian Academy of Sciences

Gál, E. & Kessler, E. 2006. Songbird remains from the Miocene (Middle Sarmatian) site Credinta (Dobrogea, South-East Romania). – In: Csiki, Z. (ed.) Volume dedicated to Dan Grigorescu on his 65th birthday. – University of Bucharest Printing House

Gilbert, B. M., Martin, L. D. & Savage, H. G. 1981. Avian Osteology. – Library of Congress, Wyoming

Hamar, M. & Csák, K. 1969. Contribuţii la cunoaşterea faunei de vertebrate pleistocene din Dealul Burzău (com. Rîpa, jud. Bihor) – jung Wurm [Contributions to the knowledge of pleistocene vertebrate fauna in Burzau Hill (Ripa, Bihor County) – jung Wurm]. – Studii şi cercetări. Biologice Seria Zoologie 21(6): 4–25.

Jarvis, E. D. *et al.* 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. – Sciences 346(6215): 1320–1331. DOI: 10.1126/science.1253451

Jánossy, D. 1952. Az Istállóskői barlang aurignaci faunája [The Aurignacian cave fauna from Istállóskő]. – Földtani Közlöny 82(4–6): 181–203. (in Hungarian)

Jánossy, D. 1954. Fossile Ornis aus der Höhle von Istállóskő [Fossile birds from the Istállóskő Cave]. – Aquila 55–58: 205–223. (in German)

Jánossy, D. 1955. Die Vogel-und Saugetierreste der Spätpleistozänen Schichten der Höhle von Istállóskő [The bird and mammalian remains of the Late Pleistocene Layers of the Istállóskő Cave]. – Acta Archaeologica Academiae Sciencentiarum Hungaricae 5: 149–181. (in German)

Jánossy, D. 1964. Letzinterglaziale Vertebratenfauna aus der Kálmán Lambreht Höhle (Bükk-Gebirge, Nordost Ungarn) [Vertebrate fauna in the end of interglacial from Kálmán Lambrecht cave (Bükk Mountains, northeast Hungary)]. – Acta Zoologica Hungarica 9: 139–197. (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. 1979. Plio-pleistocene Bird Remains from the Carpathian Basin. IV. Anseriformes, Gruiformes, Charadriiformes, Passeriformes. – Aquila 85: 11–39.

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. Humeri of central European smaller Passeriformes. – Fragmenta Mineralogica et Paleontologica 11: 85–112.

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

Jánossy, D. 1990. Vertebrate fauna of site II. – In: Kretzoi, M. (ed.) Vértesszőlős: site, man and culture, 187–229. – Akadémiai Kiadó Budapest

Jánossy, D. 1991. Late Miocene bird remains from Polgárdi (W-Hungary). – Aquila 98: 13–35.

Jánossy, D. 1992. Lower Pleistocene Bird Remains from Beremend (S-Hungary, Loc. 15. and 16.). – Aquila 99: 9–25.

Jánossy, D. 1995. A Late Miocene avifauna from Polgárdi, Western Hungary. – Acta Palaeornithologica, Courier Forschungsinstitut Senckenberg 181: 203–206.

Jánossy, D. 1996. Lower Pleistocene vertebrate faunas from the localities 16 and 17 of Beremend (southern Hungary). – Fragmenta Mineralogica et Paleontologica 18: 91–102.

Jánossy, D. & Vörös, I. 1987. Die mittelpleistozäne Fauna der Höhle des Hungária-Berges bei Dorog (Gerecse Gebirge, Ungarn) [The Middle Pleistocene fauna of the cave of the Hungaria Mountain near Dorog (Gerecse Mountains, Hungary)]. – Fragmenta Mineralogica et Paleontologica 13: 97–110. (in German)

Jurcsák, T. & Kessler, E. 1986. Evoluţia avifaunei pe teritoriul României (I) [Evolution of avifauna on Romanian territory (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 Romanian territory (III)]. – Crisia 18: 647–688. (in Romanian with English Summary)

Kessler, E. 1974a 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. 1974b 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. 1975. Contribuţii noi la studiul avifaunei fosile de la Betfia, jud. Bihor [New contributions to fossile avifauna from Betfia, Bihor County]. – Nymphaea 3: 53–59. (in Romanian)

Kessler, E. 1977. Avifauna postglaciară de la Vadu Crişului, jud. Bihor [Postglaciar avifauna from Vadu Crişului, Bihor County]. – Tibiscus 1977: 255–260.

Kessler, E. 1979. Noi date paleornitologice din pliocenul României [New paleornithological data from the pliocene of Romania]. – Nymphaea 7: 135–138. (in Romanian)

Kessler, E. 1981. Noi date privind avifauna pleistocenă a Văii Ierului (jud. Bihor) [New data on the Pleistocene bird fauna of Valea Ierului (Bihor County)]. – Nymphaea 8–9: 259–264. (in Romanian)

Kessler, E. 1982. Avifauna fosilă şi subfosilă a Munţilor Apuseni [Fossil and subfossil bird fauna from Apuseni Mountains]. – Nymphaea 10: 171–181. (in Romanian)

Kessler, J. 2010. Új eredmények a Kárpát-medence neogén és negyedidőszaki madár-világához III. [New results with regard to the neogene and Quaternary avifauna of the Carpathian Basin, Part III.]. – Földtani Közlöny 140(1): 53–72. (in Hungarian with English Summary)

Kessler, E. 2013a A Kárpát-medence madárvilágának őslénytani kézikönyve [Paleontological Handbook of birdlife in the Carpathian Basin]. – Könyvműhely, Miskolc, Hungary (in Hungarian)

Kessler, E. 2013b Neogene songbirds (Aves, Passeriformes) faunae from Hungary. – Hantkeniana 2013: 37–149.

Kessler, J. (E). 2015. Osteological guide of songbirds from Central Europe. – Ornis Hungarica 23(2): 62–156. DOI: 10.1515/orhu-2015-0009

Kessler, E. & Gál, E. 1997. Resturi fosile şi subfosile de păsări din Banat [Fossil and subfossil bird remains in Banat]. – Analele Banatului – Ştiinţele Naturii 3: 141–144. (in Romanian with English Summary)

Kessler, E. & Gál, E. 1998. Resturi fosile si subfosile de pasari in siturile paleolitice si neolitice din Cheile Turzii si Cheile Turenilor (Judetul Cluj) [Fossil and sub-fossil remains of birds in the Paleolithic and Neolithic sites of the Turzii Gorge and the Gorges of Tureni (Cluj County)]. – Angvistia 3: 9–122. (in Romanian)

Kessler, E. & Moldvai, M. 1993. Studii biometrice şi morfologice asupra scheletului membrelor la Corvidae (Aves) (Partea I) [Biometrical and morphological studies on limb skeleton at Corvidae (Aves) (Part I.)]. – Studia Universitatis Babes-Bolyai, Series Biologia 38: 69–80. (in Romanian)

Kessler, E. & Venczel, M. 2009. Bird remains from the Middle Miocene of Subpiatră (W-Romania). – Nymphaea, Folia Naturae Bihariae 36: 27–36.

