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The Great Bustard: past, present and future of a globally threatened species

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Abstract Great Bustards are still vulnerable to agricultural intensification, power line collision, and other human-induced landscape changes. Their world population is estimated to be between 44,000 and 57,000 individuals, showing a stable demographic trend at present in the Iberian peninsula, its main stronghold, but uncertain trends in Russia and China, and alarming declines in Iran and Morocco, where it will go extinct if urgent protection measures are not taken immediately. Our knowledge of the behaviour and ecology of this species has increased considerably over the last three decades, allowing us to control the major threats and secure its conservation in an appropriately managed cereal farmland. This species became '**The Bird of the Year**' in Hungary in 2014.

Keywords: conservation, Great Bustard, demographic trend, world status

Összefoglalás A túzok populációit napjainkban is veszélyezteti a mezőgazdaság intenzifikációja, a légkábelekkel való ütközésekből eredő elhullások, és az emberi hatásokra bekövetkező tájváltozások. A faj világállománya 44 000 és 57 000 egyedre tehető. Az Ibériai-félszigeten található legerősebb populáció stabil demográfiai trendet mutat, az orosz és a kínai állományok változásait jelentős bizonytalanság terheli, valamint Iránban és Marokkóban riasztó állománycsökkenés figyelhető meg, ami megfelelő védelmi intézkedések hiányában a lokális populációk kipusztulásához fog vezetni a közeljövőben. Az elmúlt három évtizedben a faj magatartásbiológiájára és ökológiai igényeire vonatkozó ismeretek jelentősen bővültek, ami lehetőséget biztosít a jelentős veszélyeztető tényezők kontrollálására, valamint a túzok védelmével összeegyeztethetően hasznosított mezőgazdasági területeken a faj megőrzésére. Ez a faj lett 2014-ben az **Év Madara.**

Kulcsszavak: természetvédelem, túzok, állományváltozás, világállomány

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Current world status and recent demographic trends

The recent history of published estimates of the Great Bustard world population shows an increasing trend, from the ca. 28,000 individuals in the early 1990's to the 44,000-57,000 individuals in 2010 (details in Alonso & Palacín 2010). However, we are convinced that this trend is partly influenced by the increasing quality of the counts during the last three decades and should therefore be interpreted with caution. During previous centuries (years 1600's-1800's), the species had been reported as a breeding bird in many more European countries than nowadays, from Great Britain to Greece, and as far north as in Sweden (Glutz *et al.* 1973). The marked declines during the 19th and 20th centuries in most central Europe are attributed to agricultural intensification, but surely hunting, and in the last decades collision with power lines also played an important role. The effects of hunting are well documented in Spain, where official hunting bags reached up to 2057 birds annually in the decades just before a hunting ban was established in 1980 (Trigo de Yarto 1971). A 70% of the leks for which we have been able to assess the cause of extinction disappeared between 1960 and 1980, the period when hunting pressure was presumably the highest in Spain. We guess that approximately half of these leks disappeared due to hunting (Alonso *et al.* 2003b, 2004a).

Although census accuracy has generally improved through the last years in most countries, and some areas might contribute to exaggerate the real increases, we think that the world total of Great Bustards has not decreased significantly during the last two or three decades (Palacín & Alonso 2008, Alonso & Palacín 2010). This conclusion is based on the trend observed in the Iberian Peninsula, where a major fraction (60-70%) of that world total lives, and where many regional populations have shown stability or even a tendency to increase in the last years. We suggest that in Spain, after several decades of decline the hunting ban established in 1980 allowed a recovery of the species in most regions, whereas in other regions populations had no capacity to recover any longer after having been decimated to just a few birds, and just continued decreasing to extinction (Alonso *et al.* 2003b).

The positive demographic trend in the Iberian Peninsula contrasts with those of Morocco and Iran, where the two most endangered populations of the species face a real threat of extinction (Alonso *et al.* 2005, Barati *et al.* 2014, Palacín *et al.* 2014). The species has also probably decreased in other main parts of its distribution range, e.g. Russia and China (Chan & Goroshko 1998, Antonchilov 2008, 2011). Finally, even in the Iberian peninsula, where the species seems to be doing better, a contraction of its distribution range is apparently occurring in many areas, due to habitat deterioration linked to a conspecific attraction tendency, which leads to the disappearance of smaller and marginal breeding groups while dispersing birds aggregate at large breeding groups (Alonso *et al.* 2004b, Pinto *et al.* 2005). All of these negative facts have been fundamental when international experts made the recent status assessment of the species, and finally agreed on the convenience of maintaining the Great Bustard listed under the *vulnerable* category (BirdLife International 2013), at least until better information is gathered in those countries where its current status and trends are not well known.

Today the world population of Great Bustards is estimated to be between 44,000 and 57,000 individuals, of which the largest fraction (60-70%) occurs in Spain *(Table 1)*. Compared to the last published estimate (Alonso & Palacín 2010), there is little new data for most of the countries with the largest populations, therefore the conclusions presented four years ago are still valid today. Perhaps the only interesting observation we can appreciate in the last four years is a slow but consistent recovery of the species in Austria and Germany, and a decrease in Iran and Morocco. Interestingly, numbers of Great Bustards in Iran and Morocco are at present similar to the minimum numbers reached two decades ago in Germany and Austria (in both countries, ca. 60 individuals in the 1990's; www.grosstrappe.at, www.grosstrappe.de), which shows that extinction could theoretically be avoided in Iran and Morocco. Unfortunately however, socio-economic conditions in Iran and Morocco are not equal to those in the two central European countries, making the recovery of the species much more difficult. International efforts should be urgently devoted to try to save the Iranian and Moroccan bustards from extinction.

	min-max	reference	year of estimate	quality of estimate
Spain	29,400 – 34,300	Alonso & Palacín 2010	2004-2010	high
European Russia	8000 – 12,000	Malikov *et al.* 2000, Khrustov *et al.* 2003, Antonchikov 2006, Watzke *et al.* 2007	1995-2005	low
NW China (Xinjiang)	400 – 2400	Gao *et al.* 2008, Ying *et al.* 2010	1990-2002	low
Mongolia + SE Russia +NE China [b]	1200 – 2200	Tian & Wang 2001, Tseveenmyadag 2002, Goroshko 2010, Kessler *et al.* 2013, Tian pers.com.	1961-2002	low
Portugal	1893	Pinto & Rocha pers. com. 2010	2009	high
Hungary	1466	L. Miklós pers. com. 2014	2014	high
Turkey	400 – 1000	Kiliç & Eken 2004, Özbagdatli & Tavares 2006, Karakas & Akarsu 2009	1990-2008	low
Ukraine	520 – 680	Yaremchenko & Bakhtiyarov 2006, Dudkin & Domashlinets pers. com. 2008	2006	low
Austria	275 – 364	R. Raab pers. com. 2015	2014	high
Germany	165	Staatliche Vogelschutzwarte Brandenburg & Förderverein Großtrappenschutz, unpubl.	2014	high
Morocco	50 – 80	Alonso *et al.* 2005, Palacín *et al.* 2014	2014	high
Iran	43 – 48	Barati *et al.* 2014	2011	high
Kazakhstan	0 – 50	Acad. of Sciences of Kazakhstan 1996	1990-1996	low
Serbia and Montenegro	35 – 36	Garovnikov 2004	2004	high
Slovakia	0 – 3	National report 2008 [c]	2008	high
Czech Republic	0 – 2	National report 2008 [c]	2006-2007	high
Romania	0 – 8	National report 2008 [c]	2008	high
Total	**43,847 – 56,695**			

Table 1. World status of the Great Bustard in 2014 (updated from Alonso & Palacín 2010). In countries not listed in this table the species is currently considered extinct [a]

1. táblázat A túzok világállománya 2014-ben

[a] Great Bustards released in Great Britain are not included in this *Table*, because they cannot be considered a self-sustaining wild population

[b] Subspecies *Otis tarda dybowskii*

[c] Communicated during the Second Meeting of the Great Bustard MoU held in Feodosia, Ukraine, in November 2008

Collision with power lines, a major concern

Collision with power lines represents today the most important cause of mortality of adult and immature Great Bustards (Palacín *et al.* 2004, Martín *et al.* 2007, Barrientos *et al.* 2012, Raab 2012). Mortality rate due to this cause may reach values of 6%-13% in some populations (Martín 2001, Alonso *et al.* 2007), and these mortality rates may seriously affect population viability (Martín 2008). An example of the devastating effect of a power line is the case of a lek in Madrid region, where numbers of males went down from 15 in 1988 to just a single male seen there at present in spring (Alonso *et al.* 2003a). Various possible causes of this high collision rate include their low manoeuvrability in flight due to their large size, their narrow field of view in the frontal plane, and possibly their low-resolution frontal vision (Martín & Shaw 2010, Martin 2011). Marking power lines with flight diverters to increase their visibility reduces bird mortality significantly but sometimes only slightly in terms of numbers of casualties (Alonso *et al.* 1994, Barrientos *et al.* 2011, 2012). The only way to completely eliminate mortality is burying the line, which is expensive and not affordable as an extensive conservation measure in most areas (Raab *et al.* 2012).

A brief history of the first Great Bustard captive breeding attempts

Captive breeding has traditionally been regarded as a suitable method to recover threatened wild Great Bustard populations. The first attempts to breed Great Bustards in captivity were carried out in Hungary (Chernel 1904), although the first successful reintroductions to the wild took place in Dobrudsha (Romania), where four individuals hatched by a Turkey *(Meleagris gallopavo gallopavo)* in 1919 were released after being kept in semi-wild conditions for several years (Rayner 1942). In the following years, similar programs were undertaken in different central European countries, urged by the alarming decreases of some populations due to agricultural intensification. The aim of these captive breeding stations was, on one hand, to reintroduce young reared from artificially incubated eggs into the wild, and on the other hand to create captive groups of breeding individuals that assured the survival of extremely threatened populations. Among those pursuing the former objective, the main stations were Steckby and Buckow in Germany, and Dévaványa in Hungary (Fodor *et al.* 1981, Dornbusch 1983a,b, Litzbarsky & Litzbarsky 1983, Sterbetz 1986, Faragó 1990). Other attempts were carried out in Portugal (Pinto 1981), Russia (Ponomareva 1983), and Slovakia (Randik & Kirner 1983). Attempts to establish a captive-breeding flock were made in Spain (Hellmich 1991), Poland (Graczyk 1980, 1983, Graczyk *et al.* 1980), and the United Kingdom (Collar & Goriup 1980, Goriup 1985, and more recently, www.greatbustard.org).

BirdLife International established an Action Plan for the Great Bustard in Europe, including among other points the study and evaluation of the current captive breeding programs, focusing on the survival and reproductive success of released individuals (Heredia *et al.* 1996). That year we made a preliminary evaluation of the efficiency of these captive breeding programs, in the light of the results from our long-term studies of the species' behaviour. We concluded that the success of these captive breeding and reintroduction programs had generally been low or very low, due to the absence of the long maternal dependence period in captive released birds, and their consequently high mortality. Young Great Bustards depend on their mothers until they are 6-18 months old, and this training period is vital for their subsequent survival and success as breeding adults (Martín 1997, Alonso *et al.* 1998). In addition, the success of these projects was often unknown due to the lack of adequate tracking of released birds (Martín *et al.* 1996). The lack of such maternal dependence period in all past and current captive breeding programs represents an important handicap that will always limit the success of such attempts. Finally, the delayed reproductive maturity and complicated mating system of this species adds further difficulties to these programs.

Current conservation projects

Since the publication of the European Action Plan in 1996 (Heredia *et al.* 1996, updated in Nagy 2009), and the Asian Action Plan in 1998 (Chan & Goroshko 1998), many habitat management programmes have been carried out in Spain, Portugal, Austria, Hungary, Germany, Serbia, financed with LIFE or other EU funding sources, and here we will not go through all of the details of these projects. However, we should say that most of them implement agri-environmental measures without appropriate tests of their efficiency, and without optimizing costs. However, habitat management is the best way to invest in conservation of the Great Bustard, including some good examples that show how declines of small populations have been stopped just through habitat improvement measures (e.g. www.grosstrappe.at, www.juntadeandalucia.es). On the opposite, reintroduction trials still show little or no success.