Kordos, L. 1984. A bodajki Rigó-lyuk újholocén kitöltésének vizsgálata [Investigating the Holocene filling of the Bodajk-Rigó Hole]. – Folia Musei Historico-Naturalis Bakonyensis 3: 31–42. (in Hungarian)

Kormos, T. 1913. Kleinere Mitteilungen aus dem Ungarischen Pleistozän [Small releases from the Hungarian Pleistocene]. – Centralblatt für Mineralogie, Geologie und Palaeontologie, 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, 498–505., 531–540. (in Hungarian)

Kretzoi, M. 1954. Befejező jelentés a csákvári barlang őslénytani feltárásáról [Final report on the Paleontological Exploration of the Csákvár Cave]. – A Magyar Állami Földtani Intézet Évi Jelentése az 1952 évről, 37–69.

Kretzoi, M. 1962. Madár-maradványok a betfiai alsópleisztocén faunából [Bird remains in the Lower Pleistocene fauna from Betfia]. – Aquila 67–68: 167–174. (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 pleisztocénből [Fossil's Eagle Owl (*Bubo maximus* Flemm.) and other bird remains in Hungarian Pleistocene]. – Aquila 22: 177–187. (in Hungarian)

Lambrecht, K. 1916. Az első magyar preglaciális madárfauna – Die erste ungarische praglaziale Vogelfauna [The first Hungarian Preglaciale bird fauna]. – Aquila 22: 165–172. (in Hungarian and German)

Lambrecht, K. 1933. Handbuch der 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]. – In: Deveti jugoslavenski speleoloski kongres, Zbornik predavanja, 711–719. (in Croatian)

Malez, V. 1986. Paleoornitološka istrazivanja u našim krajevima [Paleornithological research in our region]. – In: Mestrov, M. & Sušić, G. (eds.) Ornitologija u Hrvatskoj, 205–212. (in Croatian)

Malez, V. 1988. Pleistocenska ornitofauna iz spilje Vindije u sjevernozapadnoj Hrvatskoj [Pleistocene bird fauna from Vindija cave in North-western Croatia]. – Rad Jugoslavenske Akademije Znanosti i Umjetnosti, Varazdin 2: 31–203. (in Croatian)

Malez-Bačić, V. 1979. Pleistocenska ornitofauna iz Šandalje u Istri te njezino stratigrafsko i paleoekološko značenje [Pleistocene bird fauna from Šandalja in Istria and its stratigraphic and paleoecological significance]. – Palaeontologia Jugoslavica 21: 1–46. (in Croatian)

Milne-Edwards, A. 1868. Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France [Anatomical and paleontological research to serve a history the fossil birds of France]. Vol. 1. – Victor Masson et Fils, Paris, 472+ pls 96 (in French)

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

Monroe, B. L. jr. & Sibley, C. G. 1993. A World Checklist of Birds. – New Haven and London, Yale University Press

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 Jahrbuche der Königlich Ungarischen Geologischen Anstalt 35: 13–39. (in German)

Mottl, M. 1953. Die Erfrorschung der Höhlen [The exploration of the caves]. – Jahrbuch Naturwiessenschaft Abteilung Johanneum, Graz, 19–58. (in German)

Mourer-Chauviré, C. 1975. Les oiseaux du Pléistocène moyen et supérieur de France [The Middle and Upper Pleistocene birds of France]. – Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 64: 1–624 (in French)

Musil, R. 1980. Die Grossauger und Vögel der Teufelsbrücke [The big auger and birds of the Teufelsbücke]. – In: Feustel, R. (ed.) Magdalenienstation Teufelsbrücke [Magdelenian Station Devil's Bridge]. – Weimarer Monographien zur Úr-und Frühgeschichte 3: 5–27. (in German)

Olson, S. L. & Rasmussen, P. C. 2001. Miocene and Pliocene birds 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 Neolithic Ecsegfalva 23 SE Hungary. – Journal of Taphonomy 2(4): 221–246.

Sibley, C. G. & Ahlquist, J. E. 1990. Phylogeny and classification of birds. – Yale University Press, New Haven

Solti, B. 1996. The comparative osteomorphological study of the European small-statured Falcons (Aves: Falconidae). – Folia Historico Naturalia Musei Matraensis 21: 5–282.

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, 93–107. (in German) Tassi, M. 2006. Szendrő-Felsővár állatcsontanyaga [Animal bone material form Szendrő-Felsővár]. – Visegrádi Múzeumok Közleményei 2006, 15–30.

Tomek, T. & Bocheński, Z. M. 2000. The comparative osteology of European corvids (Aves: Corvidae), with a key to the identification of their skeletal elements. – Instytutu Systematyki i Ewolucji Zwierząt PAN.

Tyrberg, T. 1998. Pleistocene birds of the Palearctic: a catalogue. – Cambridge, Mass.: Nuttall Ornithological Club, ix, 720. [Publications of the Nuttall Ornithological Club, No. 27.]

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)

Ornis Hungarica 2020. 28(1): 169–175.
DOI: 10.2478/orhu-2020-0010

Foraging Eurasian Jays *(Garrulus glandarius)* prefer oaks and acorns in central Europe

Cezary Mitrus[1,*] & Josif Szabo[2]

Received: December 14, 2019 – Revised: February 17, 2020 – Accepted: February 18, 2020

Mitrus, C. & Szabo, J. 2020. Foraging Eurasian Jays *(Garrulus glandarius)* prefer oaks and acorns in central Europe. – Ornis Hungarica 28(2): 169–175. DOI: 10.2478/orhu-2020-0010

Abstract The Eurasian Jay *(Garrulus glandarius)* is considered as the most important factor in the dispersal and spread of oak species. We conducted studies in oak stands in four countries (Poland, Hungary, Romania, Ukraine) in the autumn of 2015 and 2016. To identify the preferences of Jays for both acorns and trees, we compared the size of acorns and tree characteristics between each selected tree and the closest unused oak. We found that acorns from selected oaks were smaller (narrower) than those from unused trees. We found no differences in the characteristics of selected and unused oaks. These results indicate that the size of acorns can be an important indicator determining the choices of foraging birds. The Jays' preferences for specific trees may influence the composition of oak populations. Trees with certain phenotypic and genomic characteristics may be favoured and dominate in the ecosystem.

Keywords: dispersion, trees, birds, preferences, coevolution

Összefoglalás A szajkó *(Garrulus glandarius)* a legfontosabb faktornak tekinthető a tölgyfajok terjedésében. Vizsgálatainkat négy ország (Lengyelország, Magyarország, Románia, Ukrajna) tölgyeseiben végeztük 2015 és 2016 őszén. A szajkók tölgyfa és makk preferenciáinak vizsgálatához összehasonlítottuk a szajkók által választott fák és azok makkjainak jellemzőit a legközelebbi, nem választott tölgyfával és annak makkjaival. A madarak által választott makkok kisebbek (keskenyebbek) voltak a nem választott fák makkjaihoz képest. Más vizsgált jellemzőben nem találtunk különbséget a választott és nem választott tölgyfák között. Az eredmények rámutatnak arra, hogy a makkok mérete fontos indikátor lehet a madarak táplálékválasztásában. A szajkók preferenciái kihathatnak a tölgyállományok összetételére. Bizonyos feno-, illetve genotípusú fák kedveltebbek lehetnek, így uralhatják az ökoszisztémát.