Below, we briefly review only some of the historically most significant conservation projects or recent reintroduction trials.

Germany:
Intensification of agriculture caused a dramatic decline of the Great Bustard population in Germany, from ca. 4000 birds in 1940 to 55 counted in 1995. The continued conservation efforts of the association Großtrappenschutz e. V. resulted in the recovery of this population to 165 birds counted in March 2014 (www.grosstrappe.de). In spite of the high predation rate by foxes, white-tailed eagles and ravens, the protection of the small remaining habitat patches and the captive breeding program running since 1973 have succeeded in the prevention of the extinction of the species in Germany. This program started at the Biological Station Steckby and continued since 1979 in Buckow. The eggs from wild nests are collected and incubated artificially. In the past, only eggs from disturbed nests were collected, but nowadays first clutches are taken systematically (40-74 yearly during the last years) based on the assumption that first clutches suffer from much predation pressure, and on the fact that females usually lay a replacement clutch. The eggs collected are incubated artificially, and young birds are fed by hand and moved to increasingly larger pens. During fledging, they eventually fly out to join adult groups. There is evidence that the artificial breeding program prevented the German population from extinction, and today insemination rate, hatching rate and release success have improved much compared to the first years, although survival of the released birds is still highly variable depending on predation pressure.

Austria – Western Hungary:

The West-Pannonian Great Bustards (birds living in Austria, Western Hungary and Slovakia) declined from 3500 individuals in 1900 to 130 in 1995 (ca. 60 of them in Austria), mostly due to agricultural transformations, the development of human infrastructures, and hunting (Raab *et al.* 2010). As a result of intensive and cross-border habitat protection measures, including establishment of protected areas, habitat management, agri-environmental measures, and burying of power lines, the population has recovered to around 400 birds (ca. 300 of them breeding in Austria, Raab 2013, Faragó *et al.* 2014, Raab pers. com., www.grosstrappe.at).

Hungary:

Dévaványa, in the region of the Körös-Maros National Park, is one of the most important areas for Great Bustards in Hungary. Dévaványa Landscape Protection Area was established there in 1975 to safeguard Hungary's largest population of Great Bustards. Around 30-40 eggs found to be endangered are taken each spring from wild nests, replaced by fake ones made of wood, and incubated artificially at the Great Bustard Conservation Centre. The chicks hatched at the Centre are later released in the wild. In addition, a large pen holds up to 40 displaying males and some 50 females in spring, and the numbers of females nesting in that area have increased in the last years due to active land management, including the creation of a mosaic of grassland, wheat, alfalfa, rape and fallow fields. More information can be found at www.tuzok.hu.

Russia:

Russia holds the second largest Great Bustard population in the world, with an estimated 8000-12,000 birds, most in the region Oblast, near Saratov, some 850 km south-east of Moscow. Since the 1980's the A. N. Severtsov Institute of Ecology and Evolution, a branch of the Russian National Academy of Science, has been collecting eggs from doomed nests for artificial incubation. Chicks from this scheme were originally used in various captive breeding projects across the former Soviet Union, which had so far been unsuccessful. In the last years, the Institute has been running a captive rearing and release project instead, lead by Dr. Anatoli Khrustov, bypassing the apparent pitfalls of captive breeding, and releasing Great Bustards back into the wild in Russia. They have also provided the chicks for the UK reintroduction between 2004 and 2013.

United Kingdom:

Great Bustards were once part of British wildlife but they became extinct in Britain in the 1840's, mainly because of hunting. After a failed trial to reintroduce the species in the UK in the 1970's, the Great Bustard Group was formed in 1998 specifically to run a new UK reintroduction project. Great Bustards for this new reintroduction into UK came from Russia during the first ten years of the project. Each year a number of young bustards were imported to the UK from Saratov. In this region, a large number of eggs were collected from doomed nests and incubated artificially in a local breeding station. When the young were 3-4 months old they were sent to UK, where they were released after a period spent at the release pen on Salisbury Plain. The low success during the first 10 years of the trial was due to different causes, but one was surely the migratory instinct of the Russian birds. The natural tendency of these birds to migrate to southwest in autumn became clear to the project managers only after ten years, in spite of our advice that this would be going to be the case, and of evidences from sightings of several released birds in southern England and even some in France. In 2014, eggs were taken for the first time from Spain, and the chicks hatched in the UK. However, a new mistake has been made, since only a fraction of the birds released carry radio-transmitters. This goes against the most fundamental condition of any reintroduction project, i.e. following the fate of all released individuals in order to be able to evaluate the success of the trial and to avoid mistakes in following years. The decision not to tag all birds was based on the fallacious argument of a significant mortality caused by transmitters, whereas the opposite was indeed shown by an analysis of the first seven years of release, where no significant negative effect of tagging was found on post-release survival (Burnside *et al.* in prep). More information about this reintroduction trial can be found in www.greatbustard.com.

The future of the species

As for the prediction of what will happen with Great Bustards in the future, we cannot be too optimistic, in spite of the apparent good health of the main population of the species in the Iberian Peninsula. The first reason for our cautious impression is the apparently rapid decreasing trend in Russia in recent years due to changes in agricultural practices (Antonchikov 2008, 2011), plus the uncertainty about real numbers and trends in other important populations like Mongolia, China, Turkey or Ukraine. This prevents us from providing a more precise guess about the overall global trend of the species. We can only say that establishing reliable trends in the future needs carrying out rigorous surveys as soon as possible in all countries where Great Bustards occur, and that these surveys should be repeated periodically during at least a decade, in order to establish reliable trends and their causes.

The second reason for our caution is the fact that recent evidences of hunting in central Asia, land-use changes in Eastern Europe, Russia, Mongolia and China, and collision with power lines in all areas of their distribution range, may have a significant impact on the worldwide population in the coming decades. These are some of the reasons why the Great Bustard is still classified as vulnerable at a global scale (BirdLife International 2013). It is indeed in Russia and China where more census and conservation work is needed, in order to be aware of the threats to these populations, and to improve protection measures. The fact that the species is migratory in these countries adds obvious risk factors to its current uncertain status.

Third, some climate change models predict northward shifts and contractions of the distribution ranges of several bird species in the coming decades (Jetz *et al.* 2007, Brommer & Møller 2010, Jiguet *et al.* 2010, Araújo *et al*. 2011), although in the case of Great Bustards we think that human activities may be much more important than climate change at least in the near future. Agricultural intensification and infrastructure expansion on the negative side, and agri-environmental programs and other active conservation and management actions on the positive side, may counteract much of the negative climate change effect foreseen in these models.

Fourth, in some Spanish regions hunters are launching a very strong lobby to include

Great Bustards in the list of game species again, based on the species' recent overall stability and increase in some areas. Their arguments are that hunting of a small number of 'old' males which, they say, would not participate in reproductive activities, should render economic benefits that could be applied for the conservation of the species. However, the results of our research with individually marked birds show the opposite. Older males have a higher status in the lek hierarchy, and therefore more access to females and higher breeding success than younger males (Alonso *et al.* 2010a,b). In addition, trophy hunting in spring would cause such alterations in the complicated lek hierarchy and disturbances to other displaying birds, that all the breeding system would probably be distorted. Fortunately, these attempts to legalize Great Bustard hunting have failed up to now, but this doesn't guarantee that in Spain the species will enjoy a protected status forever.

All these reasons suggest keeping the species under a vulnerable status is today the best measure to protect it from all factors that caused the decline and extinction of many of its populations in the past. We should encourage the nature conservation administrations of those countries still lacking accurate surveys of their Great Bustard populations to carry out such censuses, and to take the necessary measures that ensure conservation of this species and its habitat.

The Great Bustard as a model species in scientific research

A research project centered on the Great Bustard started at the National Museum of Natural Sciences in Madrid in the late 1980's and is still active at present (www.proyectoavutarda.org, www.jcalonso.eu). Thanks to this study, our knowledge of the behaviour and ecology of this species has increased considerably over the last decades, and today the Great Bustard is one of the best studied among endangered species in Europe, with over 70 papers published in scientific journals, and 4 books, 6 book chapters, 8 PhD theses, and numerous contributions to international congresses produced only by our group in the last 25 years.

Another example of the profound knowledge of its biology is that it was selected to represent birds in a recent review of sexual size dimorphism in the animal kingdom (Fairbairn 2013). The Great Bustard is indeed one of the heaviest flying birds and the most sexually dimorphic among all living bird species (Alonso *et al.* 2009a). The high weight of males and their size difference to females have conditioned many of the physiological, behavioral and life-history traits of this species. Male-male competition is extremely intense, and high rank within the lek hierarchy, as well as access to females are age- and weight-dependent (Alonso *et al.* 2010a,b). This strong sexual selection has likely pushed male weight up to the limit imposed by powered flight. But the other sexual selection mechanism, female choice, is also very strong in Great Bustards. Females are exceptionally choosy before accepting a male as her mate. They prefer the heaviest, old, and most intensively displaying males, and female choice acts reinforcing the male competition mechanism, making sexual selection a powerful driving force of their sexual size dimorphism, and ultimately of many aspects of their life.

Our project was based on individual marking and radio-tracking from the very beginning in July 1987, when we tagged our first chick in Villafáfila. The number of marked birds has grown since then up to over 1000 individuals, which we have followed throughout their lives, totaling over 19,000 locations on different days.

A big male has obvious advantages at the lek. High-rank males are involved in fewer aggressions during the mating season, because they are accepted by other males as dominant (Magaña *et al.* 2011). But if it comes to a real fight, a big male has also more chances to win. Honest signaling of the status of males to each other through sex traits can prevent these fights and their dangerous consequences and has therefore an important adaptive value (Alonso *et al.* 2010b).

However, getting big does not only bring rewards, it also entails some costs. The faster growth rate of young males implies higher nutritional needs and, when these are not fulfilled during periods of low food abundance, young males suffer higher mortality due to starvation. However, if a mother is able to rear a good, healthy male, that male will integrate earlier in the adult male flock, and gain an easier access to dominant positions in the male group, which in turn increases his lifetime reproductive success (Alonso *et al.* 1998).

But a higher body mass implies higher adult male mortality. Not only a higher natural mortality. Besides, males suffer from higher human-induced mortality than females through their entire lives. They were prosecuted as a hunting species through the whole human history, either as a prey in prehistoric and Middle Age times, or as trophies in modern times until hunting ban was established. And today they suffer from power line collision as their major mortality cause, which in males reaches 6%, doubling the rate of females (Martín 2008).

Sexual size dimorphism has also a negative effect on physiology. Heat dissipation is an important problem in males due to their body mass/surface ratio, and therefore in the Iberian Peninsula, males from southern, hot breeding areas migrate after breeding to cooler summering areas in the north to avoid the summer heat. Males from southern regions migrate longer distances and in higher proportions than males from northern regions, and summer migration is absent in females (Alonso *et al.* 2009b, Palacín *et al.* 2009). Sexual size dimorphism is surely also the cause of the strong sexual segregation in this species, as males and females differ considerably in their nutritional needs (Bravo 2014). Finally, sexual size dimorphism determines important differences in life history parameters between males and females (delayed sexual maturity and shorter lifespan in males, and skewed sex ratio with more females in all populations), and important differences in breeding strategies (few successful males posses many offspring, contrasting with many successful females that nest every year, although on average each female rears a young successfully only every eight years).

In sum, to maximize their lifetime reproductive success a male's objective is to secure access to females, and to achieve this they invest four months fighting for dominance at the lek. This is the first mechanism of sexual selection, called male-male competition, which favors large size in males. In contrast, the main objective of a female is rearing their single chick, in which they invest 8-15 months of maternal care. Further, females also favor large size of males through a second mechanism of sexual selection, the female choice. This is how sexual selection acts on this species favoring the most extreme sexual size dimorphism among birds, and one of the strongest among vertebrates.