Kulcsszavak: diszperzió, fák, madarak, preferenciák, koevolúció

[1] *Department of Vertebrate Ecology and Paleontology, Institute of Biology, Wrocław University of Environmental and Life Sciences, Chełmońskiego 38c, 51-631 Wrocław, Poland*
[2] *Str.Croitorilor 2/49, Odorheiu Secuiesc/Harghita 535600, România*
* *corresponding author*

Introduction

Animals are required for dispersing the seeds of many plant species in both the tropics and in temperate zones (Howe & Smallwood 1982, Jordano 2000). Based on the way in which seeds are transported, three categories of zoochory are usually distinguished: endozoochory – seeds are ingested by an animal and later regurgitated or defecated, epizoochory – seeds are accidentally attached to the outside of an animal body, for example, in the fur, and synzoochory – animals actively transport seeds and deposit them elsewhere (Jordano 2000, Hulme 2002, Will & Tackenberg 2008, Vander Wall & Beck 2012). In particular, birds play an important role in plant dispersion over long distance and this is a good example of synzoochory. In many cases, a very close association between animals and plants can be considered as coevolution (Pons & Pausas 2007). Mutualism, being advantageous both for birds and plants, is also observed (Pesendorfer *et al.* 2016). Thus, such a coexistence gives the opportunity to study relationships between birds and plants. The Eurasian Jay *(Garrulus glandarius)* is considered the most important factor in the dispersal and spread of oak *Quercus* species (Bossema 1979, Clayton *et al.* 1996, Perea *et al.* 2011, Kurek *et al.* 2018). Long distance dispersal of acorns is possible due to the ability of Jays to collect, carry and cache seeds in the ground (Bossema 1979, Mosandl & Kleinert 1998, Pons & Pausas 2007, Kurek & Dobrowolska 2016). Birds are selective and choose acorns for hoarding by visual means, mainly according to the colour and size (Bossema 1979, Pons & Pausas 2007, Richardson *et al.* 2013, Bieberich 2016). However, few studies addressed the selection of acorns by Jays (Bossema 1979, Pons & Pausas 2007, Myczko *et al.* 2014, Bieberich 2016) and knowledge on the characteristics of trees selected for foraging is lacking.

The aim of this study was to determine the foraging preferences of Jays in relation to the characteristics of oaks and acorns in central Europe. We tested the following hypotheses: Jays collect acorns from specific trees, oaks and acorns selected by birds differ from unused trees, location (country) does not influence the characteristics of trees and acorns.

Materials and methods

Study area

Observations were made in four countries (Poland, Hungary, Romania, Ukraine) in oak stands on lower (250–450 m above sea level) parts of the Carpathian region. In Poland, the studies were conducted in the oak forest near Kalwaria Pacławska (49°38’44.5”N, 22°41’48.5”E) – 30 ha, in Hungary in the Bükk National Park in the vicinity of Cserépfalu (E 47°58’00.0”N, 20°33’47.6”E) – 20 ha, in Ukraine close to Ivanivka (48°53’18.0”N 24°06’03.1”E) – 30 ha and in Romania near Homoródújfalu (46°07’50.8”N 25°24’56.1”E) – 20 ha. In the cases of Romania and Hungary, the oak stands were within pasture with the trees usually (only oaks) growing at low density. Herds of cattle and sheep grazed beneath the trees. In the case of Hungary, turkey oaks *(Quercus cerris)* dominated in the stands with only single individuals of pedunculate oak *(Quercus robur)*, also present.

In Poland and Ukraine, trees in abandoned (20–30 years ago) wood-pastures had expanded to produce mixed forest, where beside stands of pedunculate oak, there were also stands of other trees: hornbeam *(Carpinus betulus)*, beech *(Fagus sylvatica)*, sycamore *(Acer pseudoplatanus)*, small-leaved lime *(Tilia cordata)*, norway spruce *(Picea abies)*, European silver *(Abies alba)* and in the lower layers, common hazel *(Corylus avellana)*.

Field data collection

The observations were carried out in two autumn seasons (2015 in Poland and Ukraine, 2016 in Hungary and Romania) in October and November. The total observation time amounts 42 days (20 days in 2015 and 22 days in 2016). Trees used by birds were located in oak stands or pastures with solitary trees by observations of flying Jays. Only oaks where foraging Jays were observed at least twice were used in the analysis. The following information was then collected: characteristics of the selected tree (species, trunk circumference at height of 1.5 m, height of tree, radius of crown) and habitat characteristics (inside forest or in open area in the case of solitary oaks). The same characteristics were recorded for the nearest oak with acorns but not used by Jays. In the case of open areas, only unused oaks within 20 m were included in analysis. Additionally, the characteristics of fallen acorns under oaks were described. From the ground under each used and the closest unused oak, 50 randomly selected (without signs of infestation by insects) acorns were collected. After drying in the laboratory, they were measured using sliding callipers by one person (CM) recording length and width (in mm).

Statistical analyses

For comparisons of two groups of data the Mann–Whitney U test was used. To determine factors affecting the Jay's choice, Generalized Linear Model (GLM) with binominal distribution and logit function were constructed where: biometric traits of acorns and country (place of observation) were used as independent factors. Because of the number of data, this model was used only in the case of pedunculate oaks. All statistical analyses were undertaken using Statistica for Windows v.13.3.

Results

Jays used two species of oaks: *Quercus robur* in the studies in Poland, Ukraine and Romania, and *Q. cerris* in the case of study in Hungary. In total, 421 visits of Jays were observed. We characterised 25 (5 from Ukraine, 6 from Poland, 6 from Romania and 8 from Hungary) used and 12 unused oaks (3 from Ukraine, 2 from Poland, 3 from Romania and 4 from Hungary). We did not find differences in the parameters (height, size of crown and diameter of trunk) of selected and unused trees *(Table 1)*. The oaks which were used by foraging Jays in open areas were significantly shorter in height and had bigger crowns

Table 1. Characteristics of oaks selected and unused by Jays
1. táblázat A szajkók által használt és nem használt tölgyek jellemzői

	Selected				**Unused**				
	NN	**Mean**	**Min-Max**	**Sd**	**N**	**Mean**	**Min-Max**	**Sd**	**U test, p**
Height (m)	25	22.7	14–30	4.81	12	24.2	19–31	4.38	-0.69, p=0.49
Crown (m)	25	7.8	4.7–12.4	2.30	12	7.8	6.0–11.1	1.32	-0.42, p=0,67
Circumference (cm)	25	217.2	129–430	83.10	12	216.4	119–345	82.79	0.08, p=0.93

than those growing in the forest *(Table 2)*. Place (country) of observation and size (width but not length) influenced the selection of Jays in the case of *Q. robur (Table 3, 4)*. The size of acorns also depended on oak species. Acorns of *Q. cerris* were significantly longer and wider than those from *Q. robur (Table 5)*.