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Conservation of Great Bustard *(Otis tarda)* population of the Mosoni-Plain – A success story

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Sándor Faragó, Péter Spakovszky & Rainer Raab 2014. Conservation of Great Bustard *(Otis tarda)* population of the Mosoni-Plain – A success storyt. – Ornis Hungarica 22(2): 14–31.

Abstract At the turn of the 19-20th centuries, the Great Bustard population of the Kisalföld (Little Hungarian Plain) numbered 4000 specimens. By 1990, only about 100 individuals remained in the Hungarian and Austrian territories. Of the many possible negative factors of current times, the greatest pressure on the Great Bustard population stems from unfavorable crop structures, extensive use of intensive agricultural technologies and predation. During the past decades, we have seen a shift in nesting place locations from natural-like habitats to agrar-type habitats. This change may be explained by the more favorable structure and microclimate of this latter habitat type paralleled with greater food source availability. In order to escape this ecological trap, we have to engage in active conflict resolution that provides protection for the region's Bustard population.

For this very reason, the MOSON Project was founded in 1992 at the northern part of the Mosoni-Plain in the territory of Lajta-Hanság Co. Later, several Austrian regions joined the project. On these territories, out of the above mentioned 100 specimens, only 20 birds lived at the time. As the result of active habitat management of Great Bustards and coexisting small game species (mostly due to the influence of set-aside areas) as well as effective predator control (especially the Red Fox) resulted in an increase of the Great Bustard population. By the end of the 1990's, the population grew to 120-130 individuals which number was limited by the carrying capacity of this territory. Consequently, the species continued to reoccupy new regions in the Hungarian and Austrian territories. These days, the number of Great Bustards in these protected regions is estimated to be 400 individuals.

In 1998, the Mosoni-plain was given IBA (HU-001) status, and in 2004, the region was protected under the Natura 2000 EU nature conservation network.

Keywords: *Otis tarda*, MOSON Project, habitat improvement, predator control, agri-environmental scheme

Összefoglalás A 19-20. század fordulóján a Kisalföld túzokállománya még mintegy 4000 példány volt. 1990-re ebből a létszámból már csak mintegy 100 példány maradt fenn Magyarország és Ausztria területén. A sok negatív tényező közül napjainkban a kedvezőtlen vetésszerkezet, az intenzív termesztéstechnológiák és a predáció fejti ki a legnagyobb nyomást a túzokpopulációra. Az elmúlt évtizedekben a faj fészkelőhely váltását figyelhettük meg a természetszerű élőhelyek rovására, egyszersmind a szántóföldi habitatok javára. A váltás utóbbi élőhelyek kedvezőbb struktúrájával, mikroklímájával, valamint jobb növényi és állati eredetű táplálék kínálatával magyarázható. Ebből az ökológiai csapdából csak aktív, a konfliktusokat feloldó túzokvédelmi tevékenységgel tudunk kikerülni.

E célt szolgálja a Mosoni-sík északi részén, a Lajta-Hanság Zrt. területén 1992-ben alapított MOSON Project, melyhez csatlakoztak a későbbiekben osztrák területek is. E területen az említett 100 példányból 20 madár élt. A túzok és a koegzisztens apróvad fajok érdekében végzett aktív élőhelygazdálkodás (mindenekelőtt a set-aside területek dominanciája), valamint predátor (főként róka) kontrol azt eredményezte, hogy a túzokpopuláció az 1990-es évek végére elérte a 120-130 példányt, ami a terület eltartó képességének tekinthető. Ezt követően a faj mind magyar, mind osztrák területen újabb területeket foglalt vissza, s mára a térség túzokállományát mintegy 400 példányra becsüljük.

A Mosoni-sík 1998-ban IBA (HU-001), 2004-ben pedig Natura 2000 terület lett.

Kulcsszavak: *Otis tarda*, MOSON Project, élőhelyfejlesztés, predátor szabályozás, AKG program

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Introduction

At the turn of the 19th/20th century, the Great Bustard population of the Kisalföld spread across significantly larger territories than today and numbered approximately 800-900 individuals. There was also a large population of the species present in Austria with approximately 1000 birds, and in regions of the present-day Slovakia with about 2000 individuals. These population numbers were fairly constant up until the winter of 1928/1929. In the 1941 national survey, as direct consequence of the aforementioned year's winter conditions, only 500 bustards were counted in the Kisalföld region. After the war, in the 1950's, estimated size of the population was around 300 individuals; but by 1969 when the Great Bustard was given protection status, the population reduced to only 137 birds (Faragó 1978, 1993). Even though there is statistical data available from the hunting seasons of 1969-2003, due to the unsynchronized nature of the applied counting methods, in many cases, reported results differed significantly from the actual population size of the time. During 1973 and 1976, the population consisted of only 94-101 individuals. Five years later, in 1981, this continuous decline in population size was already apparent as we counted only 80-87 individuals. By 1989, the nesting population was made up of only 55-61 birds. During this period, almost the entire South-Hanság subpopulations disappeared, paralleled with notable declines in the Jánossomorja (Tóbi-liget) and Császárrét regions (Faragó 1982, 1986a, 1988, 1993, 1996a, Faragó *et al.* 1987).

In an attempt to identify the causes of this dramatic decline in population size (Faragó 2006), we determined nine key factors which have negatively influenced population dynamics: (1) harsh winters, (2) floods, drainage waters and extreme precipitation during breeding season, (3) fire damages, ground fires, (4) decline of suitable habitat for the Great Bustard due to changes in habitat structures, (5) effects of land ownership changes, (6) changes in crop structure on agricultural lands, (7) intensive crop production technologies (8) predation and (9) hunting pressure. Of these factors, there are several which no longer have an effect on the current population (2, 3, 4, 5, 9), while others rarely have an impact (1 and in part 2). Of the remaining negative factors of current times, the greatest pressure on the Great Bustard population stems from unfavourable crop structures, extensive use of intensive agricultural technologies and predation. These negative factors are even more intensified by the fact that the bustard is relatively conservative in its choice of lek territory as the birds show strong preference for specific sites. This behaviour can also be seen in the Kisalföld population (Faragó 1978, 1990). In addition, there is also a strong pattern for nesting site changes where the birds preferentially relocate to cropped agricultural sites from naturally occurring habitats. This change may be explained by the more favourable structure and microclimate of agricultural habitats paralleled with greater food source availability (Faragó 1979, 1981, 1986b). In order to escape this ecological trap, we have to engage in active conflict resolution which addresses the above issues and which provides protection for the region's Great Bustard population (Faragó 1989, 1996b).

Taking into consideration all these aspects, in 1992, we have established the MOSON Project in the Northern part of the Mosoni-plain in the Rajka/Hegyeshalom region, which encompassed 1232 hectares. The Great Bustard conservation program on the Lajta-Hanság Co. territory was initiated by the University of Sopron, Department of Game Management (today the University of West-Hungary, Institute of Wildlife Management and Vertebrate Zoology) in partnership with the Lajta-Hanság Co., the Fertő-Hanság National Park and WWF Austria. The aim of the conservation program was to increase the size of the population, which numbered only 20 individuals at the time, by means of facilitating ecologically supportive technologies (Faragó *et al.* 2001, Spakovszky *et al.* 2011).

Material and Methods

Before 1992 prior to initiation of the MOSON Project, the area of the Lajta-Hanság Co. was utilized for agricultural activity with all of the negative impacts of large scale habitat structures and applied growing technologies. Until 1991, most of the area was used for grain and rape (sometimes maize) production, further 169 hectares of land was utilized for sheep pasture and 20 hectares was left for meadows. When the Project began, grasslands and pastures were left uncut and the previously uncultivated agricultural lands were unutilized. Size of this area was 543 hectares which was a total of 44% of the Project's entire territory. As a result of extreme drought in 1991, the rape plantation yield was so low that harvesting costs would have outweighed any expected profits; therefore, that year's harvest was forgone. As a result of this, we have gained another 351 hectares of untouched land which expanded the protected 'bustard-friendly' region to 894 hectares (73%). The Project Directives – as entered into contract – were the following:

Agricultural activity

- Sheep pastures may only be utilized earliest from the middle of June but preferentially from the end of July
- Meadows may not be utilized for hay harvesting; cutting of meadows has to be done in September and/or October of every second year. This can also be achieved by means of grazing in September or October of these given years
- From 1994 onwards, winter barley should be changed to winter wheat which requires 3-4 weeks of delayed harvest
- Rye may not be treated with pesticides at all, whereas winter barley and winter wheat may only be treated up until the 15th of April
- Up until the date of harvest, no agricultural activity of any kind may be performed in the area
- Rape fields may only be treated against pests up until April 30th the latest
- In the event that some unexpected condition arises, which may have a negative impact (for example drought), harvesting of rape must forgo. In such years, the WWF Austria may offer monetary compensation for loss of harvest in certain

rape-planted agricultural areas to ensure protection of nesting birds.
- Feeding of green-stage plants and top-dressing-type fertilization of vegetation during the growing season are prohibited in case of all four crops.

Hunting / game management

- The LAJTA-HANSÁG Co. Hunting and Tourism Operation and their Austrian partner JAGDVERWALTUNG FLICK have agreed upon parallel time hunting utilization of the territory. The agreement ensures that during breeding season and in the nesting period, the birds remain undisturbed, as well as the agreement guarantees equal hunting opportunities for both parties.
- In case of Roe Deer *(Capreolus capreolus)* hunting, the parties have agreed to a hunting period different from the otherwise accepted hunting seasons in Hungary or in Austria. According to this: hunting period for Roe bucks is set between July 20th to September 30th,
- and hunting for does and fawns is only permitted between October 1st and February 15th.
- Within this time frame, both countries shall follow their own hunting season guidelines. The permitted hunting season date may be adjusted depending on any changes to the hunting guidelines of each country.
- During hunting (of Roe Deer), use of cars is strictly restricted to road ways in order to minimize any disturbance of Great Bustards who are guiding their chick.

Predator control is an ultimate necessity of any effective conservation program that aims to protect Great Bustards, birds in general or any other types of game. In light of this, in the 1990's, we annually placed 500 pieces of F2-treated eggs (with 3-chloro-4-methylaniline hydrochloride active substance specifically selected for crows) to limit the local crow population (of course this population was also under armed control). As a result, there were no Magpies *(Pica pica)* or Hooded Crows *(Corvus corone cornix)* nesting in the conservation territory. Population control of the Red Fox *(Vulpes vulpes)* was intensively performed by means of gun control, trapping and den hunting, especially since the vaccination (immunization) program against rabies – which began in 1993 – included the Project's territory as well.

Based on the above parameters, records were kept continuously and summarized annually. These included data on changes in habitat structures including developments, recording and mapping of habitats, agricultural land use and activity.

Continuous survey of the Project's region enabled us – based on *complete population assessment* – to estimate the size of the local Great Bustard population especially during the mating and autumn seasons. We also recorded sex ratios and successfully reared offspring output for the population. During the mating season and in winter, by synchronous counting, we were able to survey the West-Pannonian Great Bustard population as well (Raab *et al.* 2010).

Due to the nature of wildlife in the region, we also recorded the size and dynamics of hunting bags for Brown Hare *(Lepus europaeus)* and Roe Deer for each year.

We determined changes in predation pressure based on Red Fox hunting bag size.

Student t-test was used to compare the number of Red Foxes before and after 2000. We used linear regression to estimate trends in the number of individuals (Reiczigel *et al.* 2007).