Table 2. Comparison of oaks growing in two different habitats
2. táblázat A tölgyfák jellemzőinek összehasonlítása nyílt és zárt állományban

	Open area				**Forest**				
	N	**Mean**	**Min-Max**	**Sd**	**N**	**Mean**	**Min-Max**	**Sd**	**U test, p**
Height (m)	25	18.8	14.0–30.0	5.26	12	24.5	19.0–31.0	3.64	2.80, p<0.01
Crown (m)	25	8.8	4.7–12.0	2.12	12	7.4	5.1–12.4	1.88	-1.95, p<0.05
Circumference (cm)	25	224.3	120–430	82.52	12	18.75	119–330	83.00	-0.79, p=0.43

Table 3. Characteristics of acorns from selected and unused trees by Jays
3. táblázat A szajkók által használt és nem használt makkok jellemzőinek összehasonlítása

	Selected				**Unused**			
	N	**Mean**	**Min-Max**	**Sd**	**N**	**Mean**	**Min-Max**	**Sd**
Length (mm)	1235	25.49	9.7–24.4	3.84	520	28.69	9.1–22.8	2.33
Width (m)	1235	14.94	14.2–37.1	1.79	520	16.10	16.5–39.0	4.98

Table 4. Results of Generalised Linear Model testing the relationships between Jays' choice and parameters of acorns and place of observation
4. táblázat Az általánosított lineáris modellek eredményei a szajkók által választott makkok hossza, szélessége és a vizsgálat országai szerint

	Degrees of freedom	**Wald's Statistic**	**P**
Length (mm)	1	8.68	0.003
Width (mm)	1	0.02	0.900
Country	1	65.08	<0.001

Table 5. Comparison of acorns of two species of oaks
5. táblázat A szajkók által használt makkok jellemzőinek fajok közötti összehasonlítása

	Q. robur				**Q. cerris**				
	N	**Mean**	**Min-Max**	**Sd**	**N**	**Mean**	**Min-Max**	**Sd**	**U test, p**
Length (mm)	1155	24.79	14.2–37.3	3.76	600	28.69	17.4–39.0	3.96	-21.63, p<0.01
Width (mm)	1155	14.79	9.1–24.4	1.95	600	16.10	11.8–24.3	1.84	-14.35, P<0.01

Discussion

Our results indicated that the characteristics of acorns are the most important factors for foraging Jays. Birds collected acorns which were smaller than those growing on neighbouring unused trees. Earlier studies also showed experimentally that the size of acorns was an important factor for Jays collecting food (Pons & Pausas 2007). However, these authors showed that Jays preferred bigger acorns. Preference for bigger acorns has implications for the process of oak dispersion and according to these results large acorns appear to have a higher chance of being dispersed, and in this way, an increased probability of germination and seedling establishment (Tripathi & Khan 1990, Sonensson 1994, Bonfil 1998, Gómez 2003). Selection for bigger acorns could also lead to an increase in the size of acorns in oaks, but this evolutionary process can be limited by the physical constraints on Jays for handling, swallowing and transporting very big acorns (Pons & Pausas 2007). This ability is related to the size of their bill and throat (Gómez 2004). Pons and Pausas (2007) suggested that the limiting size of acorns is 17.2 mm in width. Thus, as observed in our study, the size of acorns collected from preferred oaks are an appropriate size for Jays to swallow.

Our studies also indicated a preference by Jays for specific trees for foraging, although, the morphological characteristics of the oaks were not significant for birds whereas the size of acorns was important. Bigger acorn should be preferred by Jays because the size can be related to the nutritional content and indicates the condition of the acorn (Gómez 2004, Pons & Pausas 2007). However, studies about acorns' chemical composition are scarce (Johnson *et al.* 1993, Fleck & Woolfenden 1997, Kilic *et al.* 2010). Features of acorns of specific trees can differ not only in size but also in chemical composition. Łuczaj *et al.* (2014) indicated that acorns differ in tannin content not only between species of oaks but also between individual trees of the same species. Thus, preferences of Jays for specific trees can be related to various aspects. It may be connected not only with size of acorns but also to their nutrient characteristics. The other factor influencing Jays' choices may be related to infestation of acorns. Other studies indicated that Jays preferred undamaged acorns (Bossema 1979, Pons & Pausas 2007). The specific individual trees can differ in level of infestation by arthropods and Jays can prefer trees with a lower incidence of affected acorns. Similar to other corvids (Emery & Clayton 2004), preferences for specific trees can be perpetuated by observation and repeated choices of other individual Jays.

Jays' selection in relation to the size of acorns and for specific trees can involve not only phenotypic characteristics of acorns but also features of the trees and as a consequence, Jays can help them to disperse their seeds. Thus, Jays' preferences can influence the composition of oak populations, trees with certain phenotypic and genomic characteristics may be favoured and become dominant in the ecosystem assuming that Jays' preferences are consistent across years.

Acknowledgements

Financial support was received through the project 'Oak woods in rural landscapes of the Carpathian region: origin, dynamics and conservation values, financed by the National Science Centre, Poland, following the decision DEC-2013/11/B/NZ9/00793. We are grateful to Shelley Hinsley and Magda Górowska for providing comments that improved the quality of the manuscript and for correcting the English version.

References

Bieberich, J. 2016. Acorns of introduced *Quercus rubra* are neglected by European Jay but spread by mice. – Annals of Forest Research 59(2): 1–10. DOI: 10.15287/afr.2016.522

Bonfil, C. 1998. The effect of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugose* and *Q. laurina* (Fagaceae). – American Journal of Botany 85(1): 79–87. DOI: 10.2307/2446557

Bossema, I. 1979. Jays and oaks: An eco-ethological study of asymbiosis. – Behaviour 70(1–2): 1–116. DOI: 10.1163/156853979X00016

Clayton, N. S., Mellor, R. & Jackson, A. 1996. Seasonal patterns of food storing in the Jay *Garrulus glandarius*. – Ibis 138(4): 250–255. DOI: 10.1111/j.1474-919X.1996.tb04336.x

Emery, N. J. & Clayton, N. S. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. – Science 306(5703): 1903–1907. DOI: 10.1126/science.1098410.

Fleck, D. C. & Woolfenden, G. E. 1997. Can acorn tannin predict scrub-jay caching behavior? – Journal of Chemical Ecology 23(3): 793–806.

Gómez, J. M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by Jays in a heterogeneous landscape. – Ecography 26(5): 573–584. DOI: 10.1034/j.1600-0587.2003.03586.x

Gómez, J. M. 2004. Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. – Evolution 58(1): 71–80. DOI: 10.1111/j.0014-3820.2004.tb01574.x

Howe, H. F. & Smallwood, J. 1982. Ecology of seed dispersal. – Annual Review of Ecology and Systematics 13: 201–228.

Hulme, P. E. 2002. Seed-eaters: Seed dispersal, destruction and demography. – In: Levey, D. J., Silva, W. R. & Galetti, M. (eds.) Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. – CABI, Wallingford, UK, pp. 257–273.

Johnson, W. C., Thomas, L. & Adkisson, C. S. 1993. Dietary circumvention of acorn tannins by Blue Jays. – Oecologia 94: 159–164.

Jordano, P. 2000. Fruits and frugivory. – In: Fenner, M. (ed.) Seeds: The Ecology of Regeneration in Plant Communities. – CABI, Wallingford, UK, pp. 125–165.

Kurek, P. & Dobrowolska, D. 2016. Acorns dispersal by Jays *Garrulus glandarius* onto clear-cuts and under the forest canopy. – Sylwan 160(6): 512–518.

Kurek, P., Dobrowolska, D., Wiatrowska, B. & Dylewski, L. 2018. What if Eurasian Jay *Garrulus glandarius* would larder acorns instead of scatter them? – Forest 11(5): 685–689. DOI: 10.3832/ifor2793-011

Kilic, U., Boga, M. & Guven, I. 2010. Chemical composition and nutritive value of oak *(Quercus robur)* nut and leaves. – Journal of Applied Animal Research 38(1): 101–104. DOI: 10.1080/09712119.2010.9707165

Łuczaj, Ł., Adamczak, A. & Duda, M. 2014. Tannin content in acorns (*Quercus* spp.) from Poland. – Dendrobiology 72: 103–111. DOI: 10.12657/denbio.072.009

Mosandl, R. & Kleinert, A. 1998. Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus silvestris* L.) stands. – Forest Ecology and Management 106(1): 35–44. DOI: 10.1016/S0378-1127(97)00237-5

Myczko, Ł., Dylewski, Ł., Zduniak, P., Sparks, T. H. & Tryjanowski, P. 2014. Predation and dispersal of acorns by European Jay *(Garrulus glandarius)* differs between a native (pedunculate oak *Quercus robur*) and an introduced oak species (northern red oak *Quercus rubra*) in Europe. – Forest Ecology and Management 331: 35–39. DOI: 10.1016/j.foreco.2014.07.027

Perea, R., San Miguel, A. & Gil, L. 2011. Flying vs. climbing: Factors controlling arboreal seed removal in oak-beech forests. – Forest Ecology and Management 262(7): 1251–257. DOI: 10.1016/j.foreco.2011.06.022

Pesendorfer, M. B., Sillett, T. S., Koenig, W. D. & Morrison, S. A. 2016. Scatter-hoarding corvids as seed dispersers for oaks and pines: a review on a widely distributed mutualism and its utility to habitat restoration. – The Condor 118(2): 215–237. DOI: 10.1650/CONDOR-15-125.1

Pons, J. & Pausas, J. G. 2007. Not only size matters: acorn selection by the European Jay *(Garrulus glandarius)*. – Acta Oecologica 31(3): 353–360. DOI: 10.1016/j.actao.2007.01.004

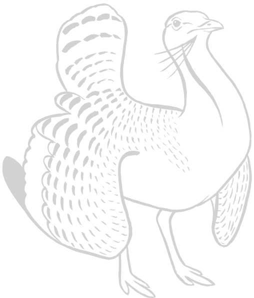
Richardson, K. B., Lichti, N. I. & Swihart, R. K. 2013. Acorn-foraging preferences of four species of free-ranging avian seed predators in eastern deciduous forests. – The Condor 115(4): 863–873. DOI: 10.1525/cond.2013.120189

Sonensson, L. K. 1994. Growth and survival after cotyledon removal in *Quercus robur* seedlings, grown in different natural soil types. – Oikos 69(1): 65–70. DOI: 10.2307/3545284

Tripathi, R. S. & Khan, M. L. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. – Oikos 57(3): 289–296. DOI: 10.2307/3565956

Vander Wall, S. & Beck, M. J. 2012. A comparison of frugivory and scatter-hoarding seed-dispersal syndromes. – Botanical Review 78: 10–31. DOI: 10.1007/s12229-011-9093-9

Will, H. & Tackenberg, O. 2008. A mechanistic simulation model of seed dispersal by animals. – Journal of Ecology 96(5): 1011–1022. DOI: 10.1111/j.1365-2745.2007.01341.x



Ornis Hungarica 2020. 28(1): 176–180.
DOI: 10.2478/orhu-2020-0011

Differences in eggshell pigmentation pattern between Common Moorhen *Gallinula chloropus* and Eurasian Coot *Fulica atra* eggs

Valentin Adrian Kiss*[1,2], Liviu Răzvan Pripon[3] & Attila Marton[4,5]

Received: April 27, 2020 – Revised May 11, 20202 – Accepted: May 12, 2020

Kiss, V. A., Pripon, L., R. & Marton, A. 2020. Differences in eggshell pigmentation pattern between Common Moorhen *Gallinula chloropus* and Eurasian Coot *Fulica atra* eggs. – Ornis Hungarica 28(1): 176–180. DOI: 10.2478/orhu-2020-0011

Abstract Facultative avian brood parasites increase their reproductive output by laying eggs in the nests of conspecifics or closely related species. The Common Moorhen *Gallinula chloropus* is a well-known facultative brood parasite that nests in wetlands, which are utilised also by a wide range of waterfowl, including the Eurasian Coot *Fulica atra*. The two species breed in similar habitats and have a similar egg pigmentation pattern; thus, the Coot can be a suitable host of brood-parasitic Moorhen. To study whether there is any discernible difference between the spotting pattern of Coot and Moorhen eggs, we compared the density of different sized spots on eggs of the two species. Our results show that Coot eggs have a significantly higher density of small speckles then Moorhen eggs, while the latter species has eggs with more conspicuous larger spots. Therefore, Coots can possibly rely on these differences in eggshell pattern to recognize and eject the brood parasitic Moorhen eggs.

Keywords: aquatic birds, interspecific brood parasitism, egg morphology, Rallidae

Összefoglalás A fakultatív költésparazita madárfajok növelhetik szaporodási sikerüket azáltal, hogy tojásaik egy részét azonos vagy közelrokon fajok fészkébe tojják. A vizes élőhelyeken fészkelő vízityúk *(Gallinula chloropus)* egy közismert fakultatív költésparazita, amely néha a szárcsát *(Fulica atra)* is parazitálja. A két faj hasonló élőhelyen költ, és hasonló tojásmintázattal rendelkezik, így a szárcsa kézenfekvő gazdafaj lehet a vízityúk számára. Összehasonlítottuk a két faj tojásain található, különböző méretű foltok gyakoriságát azért, hogy megvizsgáljuk, van-e olyan észlelhető különbség a tojásaik mintázata között, amely révén a szárcsa felismerheti a fészekidegen tojásokat. Eredményeink azt mutatják, hogy a szárcsa tojásai jelentősen sűrűbben szeplőzöttek a vízityúkénál, míg utóbbi tojásain, gyakrabban előfordulnak szembetűnőbb, nagyobb foltok. A tojások mintázatbeli különbsége lehetővé teheti a szárcsa számára, hogy felismerje a vízityúk tojásait, és elkerülje a költésparazitizmussal járó költségeket.