Results

Habitat development

In the autumn of 1992, we established a so-called 'bustard-field' area which spanned over 25 hectares. On this land we planted a seed mixture of rape (5 kg/ha), alfalfa (20 kg/ha) and winter barley (100 kg/ha). Unfortunately, severe drought in that season hindered seed germination; therefore, the crop mixture was only able to provide food source in the seedling stage. Later, the seedlings got frost bitten and perished in the winter cold. However, even in such conditions, weeds germinated along with the crop mix offered large sources of green plant food in the spring time. In 1993, that multilateral agreement came into effect which specified the following habitat structure for the Project: Meadow: 20 ha, fallow: 746 ha, Bustard-field strips: 25 ha, Rape: 95 ha, Winter Barley: 72 ha and Rye: 105 ha (Total 1232 ha).

Agricultural activity was limited to only 22.1% of the territory, whereas 'bustard-friendly' territories extended to 77.9% (960 hectares). Due to the effect of extreme drought, the rape fields remained unharvested; therefore, we gained another 95 hectares of undisturbed territory. The only crops harvested in that year were barley (72 ha of land) and rye (105 ha of land). In the fall, withered tall weed-type vegetation was partly ploughed, while remaining weedy vegetation was flattened by heavy smoothing-plane before hunts in the area. In 1993/1994, 25 hectares of 'bustard-field' was planted with 100% rape. The plantation was fairly successful; therefore, it provided adequate food source for the winter. In addition to making the habitat structure of the territory more 'bustard-friendly', we also tried, as much as possible, to make the crops and associated agricultural practices less destructive to the population.

From 1994 onwards, we diversified the vegetation cover of the MOSON Project's territory by breaking up the monotony of the grass and uncultivated agricultural land areas and planted strips of rape, rye and spring barley. Location of these strips changed every year and as a result, these areas became 1-2-3-4 etc. year old fallows that each supported different flora and Arthropod fauna. In order to maintain desirable vegetation structures of uncultivated agricultural lands, it was unavoidable that we do some form of management; therefore, at the end of September/ beginning of October, the tall vegetation of these areas (mostly 1st and 2nd year fallows) were shredded. Every year, these associated costs were funded by the WWF Austria. This type of habitat management and the resulting habitat characteristics of the region continued until 2003. In 1995, as a result of state compensations (restitutions), four parcels of land from the Northeast region of the Project, as well as portion of the parcel located beside the left bank of the Lajta river canal, got out of the Lajta-Hanság Co.'s management; therefore, the Project's habitat-managed region decreased by 842 hectares.

Between 2004-2009, the Lajta-Hanság Co. won support of the so called '*Agricultural crop production based on bustard habitat development guidelines*' agri-environment scheme management program, which yielded 5042 hectares of protected land of which the MOSON Project was also a part of. As part of the implementation program in the Project's region, which now was concentrated to 872 hectares, we continued with the already utilized strip type habitat management technique and established various grains (winter wheat, winter bar-

Habitat (%)	2005/2006	2006/2007	2007/2008	2008/2009
Winter wheat	3.5	0.0	0.0	0.0
Winter crops (mixed)	0.0	0.0	0.0	6.5
Triticale	0.0	7.7	8.4	0.0
Crimson clover	0.0	0.5	0.0	0.0
Pea	8.4	0.0	0.0	0.0
Rape	0.0	1.4	3.5	2.6
Fallow	0.0	0.5	0.0	0.0
Total cultivated land	*11.9*	*10.1*	*11.9*	*9.1*
Total uncultivated agricultural land – fallow	*88.1*	*89.9*	*88.1*	*90.9*
Total MOSON Project	100	100	100	100

Table 1. Changes of the habitat structure between 2005–2009 in the MOSON Project
1. táblázat Az élőhely-szerkezet alakulása 2005–2009 között a MOSON Projectben

ley, triticale) and cow-grass, peas and rape in alternating plantation strips. 9.1-11.9% of the territory became cultivated agricultural land, whereas 88.1-90.9% was left as fallow area *(Table 1).*

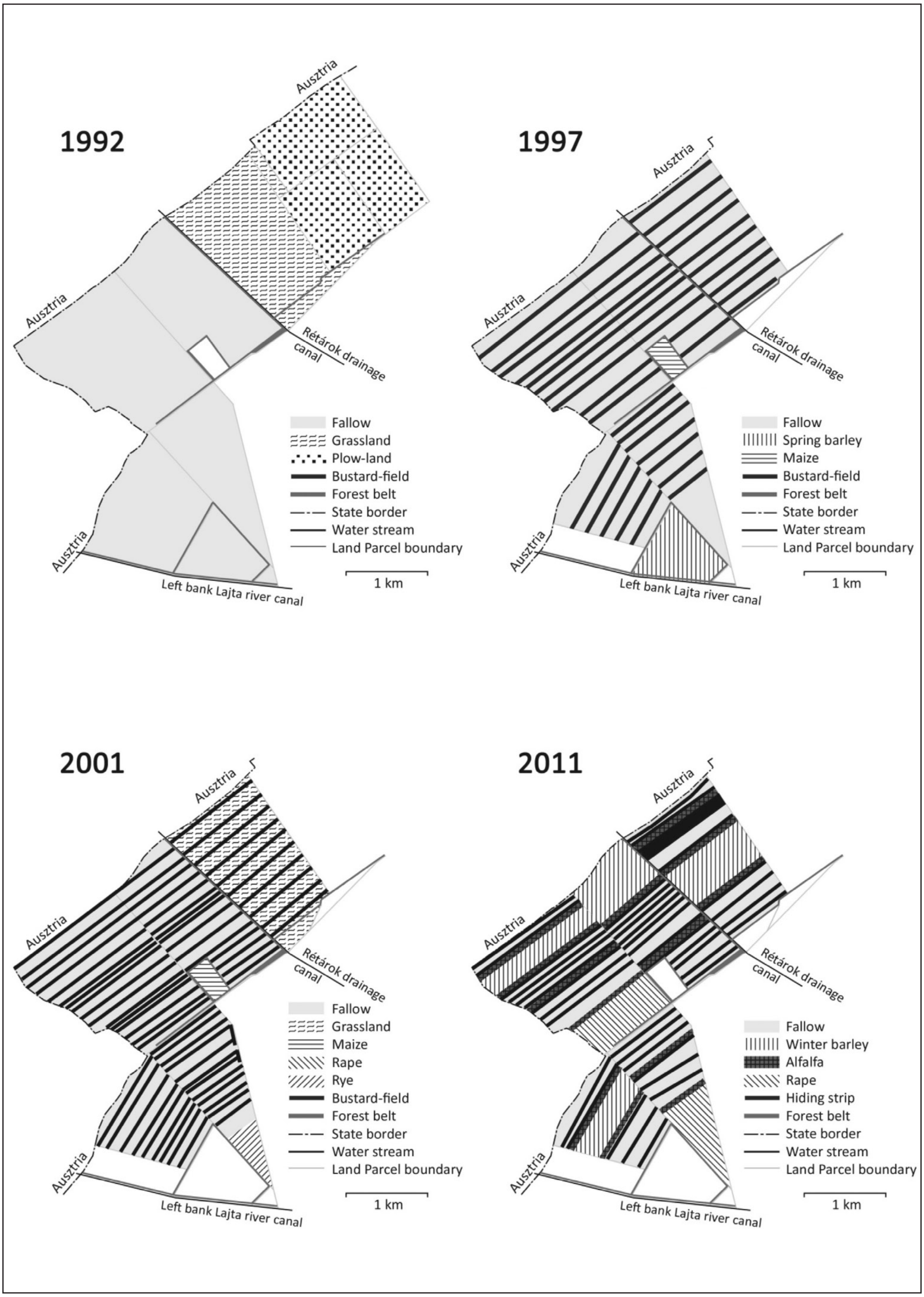
In 2009, the land owner was awarded funding by the AKG (agri-environment scheme management program) for another 5 year period. However, the 'migrating' bustard-land management technique could no longer be followed by the land registry. Therefore, we converted to a management technique which enabled us to perform fallow land management for a maximum of 3 years after a 1 year of active cultivation period of the land. The proportion of alfalfa in the Project was 7.5% (64.7 ha) which was distributed in 13 land strips. In addition, in one of the years, partly due to crop rotation and limitations of the agricultural region, we also planted rape (97.3 ha – 11.3%). From grains, due to local technological limitations, we chose winter barley to be grown in the area (35.1-262.0 ha – 4.1-30.4%). However, most of the territory remained as fallow lands (502.4-796.8 ha – 58.3-92.5%) *(Table 2, Map 1).*

Predator control

The Lajta-Hanság Co., as we have already discussed, continues to engage in intensive

Habitat (%)	2009/2010	2010/2011	2011/2012	2012/2013	2013/2014
Fallow	92.5	58.3	64.6	62.1	88.4
Alfalfa	7.5	7.5	7.5	7.5	7.5
Winter barley	0.0	22.9	27.9	30.4	4.1
Rape	0.0	11.3	0.0	0.0	0.0
Total MOSON Project	100	100	100	100	100

Table 2. Changes of the habitat structure between 2009–2014 in the MOSON Project
2. táblázat Az élőhely-szerkezet alakulása 2009–2014 között a MOSON Projectben



Map 1. Habitat development in the MOSON Project
1. térkép Élőhelyfejlesztések a MOSON Project-ben

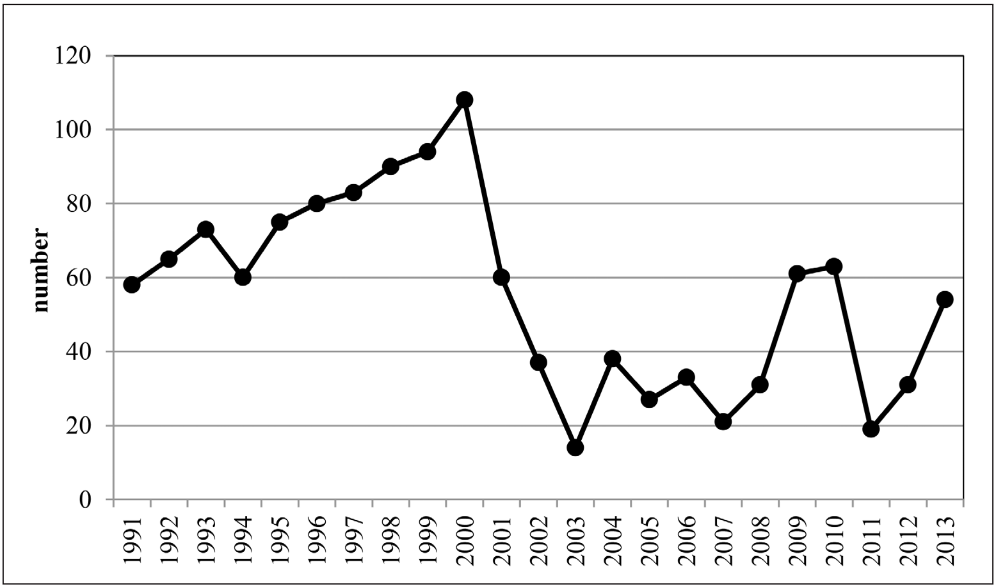


Figure 1. Red Fox hunting bag dynamics between 1990–2013 in the MOSON Project
1. ábra A vörös róka terítékdinamikája 1990–2013 között a MOSON Projectben

predator control in the region since the beginning of the Project. In case of the Corvidae (which have not nesting colony present locally), the control focuses on settlement avoidance from the adjacent Szigetköz area or Austrian territories. For Magpies, this type of management is highly effective. However, in case of the Hooded Crow, the incoming transient population from the Szigetköz and Austria is significant enough for these birds to continue to be present in the Project's territory. The most intensive work concentrated on predator control of the Red Fox population *(Figure 1)*. Foxes decreased by 41 (CI: 26.7; 55.2, $P<0.0001$) after 2000.

Great Bustard population dynamics

Based on the sprig population assessment of the MOSON Project, the initial Great Bustard population of the region was 20 individuals *(Figure 2)*. As of 1992, this population size began to grow as a direct result of the implemented habitat management measures. These changes had a positive impact on offspring survival to adulthood, which up until that point most often perished due to the destructive nature of the past agricultural activities of the region. Significant recovery was finally seen from 1995 when the successfully reared female chicks born in 1992 reached sexual maturity. They then increased the reproductively active population of hens who laid eggs and successfully reared their own chicks. From 1998, a significant population boom was expected which was reflected in the spring and autumn population surveys where the number of Great Bustards reached or exceeded 120 individuals. Assuming a linear trend, the yearly rate of growth is 5.7 ($SE=0.73$, $P<0.0001$) individuals in case of spring during the whole time period, and 14.1 ($SE=3.5$, $P=0.0007$) individuals until 1999 in case of autumn. After 1999 no trend can be seen in the number of Great Bustards in autumn. We specu-

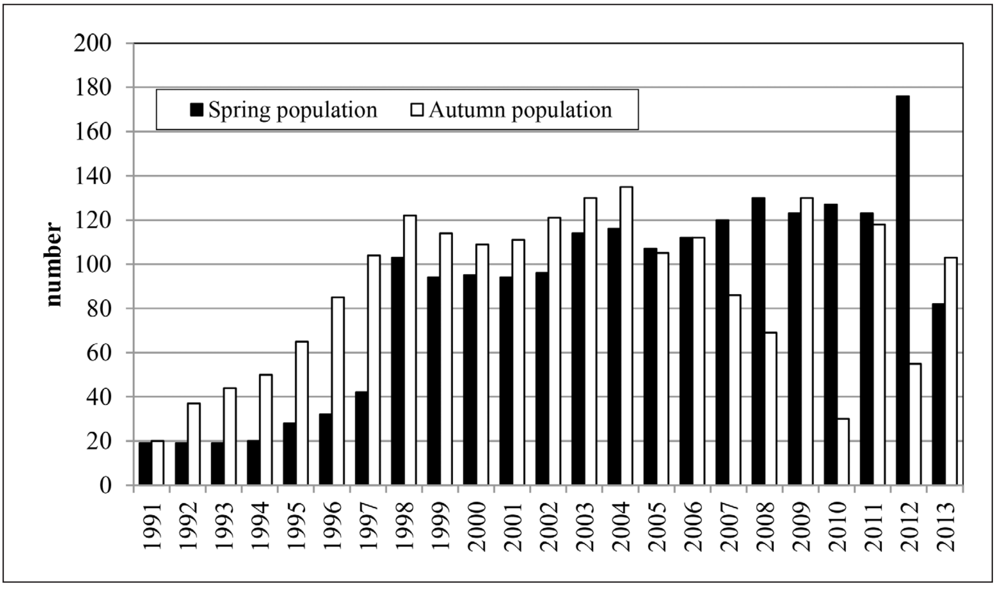


Figure 2. Great Bustard population dynamics between 1991–2013 in the MOSON Project
2. ábra A túzokállomány dinamikája 1991–2013 között a MOSON Projectben

	1991	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**
Cock	6	6	6	6	6	10	14	41	24	22
Hen	13	13	13	14	22	22	28	62	70	73
Spring population	19	19	19	20	28	32	42	103	94	95
Chick	1	17	9	13	15	26	19	19	20	14
Fall population	20	37	44	50	65	85	104	122	114	109

	2001	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**
Cock	22	21	26	29	45	52	54	56	49	45
Hen	72	68	88	87	62	60	66	74	74	82
Spring population	94	96	114	116	107	112	120	130	123	127
Chick	17	18	16	19	11	5	7	8	6	2
Fall population	111	121	130	135	105	112	86	69	130	30

	2011	**2012**	**2013**
Cock	40	57	48
Hen	83	119	34
Spring population	123	176	82
Chick	8	4	7
Fall population	118	55	103

Table 3. Estimated size of the Great Bustard population between 1991–2013 in the MOSON
3. táblázat A túzokállomány becsült létszáma 1991–2013 között a MOSON Projectben

Year	Heideboden (A)	Parndorfer Platte (A)	Hanság (A)	Kisalföld (H)	Total
1990	0	6	16	86	108
1996	1	6	14-16	65-66	86-89
2000	14	8	10-14	89	121-125
2003	34-67	9-10	16-17	114	173-208
2005	60-82	8	18-21	89-105	175-216
2006	76-93	8	24-27	104	212-232
2007	85-98	14	26-27	103-114	228-253
2008	93-101	25-26	22-24	80-111	220-262
2009	92-112	20-26	16-23	93-137	227-298
2010	130-155	24-26	20-24	78-116	252-321
2011	127-150	20-27	19-25	100-127	266-329
2012	117-145	13-19	22-26	145-178	297-368
2013	211-271	18-23	20	74-83	323-397

Table 4. Dynamics of the Kisalföld's (Hungary and Austria) spring Great Bustard population between 1990–2011 (Raab *et al.* 2010 and updated)

4. táblázat A Kisalföld (Magyarország és Ausztria) tavaszi túzokállományának dinamikája 1990–2011 (Raab *et al.* 2010 és aktualizálva)

late that this population size is limited by the carrying capacity of this territory.

Around this time, however, we also noticed a gradual resettlement of the Great Bustards in the neighbouring Austrian and Slovakian regions (Raab *et al.* 2010), and they also appeared south of the Mosonszolnok region of the LAJTA Projects, as well as in the Lébény range (Faragó & Spakovszky 2012) *(Table 4, Maps 2 – 3)*.

Some of the data showed drastic changes from year to year in certain regions which can be explained by the leks which were originally undisturbed areas and as such were frequently visited by the birds. The most significant accomplishment of this conservation effort was that, when compared to the initial population size of the Project in the early days, the bustard population later quadrupled and numbered over 400 individuals in the region!

Population dynamics of huntable coexisting species

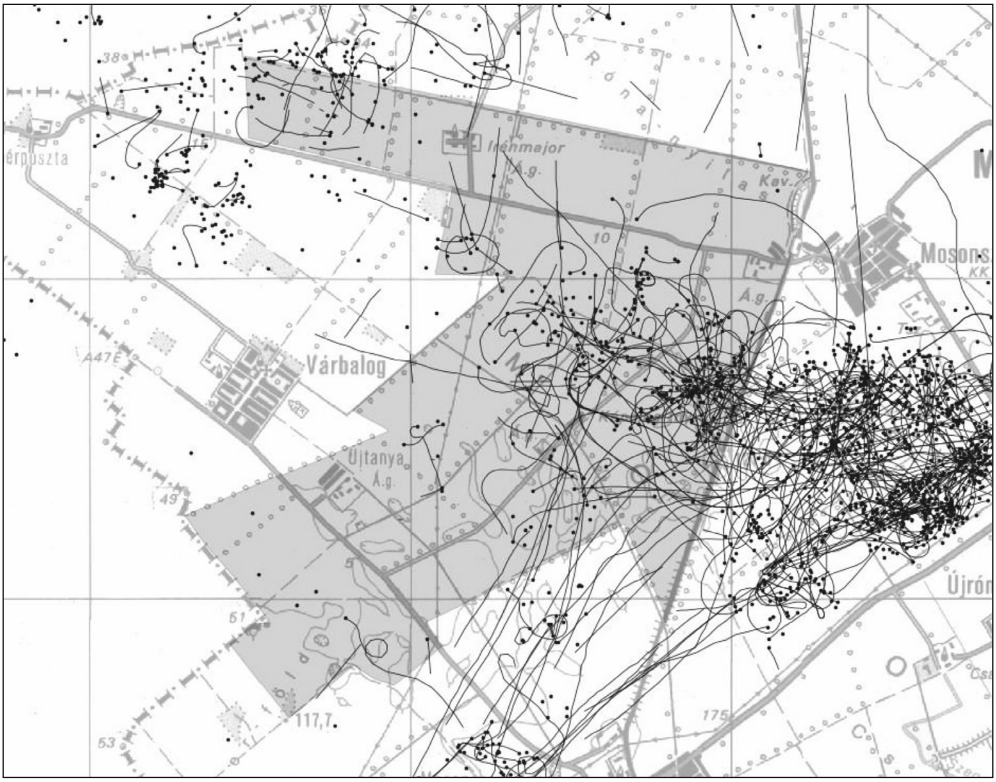
Based on the 'wise use' concept (Robertson 1991), there can be no doubt that any improvement to the habitat structures and reduction in disturbance not only positively impact on the Great Bustard population but also positively influence other coexistent protected bird and huntable game populations.

Along with a slight increase in population numbers, we also observed a concentration of Roe Deer in the area, especially between September and April. Exact numbers can be determined from the changes of hunting bag sizes *(Figure 3)*. Hunting bag of the Roe Deer reflects the population dynamics of this species. The Roe Deer population, numbering almost 300 individuals, is significantly underutilized in the Project's region,

Map 2. Distribution and movement of the Great Bustard population in the MOSON Project region
2. térkép A túzok elterjedése és mozgása a MOSON Project térségében

which situation has improved somewhat in the latter years. In spite of this underutilization, the Project has been able to produce trophies every year which had a medal or even sometimes the gold medal awarded. The number of Roe Deers significantly increased by 2.8 (SE=0.8, P=0.00275) animals during the years.

The greatest positive result was seen in the dynamics of the Brown Hare hunting bag. Since the initiation of the Project, the original number of hunting bag of this species (333 individuals) almost doubled after the first years, which resulted in the shooting of an additional 280 animals in 1992 compared to 1991, and 314 animals more in 1993. As a direct consequence of all the habitat development in the area, the hunting bag grew over 1000 animals by 1994 and over 1500 animals by 1995. Within 5 years, the hunting bag for the Brown Hare has quintupled. In 1997, there was a slight decline in the size of that year's hunting bag as the hunts resulted in the shooting of only 1200 animals, but in 1999, the hunting bag of the Hare again numbered 1200 individuals. As it was already mentioned in case of the Great Bustard population, in 2000 and 2001, the extreme drought event that occurred during the breeding season also had a negative impact on the Brown Hare population. In these years, the hunting bags of 2000 and 2001 had only 800 and 464 individuals, respectively, even though in the



Map 3. Distribution and movement of the Great Bustard population in the LAJTA Project region
3. térkép A túzok elterjedése és mozgása a LAJTA Project térségében

spring, these numbers were expected to be much higher. After a short increasing period, there was a significant decrease in the number of Brown Hares after 1996. The yearly decreasing rate was 54.7 (SE=14.8, P=0.00192) animals.