Kulcsszavak: vízi madarak, fajok közötti fészekparazitizmus, tojás színezet, guvatfélék

[1] *Babeş-Bolyai University, Faculty of Biology and Geology; 400006 Cluj-Napoca, Str. Clinicilor nr 5–7., Romania, e-mail: kissvalentinadrian@gmail.com*

[2] *Babeş-Bolyai University, Student College for Advanced Performance Studies; 400376 Cluj-Napoca, Str. Pandurilor nr 7., Romania*

[3] *Babeş-Bolyai University, Faculty of History and Philosophy; 400084 Cluj-Napoca, Str. Mihail Kogălniceanu nr 1., Romania*

[4] *Department of Evolutionary Zoology and Human Biology, University of Debrecen, 4032 Debrecen, Egyetem tér 1., Hungary*

[5] *Juhász-Nagy Pál Doctoral School, University of Debrecen, 4032 Debrecen, Egyetem tér 1., Hungary*

** corresponding author*

Introduction

Brood parasitism is a reproductive strategy found across a wide range of avian taxa (Haraszthy 2019a, b), in which females lay their eggs in the nest of conspecific or heterospecific hosts, with the aim of increasing their own reproductive output on the expense of the hosts' parental care directed towards the host's own brood (Davies 2000). While only 1% of all avian taxa are obligate brood parasites (i.e. rely solely on the parental care of heterospecific hosts), conspecific brood parasitism is a facultative strategy, and it is more common in precocial species (e.g. around 60% of all Anatidae species, Yom-Tov & Geffen 2018). Common Moorhens *Gallinula chloropus* (Moorhen hereafter) exhibit a highly diverse breeding strategy, ranging from monogamy to polygamy and polygyny, but are also notoriously brood parasitic (Gibbons 1986). Moreover, besides eggs dumped in the nests of conspecifics, Moorhen eggs were found within the clutches of Little Bittern *Ixobrichus minutus*, Eurasian Coot *Fulica atra* (Coot from hereafter), Grey Partridge *Perdix perdix*, Little Grebe *Tachybaptus ruficollis*, Black-headed Gull *Chroicocephalus ridibundus* and Ferruginous Duck *Aythia nyroca* (Engler 1983, David *et al*. 2005, Meniaia *et al*. 2014, Haraszthy 2018).

The nestlings of precocial species do not rely as heavily on the care of their parents (or foster parents) as altricial nestlings do, however, increased number of eggs in the nest might lead to nest destruction (Wang *et al.* 2013) or lower fledgling success (Lyon 1993, 2003). For example, in the Moorhen population studied by Gibbons (1986), the mean number of nestlings successfully reared from nests containing eggs from only one female was 1.70, while only 1.20 nestlings fledged from the nests containing the eggs of multiple females. Therefore, hosts are expected to evolve defences to minimize the occurrence and negative effect of brood parasitism, by recognizing the parasites as enemies, or by recognizing and rejecting brood parasitic eggs (Davies 2000).

After finding a seemingly rejected Moorhen egg next to a clutch of Coot eggs, we decided to investigate whether the differences in eggshell pigmentation may constitute reliable cues for the Coot in the recognition and rejection of Moorhen eggs. We hypothesise that there are some subtle differences in the eggshell pigmentation that enable Coots to recognize foreign eggs, thus evading brood parasitism. Coot and Moorhen eggs are fairly similar in size and shape, and have fine speckles and brownish blotches of various sizes on a white-ivory background. We predict that the density of fine speckles is higher on Coot eggs, while in contrast, the density of larger blotches is higher on Moorhen eggs.

Materials and methods

The Eurasian Coot is one of the most abundant species at our study site Câmpenești fishponds, Romania (46°50'35.7"N 23°42'23.1"E), where it reproduces in large numbers despite the intense human activity around the fishpond, and forms relatively abundant flocks in winter (Kiss & Pripon 2019). Here, we found a seemingly rejected Moorhen egg next to a Coot nest containing 8 eggs in 2018. In order to quantify the differences in eggshell pigmentation, we conducted spot counts based on spot size, on Coot eggs from different nests from our study site (*n* = 5) and Moorhen eggs (*n* = 5). To have an identical sample size between the two species, besides the Moorhen egg found next to the Coot nest in 2018, we sampled four locally collected Moorhen eggs in the oological collection of Zoological Museum of the Babeș-Bolyai University.

We classified the markings on the eggs based on the diameter of the spots on the eggshell, as follows: "speckles" (< 0.5 mm), "small spots" (0.5–1 mm), "large spots" (1–3 mm) and "blotches" (>3 mm). We photographed 6 squares on each egg through a handheld magnifier glass (5× magnification) and direct visually counted the spots of different sizes. Thus, we evaluated the number of spots on 30 squares collected from Coot eggs and 30 squares collected from Moorhen eggs, and calculated their average number and relative frequency. Large spots and blotches scarcer and more dispersed then speckles and small spots, therefore are better evaluated by relative frequency within the randomly selected squares. Both evaluations reflect the density of spots on the eggshell surface.

We performed One-way ANOVA analysis using PAST programme in order to test difference between the egg markings of the two species.

Results

Although Coot and Moorhen eggs have a highly similar eggshell pigmentation pattern, we found marked differences in the abundance and relative frequency of different sized spots between the eggs of the two species *(Table 1)*.

Coot eggs had on average more speckles then Moorhen eggs ($F = 297.20$, $df = 33.54$, $P < 0.001$), while Moorhen eggs had a higher abundance of small spots ($F = 10.72$, $df = 46.31$, $P = 0.002$) and blotches ($F = 13.42$, $df = 33.83$, $P < 0.001$). We found no significant difference in the abundance of large spots (i.e. spots of 1–3 mm diameter) between the two species ($F = 2.06$, $df = 56.36$, $P = 0.157$).

Table 1. Minimum, maximum, mean (± *SD*) number of each type of spots per evaluated square (25 mm^2), and the relative frequency (*F%*) of each type of spots on Coot and Moorhen eggs

1. táblázat Különböző méretű foltok relatív gyakorisága (*F%*), illetve minimum, maximum és átlagos (±*SD*) száma 25 mm^2-es mintavételezési négyzetekben, szárcsa és vízityúk tojásokon

	Speckles		**Small spots**		**Large spots**		**Blotches**	
	Coot	**Moorhen**	**Coot**	**Moorhen**	**Coot**	**Moorhen**	**Coot**	**Moorhen**
Min	72	12	0	0	0	0	0	0
Max	185	40	4	9	4	2	1	3
Mean ±SD	111.06 ±27.12	22.40 ±7.61	1.66 ±1.44	3.40 ±2.51	0.53 ±0.97	0.86 ±0.81	0.10 ±0.30	0.83 ±1.05
F%	100%	100%	60%	90%	30%	60%	10%	46%

Discussion

The recognition of brood parasitic eggs by hosts, based on the eggshell markings is a widespread and well-studied host defence (Davies 2000). Host that fail to recognize foreign eggs and act on it accordingly, are compelled to invest parental care in non-kin offspring at the detriment of their own offspring (Lyon 2003, Wang 2013).

We found marked differences between the eggshell pattern of the facultative brood parasitic Moorhen and its occasional host, the Eurasian Coot. Therefore, our results provide evidence that Coots could rely on the differences in eggshell pigmentation to recognize foreign eggs and evade the costs of brood parasitism. The recognition of own eggs might be particularly important in this species, because besides facing the odds of the occasional interspecific brood parasitism of the Moorhen, the Coot is also known to utilize this alternative reproductive strategy as a facultative intra- and conspecific brood parasite (Samraoui & Samraoui 2007, Haraszthy 2018).

The American Coot *Fulica americana* is known to count its eggs and to recognize if there are extra eggs in its clutch (Lyon 2003), however, it is not known if this frontline defence is shared with its sister taxa, the Eurasian Coot.