Discussion

Our results show that the parameters of Great Bustard-friendly habitats outlined earlier, especially the extensively managed lek territories and surrounding regions (including fallows), have great capacity to attract and support the Great Bustard population. All factors such as the calm, undisturbed surroundings in the mating and nesting season, the diverse habitat structure, the favourable microclimatic conditions and ample food availability, all contribute to the success of such territories. The fallows and the 'bustard fields', which are specifically planted with a diverse crop selection, provide not only the necessary amount of animal food availability, mostly Arthropods, for the chicks, but also provide much needed quality and diversity in their diet. The implemented, almost entirely chemical-free, agricultural activity in the protected habitats ensures that any direct or indirect chemical exposure to pesticides is prevented. Last but not least, with this technique, we can avoid those damages and losses that occur as a result of agricultural practices that utilize mechanized

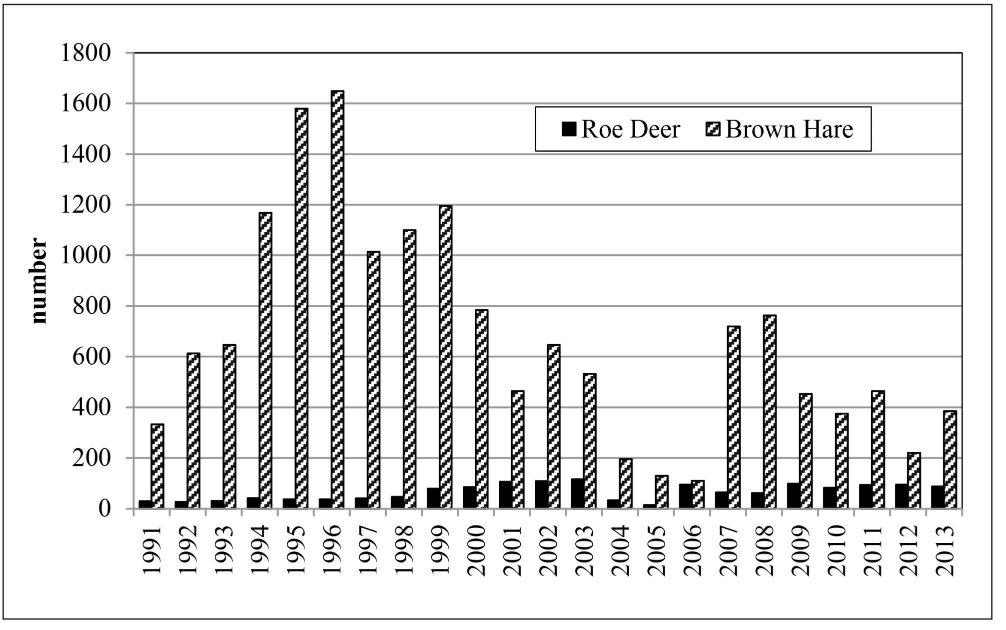


Figure 3. Utilization dynamics of the Brown Hare and Roe Deer in the MOSON Project between 1991–2013
3. ábra A mezei nyúl és az őz hasznosítás-dinamikája a MOSON Projectben 1991–2013

methods (such as mowing or cutting) and which pose the greatest danger to the Bustards. These techniques resemble conditions that are similar to those of the 19-20th century when the Hungarian agriculture was extensive and which period also coincided with the 'golden age' of small game populations (Faragó 1997). It has been conclusively shown by earlier Spanish (Alonso & Alonso 1990) and several Hungarian habitat preference studies (Faragó & Kalmár 2006, 2007, Kalmár & Faragó 2008, Faragó & Spakovszky 2012) that positive territorial characteristics and supportive habitat development have great positive influence on local communities *(Table 5)*.

The significance of fallow lands (short- and longterm fallows) / uncultivated agricultural lands, as well the presence of stubble fields, is supported by several Spanish studies (Alonso & Alonso 1990, Lane *et al.* 2001, López-Jamar *et al*. 2011). This significance is especially important in those regions where infrastructure development has taken over or where utilization of the specific land areas changes. In addition to these habitat types, preferential selection for alfalfa-type habitats has been demonstrated both by Alonso and Alonso (1990) and by our own observations in different study areas (Faragó & Kalmár 2006, 2007, Kalmár & Faragó 2008). In general, it can be concluded that there is a spatial and temporal variability in the selection of preferred habitat types (Martín *et al.* 2012). The key significance of crop lands is that they provide nesting sites for the birds (see Magaña *et al.* 2010). However, these lands are also important habitats for Great Bustards in other times of the year when these crop fields enter the stubble or fallow land phase.

Great Bustards clearly avoid urban or developed rural areas and high traffic roads (usually the artefacts of human activity), or

Habitat	2005/2006				2006/2007				2007/2008			
	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Fallow	**0.84**	**0.83**	-1.00	-0.98	**0.77**	0.42	-1.00	-1.00	**0.78**	**0.77**	-0.61	-0.65
Rape	-0.76	0.00	**0.81**	**0.86**	**0.52**	0.00	**0.74**	**0.77**	-0.13	0.00	**0.77**	**0.77**
Volunteer plants	-1.00	-1.00	**0.86**	-1.00	0.00	-0.12	**1.00**	0.00	**0.86**	-0.46	-1.00	-0.90
Winter wheat	-0.38	0.00	-1.00	-0.71	-	-	-	-	-0.60	0.00	-1.00	-0.98
Stubble	-1.00	-0.37	-1.00	-1.00	-1.00	0.26	-1.00	0.11	0.00	-0.18	0.00	0.00
Plough-land	-1.00	-1.00	-1.00	-1.00	-0.74	-0.96	-0.55	-0.77	-0.64	-0.56	-0.38	-0.73
Grassland	-	-	-	-	**0.62**	0.22	-1.00	-1.00	-	-	-	-
Alfalfa	-	-	-	-	-0.15	0.08	-1.00	-1.00	-0.67	-0.75	-1.00	0.09

Table 5. Preferred habitats (Ivlev-index) of the Great Bustard in the Mosoni-plain (2005–2008) (based on Faragó & Kalmár 2006, 2007, Kalmár & Faragó 2008)

5. táblázat A túzok élőhely preferenciái (Ivlev-index) a Mosoni-síkon (2005–2008) (Faragó & Kalmár 2006, 2007, Kalmár & Faragó 2008 alapján)

habitats where they have no clear horizontal view of their surroundings (Alonso & Alonso 1990, Lane *et al.* 2001, Osborne *et al.* 2001). All Spanish authors take note of the Great Bustards' habitat fidelity which is not only limited to their leks but also to their nesting sites and wintering territories (Alonso & Alonso 1990, Alonso *et al.* 2000, Lane *et al.* 2001, Osborne *et al.* 2001). These observations are also supported by our study and the successful rehabilitation of the MOSON Project region and its Great Bustard population.

This habitat fidelity is especially important in the West region of the Carpathian basin where winter migration of Great Bustards occurs only in extreme weather conditions (Faragó 1990b). The Spanish Great Bustard populations, however, show partial, short/medium distance migration in their area (Alonso *et al.* 1995, Alonso *et al.* 2000, Alonso *et al.* 2001). As a result of this, we can say that in the West-Pannonian region, the conservation of lek and surrounding habitats are of greatest importance to the local Great Bustard population.

Habitat management also positively influences other bird communities, as habitat structures like fallow lands, depending on duration of the resting phase, support diverse bird communities and increase population sizes, as this has been demonstrated by Kovács *et al.* (2009) on the Hevesi-Plain (NE-Hungary). We also see similar patterns in the MOSON Project and its surrounding regions in Austria (Raab *et al.* 2010). An increase in diversity and size of animal communities inherently attract larger numbers of predators which in general, as well as in case of the Great Bustard population, also intensifies predation pressure on prey species in the region. Often, like it is in the case of eagles, they can have such drastic impact on some other species that habitat selection and dispersion is greatly limited, which may even lead to relocation from that region (Spakovszky 2009). This predator pressure partly explains the drastic reduction of the Brown Hare population. However, in this case, another significant influencing factor was the appearance of the European Brown Hare Syndrome (EBHS) virus in the beginning of 2000's, which, due to the high population density in the region, became the most important population-limiting factor.

In many Western European countries most of the research work focuses on the limitations or lack of continuous coverage of agri-environmental protection programs (Llusia & Onate 2005, Kleijn *et al.* 2006), and similar conclusions were drawn in the Dévaványa region and the Bihari-plain (Nagy *et al.* 2008) or in the Kiskunság by Németh *et al.* (2009). We, on the other hand, can only attest to the success of the Mosoni-plain conservation program. The reason for that is that while others point to this as negative criticism, on the Mosoni-plain, due to the size of the Lajta-Hanság Co. territory, we were able to include in the program such key land areas (lek territory, nesting sites, wintering habitats). This had significant and relevant effect on the recovery and stability of the Great Bustard population and eventually led to the expansion of their local population. In the MOSON Project, such measures as delaying the commencement of reaping or stem-crushing further reduced those losses which would have normally occurred from these technologies.

Another important achievement of this Project was that while the Mosoni-plain was not listed as an important Hungarian bird habitat up until 1989 (Waliczky 1992), by the second half of the 1990's, the Mosoni-plain was given IBA (Important Bird Area) status based on the new criteria of the National and European significant habitats list. The Mosoni-plain was listed with the code number of HU-001, a region of 4310 hectares included and protected species were the *Otis tarda* and the *Perdix perdix* (Nagy 1998, Nagy 2000). Based on all these, in 2004, the territory was placed under Natura 2000 (European Union Nature Conservation Network) protection. The MOSON Project served as model for the creation of the Hungarian Great Bustard Conservation Program (Faragó *et al.* 2013) and it also provided the basis for the Bustard LIFE Project between 2005-2008 (Faragó & Kalmár 2006, 2007, Kalmár & Faragó 2008, Faragó & Kalmár 2011).

Acknowledgement

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Key mortality causes of the Great Bustard *(Otis tarda)* in Central Hungary: an analysis of known fatalities

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Csaba Vadász & Miklós Lóránt 2014. Key mortality causes of the Great Bustard *(Otis tarda)* in Central Hungary: an analysis of known fatalities. – Ornis Hungarica 22(2): 32–41.

Abstract In this study, we identified the key mortality causes of eggs, juveniles and adults of the Great Bustard *(Otis tarda)* and quantified the relative importance of those, based on systematic data collection that have been carried out during the period between 2005 and 2014 at the Upper-Kiskunság region in Central Hungary. Rate of mortality regarding juveniles and adults was 39.71% caused by anthropogenic factors. Within the anthropogenic factors leading to mortality, collision was represented by 81.48% of fatalities, whereas mowing/hay making represented by 18.52%. Hay making/mowing was the factor leading to unsuccessful breeding attempt with the strongest negative effect on the breeding success of the investigated population of the Great Bustard, as it was represented by 50.96% of all known mortality cases. Chemical treatment had the factor with the second strongest effect, as it was represented by 12.33% of all known mortality cases. The rate of unsuccessful breeding (hatching) caused by particular activities (hay making/mowing, tillage, harvesting) varied between 68.42% and 75.00%. It was the disturbance by passers-by which led to the highest portion of unsuccessful breeding with 83.33% unsuccessful nests.

Keywords: Great Bustard, mortality factors, collision with cables, mowing, anthropogenic disturbance

Összefoglalás Munkánkban a túzok *(Otis tarda)* tojásai elpusztulásának, illetve a juvenilis és adult korú egyedek elhullásának okait vizsgáltuk a Felső-Kiskunságban a 2005-2014 közötti időszakban. A juvenilis és adult korú egyedek elhullásának oka 39,71%-ban volt emberi hatásokra visszavezethető, ezeken belül is a légvezetékekkel való ütközés reprezentálta messze a legtöbb elhullást (81,48%). A kaszálás, mint mortalitási faktor jellemzően a pullus korú egyedek pusztulásához vezetett (18,52%). A tojások kikelésének sikertelenségéhez a kaszálás járult hozzá legnagyobb mértékben (az összes sikertelen kelés 50,96%-a erre volt visszavezethető). A szántóföldi kultúrák vegyszeres növényvédelme 12,33%-át tette ki a sikertelen kelések okainak. A különböző típusú zavarások (mezőgazdasági munkák) után a kelés sikertelensége 68,42-75,00% között változott. A gyalogos közlekedés során felriasztott tojók fészkeinek 83,33%-ánban volt sikertelen a kelés.

Kulcsszavak: túzok, elhullási okok, légvezetékkel való ütközés, kaszálás, antropogén zavarás

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Introduction

Although it is usually impossible to follow the life history of every single individual of a wild population, it would evidently be of great importance to be able to estimate the relative importance of different factors which lead to death of individuals. From nature conservation perspective, by identifying those threatening factors that can be neutralized (or minimized, at least), vulnerable populations could be enforced as habitat management could be based on real data, which would form the basis of evidence-based conservation (see Sutherland *et al.* 2004). In financial perspective, available resources can be allocated optimally (i.e. it would provide us with the possibility to finance those interventions which would contribute to stabilizing a certain population at lowest costs.

The Great Bustard is a relatively well known bird species (Alonso *et al.* 1994) via its vulnerable status (BirdLife International 2013). However, there is still poor information about the quantitative life table for its Hungarian populations. Nevertheless, by gathering information from different resources, it is possible to construct a model describing the age-specific mortality. For conservationists, these kind of models can provide important management implications. Furthermore, the recently unquantifiable units/parts of these models can assign potential topics for future scientific research.