If the Eurasian Coot is capable of true egg recognition (*sensu* Lyon 2007), the occurrence of intraspecific or conspecific brood parasitism might be higher than reported in previous studies, since hosts might immediately recognize and remove foreign eggs from the clutch. Further studies are needed to assess the extent and costs of Moorhen brood parasitism on Coots, alongside an experimental framework for testing the underlying mechanisms of brood parasitic egg recognition by Coots. However, since a closely related species showed marked egg recognition abilities during experimental egg-swaps (Lyon 1993, 2003, 2007), it is worth mentioning that for such experiments freshly collected Moorhen eggs are needed, to exclude the confounding effect of other egg recognition cues (e.g. surface ruggedness of clay eggs, low weight of eggs from oological collections etc.).

We conclude that the eggshell pigmentation patterns can serve as reliable cues for the Coot to recognize its own eggs and spot foreign eggs within its clutch, thus evading the costs posed by brood parasitism.

Acknowledgements

We express our gratitude towards Gergely Osváth for giving us the opportunity to study the eggs belonging to the ornithological collection of Zoological Museum of the Babeș-Bolyai University, Mihai Pop for his help in the field work and Horea Olosutean for his statistical guidance. We wish to thank László Haraszthy for his constructive comments during the review process of the manuscript. This research was funded by Milvus Group Association's Scholarship Grant and Babeș-Bolyai University through the Special research scholarship, both awarded to Valentin Adrian Kiss.

References

Davies, N. B. 2000. Cuckoos, Cowbirds and Other Cheats. – Poyser Publishing

David, A., Vass, C. & Coroiu, I. 2005. A new case of interspecific brood parasitism in Common Moorhen *Gallinula chloropus*. – Avocetta 29: 33–36.

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

Gibbons, D. W. 1986. Brood parasitism and cooperative nesting in the Moorhen, *Gallinula chloropus*. – Behavioural Ecology and Sociobiology 19: 221–232. DOI: 10.1007/BF00300863

Haraszthy, L. 2018. Intra- and interspecific nest parasitism of Common Moorhen (review of cases and new data). – Ornis Hungarica 26(1): 95–101. DOI: 10.1515/orhu-2018-0007

Haraszthy, L. 2019a New species on the list of species with intraspecific nest parasitism. – Ornis Hungarica 27(1): 166–206. DOI: 10.2478/orhu-2019-0010

Haraszthy, L. 2019b Cases of occasional interspecific brood parasitism and egg dumping in Hungary. – Ornis Hungarica 27(2): 115–141. DOI: 10.2478/orhu-2019-0020

Kiss, V. A. & Pripon, L. R. 2019. A reevaluation of the avifauna from Câmpenești fishing complex (Cluj County, Romania) in the context of high human impact. – Brukenthal Acta Musei XIV. 3.

Lyon, B. E. 1993. Conspecific brood parasitism as a flexible female reproductive tactic in American Coots. – Animal Behaviour 46: 911–928. DOI: 10.1006/anbe.1993.1273

Lyon, B. E. 2003. Egg recognition and counting reduce costs of avian conspecific brood parasitism. – Nature 422: 495–499. DOI: 10.1038/nature01505

Lyon, B. E. 2007. Mechanism of egg recognition in defenses against conspecific brood parasitism: American coots (*Fulica americana*) know their own eggs. – Behavioral Ecology and Sociobiology (61): 455–463. DOI: 10.1007/s00265-006-0273-2

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

Samraoui, F. & Samraoui, B. 2007. The reproductive ecology of the Common Coot *Fulica atra* in the Hauts Plateaux, Northeast Algeria. – Waterbirds 30(1): 133–139. DOI: 10.1675/1524-4695(2007)030[0133:TREOTC]2.0.CO;2

Wang, L., Canchao, Y., Hsu, Y. C., Antonov, A., Moksnes, A., Røskaft, E., Liang, W. & Stokke, B. G. 2013. Increase of clutch size triggers clutch destruction behaviour in Common Moorhens *Gallinula chloropus* during the incubation period. – Behaviour 150(2): 215–223. DOI: 10.1163/1568539X-00003046

Yom-Tov, Y. & Geffen, E. 2018. Conspecific brood parasitism among birds: the effect of phylogeny, mode of reproduction and geographic distribution. – In: Soler, M. (ed.) Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution. – Springer International Publishing. DOI: 10.1007/978-3-319-73138-4_5

Ornis Hungarica 2020. 28(1): 181–184.
DOI: 10.2478/orhu-2020-0012

Short report on probable case of Caspian Gull predation on migrating swallows observed at first time

Klaudia Litwiniak[1], Marcin Przymencki[1*] & Damian Celiński[2]

Received: December 14, 2019 – Revised: February 10, 2020 – Accepted: February 11, 2020

Litwiniak, K., Przymencki, M. & Celiński, D. 2020. Short report on probable case of Caspian Gull predation on migrating swallows observed at first time. – Ornis Hungarica 28(1): 181–184. DOI: 10.2478/orhu-2020-0012

Abstract At Mietków Reservoir (SW Poland), during the breeding season of 2019, we found 52 dead swallows in Caspian Gull *(Larus cachinnans)* colony. Most of them were Barn Swallows *(Hirundo rustica)*. The bodies of swallows were fresh and torn with traces of bill. We assume that swallows might have been in weak condition and hunted by gulls. They also could die because of bad weather conditions and hypothermia, fell into the water and then were taken. However, to our knowledge, it was the first mass event of feeding on migrating birds by Caspian Gull.

Keywords: *Larus cachinnans*, passerine, feeding on birds, predator

Összefoglalás A 2019. évi költési időszakban a délnyugat-lengyelországi Mietków Reservoir területén 52, többségében füsti fecske *(Hirundo rustica)* tetemet találtunk egy sztyeppi sirály *(Larus cachinnans)* kolóniában. A fecske tetemek frissek voltak, tépések nyomaival. A fecskék valószínűleg legyengült állapotban voltak, ezért estek a sirályok áldozatául. Ugyanakkor a rossz időjárási viszonyok és a kihűlés, sőt a vízbeesés is a pusztulásukhoz vezethetett, ami után a sirályok összeszedhették a tetemeket. Azonban jelen tudásunk szerint ez az első tömeges eset, amikor vonuló madarak tetemein táplálkozó sztyeppi sirályokat figyeltek meg.