In this study, by summing all the available information about the most numerous Great Bustard population in Hungary (see Práger 2005, Alonso & Palacín 2010), we identified the key mortality causes and quantified the relative importance of those, based on systematic data collection that have been carried out during the period between 2005 and 2014.

Materials and methods

The study area and the investigated population

The study area is located at the Upper-Kiskunság region in Central Hungary. This area is characterized by large-scale mosaics of unwooded grasslands and ploughfields, hosting the largest Pannonian Great Bustard population, which, in fact still shows continuous increase (Práger 2005). Major part of the area is designated as a Special Protection Area in the Natura 2000 network (HUKN10001 and HUKN10002). The core area of the Great Bustard population (including the displaying and the nesting sites) falls under national protection, forming parts of Kiskunság National Park.

Datasets used

Known fatalities regarding juveniles, immatures and adults

The factor leading to the death of every single individual was determined by investigating all the carcasses found during the systematic monitoring and irregular activities (e.g. notification from farmers, land owners, etc. about dead Great Bustards) between 2005 and 2014.

Known fatalities regarding eggs

Between 2005 and 2014, all the cases regarding unsuccessful attempts on hatching eggs having been laid in nests found accidently during different kind of field works and other activities (e.g. hunting) were categorized based on the type of the field work/activity.

Threatening factors of the nests

Between 2005 and 2014, the fate of all the eggs having been laid in nests found accidently during different kind of field works and other activities (e.g. hunting) was investigated. There were no efforts put into finding nests except for the ones having been revealed by the above mentioned activities.

The number of revealed nests in the case of lands with different legal/protection status

The location of each nesting site was classified based on the combination of type of utilization and protection status of the land hosting the nest. Regarding the type of utilization, three categories were set: (1) arable fields, (2) mowed meadows, (3) pastures. Regarding the protection status, four categories were set: (1) no protection with intensive utilization, (2) no protection with no utilization, (3) involvement in the agri-environmental scheme focusing on the protection of the Great Bustard, (4) regulated (restricted) by nature conservation authorities (at land falling under protection at national level). Thus, each site was assigned to one of the twelve combinations of the above mentioned categories. Due to prior experience, the probability of detection of the presence of a breeding female in the case of the particular land type is shown in *Table 1*. This probability value reflects the assumption that a female taking wings is surely observed by the person performing the disturbing activity. Accordingly, this value can be regarded as an indicator of intensity of the particular form of land use. Since the legal regulations on agri-environmental scheme focusing on the protection of the Great Bustard were different in the case of the two periods (i.e. the one between 2005 and 2009, and the other between 2009 and 2014), the set of field works allowed to be carried out was different, evidently resulting in different values of probability of detection of a certain nest. Accordingly, in this analysis nest having been revealed during exclusively the second programme (between 2009 and 2014) were included.

Results

Mortality causes of juvenile, immature and adult individuals

Between 2005 and 2014, 68 fatalities have been recorded regarding juvenile and adult individuals. The list of mortality causes are shown in *Table 2*. The portion of fatalities caused by: natural factors (including predation and diseases) is 58.82%, anthropogenic factors is 39.71% and unknown factors is 1.47%. Collision with different kind of cables (medium voltage power lines, railway cables, electric fences) was represented by 32.35% of all known fatalities. Within the anthropogenic factors leading to mortality, collision was represented by 81.48% of fatalities, whereas mowing/hay making represented by 18.52%.

Mortality causes of eggs

Between 2005 and 2014, 209.2 fatalities have been recorded regarding eggs (In the case of destroyed nests, when it was not possible to determine the clutch size (i.e. the number of eggs), the number of destroyed eggs was calculated as 1.8/nest). The list of mortality causes are listed in *Table 3*. Hay making/mowing was the factor leading to unsuccessful breeding attempt with the strongest negative effect on the breeding success of the investigated population of the Great Bustard, as it was represented by 50.96% of all known mortality cases. Chemical treatment was the factor with the second strongest effect, as it was represented by 12.33% of all known mortality cases.

Threatening factors of nest

Between 2005 and 2014, 199 nests have been revealed during different kind of field activities or works. The portion of nests characterized with unsuccessful and successful hatching in the case of specific activities that led to detection of the nests is shown in *Table 4*.

	No protection, intensive utilization	No protection, no utilization	Agri-environmental scheme focusing on the protection of the Great Bustard	Regulated (restricted) by nature conservation authorities (at land falling under protection at national level)
Arable fields	Any type of field works is likely to be carried out at least once during the incubation period, thus the probability of detection of a breeding female (i.e. the nest) is approx. 100%.	No field work is likely to be carried out, thus the probability of detection of a breeding female (i.e. the nest) is approx. 0%.	Due to the regulations of the agri-environmental scheme the probability of detection of a breeding female (i.e. the nest) is approx. 60%.	No field work is likely to be carried out, thus the probability of detection of a breeding female (i.e. the nest) is approx. 0%.
Mowed meadows	Mowing is likely to be carried out at least once during the incubation period, thus the probability of detection of a breeding female (i.e. the nest) is approx. 100%.	No mowing is likely to be carried out, thus the probability of detection of a breeding female (i.e. the nest) is approx. 0%.	No mowing is likely to be carried out during the incubation period, thus the probability of detection of a breeding female (i.e. the nest) is approx. 0%.	No mowing is likely to be carried out during the incubation period, thus the probability of detection of a breeding female (i.e. the nest) is approx. 0%.
Pastures	Since the presence of a herder/farmer is influenced by the grazing system (e.g. electric fence with no herder, traditional pasturing etc.), the probability of detection of a breeding female (i.e. the nest) is indefinable.	No grazing is likely to be carried out, thus the probability of detection of a breeding female (i.e. the nest) is approx. 0%.	Since the presence of a herder/farmer is influenced by the grazing system (e.g. electric fence with no herder, traditional pasturing etc.), the probability of detection of a breeding female (i.e. the nest) is indefinable.	Since the presence of a herder/farmer is influenced by the grazing system (e.g. electric fence with no herder, traditional pasturing etc.), the probability of detection of a breeding female (i.e. the nest) is indefinable.

Table 1. The probability of detection a certain breeding female Great Bustard (i.e. a certain nest) in the case of lands with different type of utilization and protection status based on prior experience

1. táblázat Egy, az adott típusú hasznosítás alatt álló, illetve védettségi szintű területen költő túzok tojó észlelésének (fészek megtalálásának) valószínűsége

Mortality causes	Number of detected dead individuals
Natural (excluding predation and diseases)	37
Collision with medium voltage power lines	14
Collision with railway cables	7
Hey making/mowing	5
Diseases	2
Collision with electric fence	1
Predation	1
Unknown	1
Total	68

Table 2. Mortality causes of juvenile and adult Great Bustards in Central Hungary between 2005 and 2014 based on known fatalities

2. táblázat A juvenilis és adult túzokok elhullásának okai a Duna-Tisza közi populáció esetében, a 2005 és 2014 között detektált esetekben

Mortality causes	Number of eggs (regarding unsuccessful breeding attempts)
Hey making/mowing	106.6
Chemical treatment of crops	25.8
Tillage	18.8
Unknown	14.2
Harvesting	11.8
Grazing by livestock	8
Eggs left by females due to human disturbance (passersby)	7
Secondary tillage (with cultivators)	5
Eggs left by females due to human disturbance (cars)	3
Sowing	2
Predation	2
Silage making	2
Soil preparation	2
Eggs left by females due to hunting	1
Total	209.2

Table 3. Mortality causes of Great Bustard eggs in Central Hungary between 2005 and 2014 based on known fatalities. In the case of destroyed nests, when the number of eggs could not been possible to determine, the number of destroyed eggs was calculated as 1.8

3. táblázat A túzok tojások pusztulásának okai a Duna-Tisza közi populáció esetében, a 2005 és 2014 között detektált esetekben. Azokban az esetekben, amikor a fészekalj pusztulásakor a tojásszám nem volt meghatározható, az elpusztult tojások számát 1,8-nek becsültük

Threatening factors	Number of revealed nests due to the specific activity	Portion of unsuccessful breeding attempts within all detected nests (and within the nests with known fate)	Portion of successful breeding attempts within all detected nests (and within the nests with known fate)	Portion of breeding attempts with unknown success
Hay making/ mowing (alfalfa fields)	62	62.90% (68.42%)	29.03% (31.58%)	8.06%
Hay making/ mowing (grasslands)	28	75.00% (75.00%)	25.00% (25.00%)	0.00%
Chemical treatment of crops	40	35.00% (43.75%)	45.00% (56.25%)	20.00%
Tillage	16	56.25% (75.00%)	18.75% (25.00%)	25.00%
Unknown	13	76.92% (83.33%)	15.38% (16.67%)	7.69%
Harvesting	9	66.67% (75.00%)	22.22% (25.00%)	11.11%
Grazing by livestock	9	44.44% (57.14%)	33.33% 42.86%)	22.22%
Eggs left by females due to human disturbance (passersby)	9	55.56% (83.33%)	11.11% (16.67%)	33.33%
Secondary tillage (with cultivators)	4	75.00% (75.00%)	25.00% (25.00%)	0.00%
Eggs left by females due to human disturbance (cars)	2	100.00%	0.00%	0.00%
Sowing	1	100.00%	0.00%	0.00%
Silage making	1	100.00%	0.00%	0.00%
Soil preparation	1	100.00%	0.00%	0.00%
Eggs left by females due to hunting	3	33.33%	0.00%	66.67%
Stalk chopping	1	0.00%	0.00%	100.00%

Table 4. Threatening factors of Great Bustard nests in Central Hungary between 2005 and 2014 based on data originating from discovered nests

4. táblázat A túzok fészkeket veszélyeztető tényezők a Duna-Tisza közi populáció esetében, a 2005 és 2014 között detektált esetekben, a megtalált fészkek alapján

Hay making/mowing (regarding both alfalfa fields and grasslands) led to the detection of 45.22% of all revealed nests, whereas chemical treatment of crops led to 20.10% of all revealed nests, all the soil tilling (including soil preparation, tillage, secondary tillage) led to 10.55% of all revealed nests, grazing led to 4.52% of all revealed nests and unintended disturbance (by passersby, cars, hunters) led to 6.30% of all revealed nests.

There were 11 specific activities that led to detection of more than one nest. Regarding these activities, the portion of unsuccessful breeding attempts ranged between 43.75% and 83.33%. It was chemical treatment of crops which represented the lowest negative impact on hatching probability, as 56.25% of nests with known fate were successful. Most activities (hay making/mowing, tillage, harvesting) led to unsuccessful breeding attempt (hatching) in roughly 75% (68.42% to 75.00%) of specific cases with known fate. It was the disturbance by passersby that led to the highest portion of unsuccessful breeding (hatching) with 83.33% unsuccessful nests.

Number of revealed nests in the case of lands with different type of utilization and protection status

Between 2009 and 2014, 91 nests have been revealed. The number of revealed nests assigned to the specific categories is shown in *Table 5*.

Most of the nests were found at plough fields (73.26%), at grasslands 20.88% (mowed meadows) and 2.20% (pastures) of the nests were detected.

Regarding the intensity of cultivation, 59.34% of all nests were detected at intensively cultivated lands (with no restrictions), 32.97% at lands covered by the agri-environmental scheme focusing on the protection of the Great Bustard and 7.69% at areas protected at national level.

Discussion

The Great Bustard is represented with a globally vulnerable population (BirdLife International 2013) with low average breeding success which shows expressed annual variance (Morales *et al.* 2002). Threatening factors influencing the survival of individuals belonging to particular population have been quantitatively assessed (see Alonso *et al*. 1994). Hungary hosts approximately 3% of the world population, as the Great Bustard population inhabiting the Carpathian Basin is the second largest in Europe (Alonso & Palacín 2010). Recently the largest and still growing Hungarian population of the Great Bustard is the one in Upper-Kiskunság at Central Hungary. In this study, based on known fatalities, we analysed the relative importance of different killing factors.