Kulcsszavak: sztyeppi sirály, énekesmadár, madártetemek, zsákmányszerzés

[1] Poleska 41/20, 51-354 Wrocław, Poland
[2] Najświętszej Maryi Panny 46/27, 42-217 Częstochowa, Poland
**corresponding author: marcin.przymencki@wp.pl*

Gulls (Larinae) have an opportunistic feeding ecology. Obtaining food is done in many ways, among others through predation, scavenging and kleptoparasitism (Avdanin *et al.* 1998). There are numerous studies about depredation of birds by large gulls. Great Black-backed Gulls *Larus marinus* have been known to kill swimming Slavonian Grebe *Podiceps auritus* and Lesser Scaup *Aythya affinis* (Mansueti 1961). Herring Gulls *Larus argentatus* were observed during attacking and killing sick birds, for example Curlew *Numenius arquata*, American Wigeon *Anas americana* or Little Gull *Hydrocoleus minutus* (Tinbergen 1953, Mansueti 1961, Macdonald & Mason 1973). There are also a number of reports of large gulls attacking migrants in flight over the sea, mostly passerines (Colston *et al.* 1959, Dyck 1969, Macdonald & Mason 1973, Dierschke 2001). Dierschke (2001) reported that Starlings *Sturnus vulgaris* and thrushes *Turdus* spp. were the most often found in large gulls' pellets on Helgoland Island. He also found bones of such species as Dunnock *Prunella modularis*, Robin *Erithacus rubecula*, Pied Wagtail *Motacilla alba* and Common Whitethroat *Sylvia* *communis*. Macdonald and Mason (1973) observed Herring Gulls attacking and killing migrating Starlings, Blackbirds *Turdus merula* and Redwings *Turdus iliacus* on the sea. Studies show that passerines form a part of gulls' diet mainly during their migration (Dierschke 2001). Because of being exhausted and flying over open, unsheltered space, migrating birds might be captured in easy way by gulls. Various methods of capture have been observed, among others when victim was forced into the sea by continual harrying or it was knocked into the water by the gulls' beating wings or feet (Macdonald & Mason 1973).

Caspian Gull *Larus cachinnans* is a large species feeding mainly on fishes on the western edge of its breeding area (Skórka & Wójcik 2008, Gwiazda *et al.* 2011). There is different situation in its core range, for example in Crimea (Kiselev 2009) and Caspian Sea basin (Avdanin *et al.* 1998), where gulls usually feed on rodents, like Little Ground Squirrel *Spermophilus pygmaeus*. Predation on other vertebrates by this species, especially birds, seems to be uncommon (Gwiazda *et al.* 2011) and there has not been described any case of hunting on passerines so far. This paper presents the first mass event of feeding on migrating birds by Caspian Gull.

On the 17th May 2019 we observed many dead swallows in or close to nests in a breeding colony of Caspian Gull. They were mainly Barn Swallows *Hirundo rustica* and a few House Martins *Delichon urbicum (Figure 1)*. We counted 52 dead swallows on three islands but 39 of them were found on one island. The bodies of swallows were torn with traces of bill *(Figure 2)*. We also found one Barn Swallow with wings firmly attached to the body and glued feathers *(Figure 3)*. It suggests that this one was eaten and spat out by adult gull or chick. All of swallows' bodies were fresh and probably laid there up to 2 days. Number of dead swallows presumably was higher as swallow's parts of skin with feathers or single feathers were abundant in the vicinity of some gull's nests.

Figure 1. Dead Barn Swallows and House Martin in this colony
1. ábra Füsti fecske és molnárfecske tetemek a vizsgált kolóniában

Figure 2. Barn Swallow's body torn with traces of bill
2. ábra Füsti fecske teteme tépések nyomaival

Figure 3. Barn Swallow with wings attached to the body and glued feathers
3. ábra Füsti fecske testhez simuló szárnyakkal, összeragadt tollakkal

This Caspian Gulls colony is located at inland Mietkow Reservoir (50°57'35.2"N 16°37'19.6"E) in SW Poland. It is a dam reservoir on the Bystrzyca river, nearly the Sudeten Mountains. Caspian Gulls usually nest there on one big island with grass and other vegetation up to 1 m high. This year they chose to nest nine small islands covered by willows. There were 3–50 pairs per island. The reservoir is foraging place to many species of birds when migration is going, for example waders and geese. During spring migration, there are also thousands of swallows. The most numerous species is the Barn Swallow, but there are many House Martins and Sand Martins too.

As swallows have fast and maneuverable flight and seem not to be easy-to capture prey for large gulls, we suppose that in this case birds might have been in weak condition and Caspian Gulls actively hunted them. However, observation of Glaucous-winged Gull *Larus glaucescens* capturing singing males of Fox Sparrow *Passerella iliaca* at their breeding grounds, not during migration (Nietlisbach *et al.* 2014), proves that large gulls are able to catch small passerines even in good physical condition. Another explanation might be that swallows were already dead in the moment they were captured by gulls. They could die because of bad weather conditions and hypothermia, fell into the water and then were taken. If so, other dead swallows would float on the water surface or would be found in other places of colony but that was not the case. Probably a few Caspian Gulls specialized in catching swallows during their migration and it happens every spring when gulls are in breeding colony. It is also possible that it was one-time case when some gulls followed their neighbours catching swallows. Both hypothesis are supported by the fact that 75% victims were found on only one island and 7 bodies laid at only one nest. As shows only existing study on foraging strategy of Caspian Gull, cases of preying on birds by this species have been very rare and consider three observations where Coot *Fulica atra* and Moorhen *Gallinula chloropus* chicks were killed (Skórka & Wójcik 2008). Our findings might suggest that this species can take advantage of migrating passerines through mainland as an additional food source, likewise their relatives, Herring Gulls, hunting on birds offshore (Macdonald & Mason 1973). Also, preying on birds might be more widespread in Caspian Gulls than it has been reported so far.

References

Avdanin, V. O., Viksne, Y. A., Zubakin, V. A., Kishchinsky, A. A., Litvinenko, N. M., Lobkov, E. G., Nechaev, V. A., Firsova, L. V., Flint, V. E. & Yudin, K. A. 1998. Birds of the USSR. Gulls. – Nauka, Moscow (in Russian)

Dierschke, V. 2001. Large gulls as predators of passerine landbirds migrating across the southeastern North Sea. – Ornis Svecica 11: 171–180.

Gwiazda, R., Bukaciński, D., Neubauer, G., Faber, M., Betleja, J., Zagalska-Neubauer, M., Bukacińska, M. & Chylarecki, P. 2011. Diet composition of the Caspian Gull *(Larus cachinnans)* in inland Poland: effects of breeding area, breeding stage and sympatric breeding with Herring Gull *(Larus argentatus)*. – Ornis Fennica 88: 80–89.

Kiselev, F. A. 2009. Agricultural value of the Caspian Gulls *Larus argentatus cachinnans*. – Russian Bird Watch 18: 1595–1603. (in Russian)

Macdonald, S. M. & Mason, C. F. 1973. Predation of migrant birds by gulls. – British Birds 66: 361–363.

Mansueti, R. J. 1961. Waterfowl predation by and records of the Great Black-backed Gull in Chesapeake Bay during winter and spring. – Chesapeake Science 2(1–2): 102–104.

Nietlisbach, P., Germain, R. R. & Bousquet, C. A. H. 2014. Observations of Glaucous-winged Gulls preying on passerines at a Pacific Northwest colony. – The Wilson Journal of Ornithology 126(1): 155–158. DOI: 10.1676/13-077.1

Skórka, P. & Wójcik, J. D. 2008. Habitat utilisation, feeding tactics and age-related feeding efficiency in the Caspian Gull *Larus cachinnans*. – Journal of Ornithology 149(1): 31–39. DOI: 10.1007/s10336-007-0208-3

Tinbergen, N. 1953. The Herring Gull's World. – Frederick A. Praeger, Inc. London