Regarding juvenile, immature and adult individuals, anthropogenic factors represent approximately 40% of all mortality causes in the case of the investigated population of the Great Bustard. Amongst these, collision with cables (especially medium voltage power lines and railway cables) is the mortality factor with far the strongest negative effect. Taking into consideration the fact that large part of birds cannot be found and thus are omitted from the reports (Ponce *et al.* 2010), the killing effect of cables must be even stronger. Although there are some solutions for reducing the risk of collision, such as the application of flight diverters on wires (Alonso *et al.* 1994), undergrounding of power lines would be the ultimate solu-

	No protection, intensive utilization	No protection, no utilization (abandoned lands)	Agri-environmental scheme focusing on the protection of the Great Bustard	Regulated (restricted) by nature conservation authorities (at land falling under protection at national level)	Total
Arable fields	44	0	22	1	**67**
Mowed meadows	9	0	6	4	**19**
Pastures	1	0	2	2	**5**
Total	**54**	**0**	**30**	**7**	91

Table 5. Number of revealed nests in the case of lands with different type of utilization and protection status in Central Hungary between 2005 and 2014 based on data originating from discovered nests

5. táblázat Az adott típusú hasznosítás alatt álló, illetve védettségi szintű területeken detektált túzok fészkek száma a Duna-Tisza közi populáció esetében, a 2005 és 2014 közötti időszakban

tion (Raab *et al*. 2011, Raab *et al.* 2012, Lóránt & Vadász 2014).

In the case of railway cables, the only solution for reducing the risk of collision could be the use of markings increasing the detectability of cables by the Great Bustards, and also the sustenance/establishment of alley of trees along railways. Of course, it should be considered that dense afforestations could result in fragmentation of Great Bustard habitats.

Regarding hay making/mowing, bird-friendly mowing methods and the prior announcement of mowing towards the nature conservation manager by the land user in the case of every potential Great Bustard breeding site could be the solution for reducing the number of destroyed nests and killed pulli and juveniles. Recently, mowing carried out at grasslands located in protected and/or Natura 2000 areas must be announced in advance towards the nature conservation manager (i.e. National Park Directorates).

Even predation is usually reported as one of the major killing factors in the case of the Great Bustard and other ground-nesting avian species (Langgemach & Bellebaum 2005), our dataset includes only a few records on fatalities caused by predators. The density of potential predators, such as the Hooded Crow *(Corvus corone)*, the Red Fox *(Vulpes vulpes)*, the European Badger *(Meles meles)* and Wild Boar *(Sus scrofa)* is rather high at the breeding grounds of the Great Bustard in the Upper-Kiskunság region, but with the recent monitoring techniques the probability of detection of predation equals roughly with zero. Carcasses found at warrens of mammal predators cannot be regarded as unambiguous evidence for predation, since these predators can bring carrion (i.e. Great Bustards found dead) to their warrens. Specific future investigations (e.g. analysis of droppings and/or bromatological investigations) could reveal the relative impact of potential predators on the Great Bustard populations. For same reasons, in the case of eggs having been permanently left by the females after having faced a certain kind of human disturbance, even the left eggs can be consumed by Hooded Craws, it is not nest predation which de facto led to egg mortality.

Chemical treatments of cereals seems to affect nesting success far less, than the other kind of field works, as the portion of abandoned nests is approximately half as high as it use to be in the case of other kind of disturbances, such as mowing, tillage etc. Nevertheless, the successive field works (e.g. harvesting) and the reduced amount of food (insects) after chemical treatment may further decrease the breeding success (Ponce *et al.* 2011).

Regarding the unintended disturbances (i.e. those cases, when a breeding female is frightened off the nest and it abandons the egg(s) facing an activity which is not related agriculture, e.g. due to the approach of passerby, see Sastre *et al.* 2009), the portion of unsuccessful breeding attempts is quite high. As these activities are not obligatory to be carried out (from agricultural perspective), with the modification of legal regulation (e.g. in the case of regulation of hunting at the breeding areas) and awareness raising focusing the rural communities and especially the farmers would significantly reduce the overall negative effects of unintended disturbances.

In addition, the influence of specific activities decreasing level of successful breeding attempts must be considered as an apparent value. In the case of infertile eggs, sooner or later the nest is left by the females, but apparently the eggs are abandoned due to some kind of human disturbance. In the case of eggs removed from endangered nests and transferred to the Great Bustard Protection Centre in Dévaványa (i.e. from those nests where there was no chance for the survival of eggs, e.g. in the case of those with too small buffer zone left uncut, etc.) fertility of eggs was investigated, and the portion of infertile and unviable eggs appeared to be surprisingly high, approximately 40% (unpublished data).

Regarding the natural threatening factors that have negative effect on the breeding success of the Great Bustard, it should be considered that a population of a long-living species can sustain with low level of breeding success, since the high rate of annual survival in the case of the successive stages can compensate it so that inner reproductive rate remains positive (or zero, at least). However, even relatively low level of mortality induced by anthropogenic killing factors (in relation to the level of mortality caused by natural killing effects) can decrease the inner reproductive rate, so that it can become negative, resulting in decrease in population size. Accordingly, the most important task is to eliminate (or reduce, at least) the killing effect of anthropogenic factors by the adequate concrete conservation measure (like underground cabling), modification of legal regulations and by the implementation of field works compatible with the sustenance of the Great Bustard.

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The effect of above-ground medium voltage power lines on displaying site selection of the Great Bustard *(Otis tarda)* in Central Hungary

Miklós Lóránt* & Csaba Vadász

Miklós Lóránt & Csaba Vadász 2014. The effect of above-ground medium voltage power lines on displaying site selection of the Great Bustard *(Otis tarda)* in Central Hungary. – Ornis Hungarica 22(2): 42–49.

Abstract Our study was conducted in the Upper-Kiskunság region, Central Hungary, which hosts the largest Pannonian population of the Great Bustard *(Otis tarda)*. The influence of the presence of above-ground medium voltage power lines on displaying site selection of Great Bustard males was investigated. The results revealed that displaying males totally reject the sites located within 350-400 m or closer to medium voltage power lines as displaying sites and show relative rejection towards potential displaying sites located at a distance between 500 and 1000 m far from power lines. Surprisingly, the overall negative effects influence much larger part of the potential displaying grounds, up to the distance to 3500 m from power lines. It can be declared that power lines reduce the extent of suitable displaying sites of the Great Bustards in the Upper-Kiskunság region. Accordingly, installation of new above-ground power lines (and other kind of wires, such as high voltage power lines, optical cables etc.) would further reduce the extent of suitable displaying sites.

Keywords: Great Bustard, power lines, collision, displaying site selection

Összefoglalás Vizsgálatainkat Magyarország legnépesebb túzok *(Otis tarda)* populációjának élőhelyén, a Felső-Kiskunságban végeztük. Arra kerestük a választ, hogy a középfeszültségű elektromos légvezetékek hogyan befolyásolják a túzok dürgőhely választását. Eredményeink rámutatnak arra, hogy a kakasok egyáltalán nem választanak dürgőhelyet a légvezetékek 350-400 méteres környezetében, illetve a vezetékek 500-1000 méteres környezetében is erősen alulreprezentáltak a dürgőhelyek. A teljes, illetve relatív rejekció az előbb említett távolságokban olyan erőteljes negatív hatást fejt ki a túzok kakasok dürgőhely választására, ami csak a légvezetékektől számított 3500 méteres távolságban egyenlítődik ki. Ennek megfelelően kijelenthető, hogy a légvezetékek erőteljes fragmentáló hatással bírnak a dürgőhelyekre. Újabb légvezetékek telepítése éppen ezért össze nem egyeztethető a helyi túzokpopuláció fenntartásával.

Kulcsszavak: túzok, középfeszültségű vezeték, ütközés, dürgőhely választás

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Introduction

Power lines represent risk of mortality caused by collision or electrocution for many bird species throughout the world, including many with endangered or vulnerable status (Bevanger 1998). While electrocution usually threatens species perching high and can be described with good flight ability, e.g. raptors, corvids, collision is generally a risk for fliers with poor manoeuvrability (Janss 2000), such as the ptarmigan species (Bevanger & Brøseth 2001) or the bustard species (Alonso *et al.* 1994). Especially species with small binocular field (cranes, storks, bustards) can be characterised with large blind areas in their visual field, thus being heavily threatened by collision (Martin & Shaw 2010). Although there are certain possibilities for reducing the risk of collision, e.g. by changing the design of wires of power lines (Bevanger & Brøseth 2001) or using markings and other bird flight diverters on electric wires (Alonso *et al.* 1994), it still represents a major killing factor in the case of certain populations (Lehman *et al.* 2007). Accordingly, underground cabling can be regarded as the ultimate solution for these negative impacts (Raab *et al.* 2012). In the case of the West-Pannonian and also the Central Hungarian Great Bustard population, collision with electric wires proved to be a major killing factor (Reiter 2000, Raab *et al.* 2011, Vadász & Lóránt 2014). Even these populations are still showing slow but steady increase in population size, it can be declared that by eliminating the loss caused by collision the growth could be much more rapid.

In addition to the above mentioned effects of the power lines, these linear establishments potentially influence the habitat use of particular species by modifying the structure of open landscapes (Ballasus & Sossinka 1996). However, it has not been studied whether the presence of power lines influence certain aspects of the habitat use of the Great Bustard or not. This species prefers large, open terrains (Lane *et al.* 2001), and this habitat preference is most expressed at the displaying period. Since air wires modify the structure of the landscape, it should have effect on the displaying site selection of adult males as the presence of power lines can potentially lead to rejection of certain parts of potential displaying sites thus reducing the extent of potentially acceptable ones.

Materials and methods

The study area

The study area is located at the Upper-Kiskunság region in Central Hungary. This area is characterized by large-scale mosaics of unwooded grasslands and ploughfields, hosting the largest Pannonian Great Bustard population, which, in fact still shows continuous increase (Práger 2005). Major part of the area is designated as a Special Protection Area in the Natura 2000 network (HUKN10001 and HUKN10002). The core area of the Great Bustard population (including the displaying and partly the nesting sites) falls under national protection, forming parts of Kiskunság National Park. In this issue, data originating from the above mentioned Natura 2000 sites is being analysed.

Data collection

Field data on displaying Great Bustards were collected between 2004 and 2011. ArcPad software running on handheld GPS devices was used to record the location of displaying sites. Displaying sites cover the location presence of adult male Great Bustards showing displaying behaviour independently the number of individuals. The estimated centre of the occupied displaying sites were recorded as points, however in cases of larger flocks with strong competition it might reach an area up to 4 hectares (200 m × 200 m).

During the field observations, in order to avoid any kind of anthropogenic affect disturbing the displaying Great Bustards, displaying sites were approached in a 500-1000 m distance. From this distance, the location of displaying sites could be estimated with the precision of 50-100 m using the available vector map elements (e.g. the location of field roads, paths, border of land units etc.). In the case of the Great Bustard, amongst suitable light conditions it is fairly easy to determine the age and sex of the observed individuals. During the field work all the individuals, regardless their age and sex group and behaviour, were recorded. In spite of that, in this issue only data on displaying adult males is being analysed.

Statistical methods

Our field observations and preliminary analyses revealed that Great Bustards reject the close neighbourhood of medium voltage power lines (MVPLs) as displaying sites. To determine the influence of location of MVPLs on spatial distribution of displaying sites, two alternative analytical methods were used.

'Method I' was used to describe and to evaluate the shift in location of displaying sites caused by the rejection of the potential displaying sites close to MVPLs. In this method, displaying sites were rendered based on their distance from the nearest MVPL. Regarding this method the following consecutive steps were performed:

a) The distance from the nearest MVPL was measured in the case of every single displaying site and random generated points.

b) Displaying sites and random points were ordered based on the distance measured from the nearest MVPL.

c) The following measures were computed:

- the shortest distance between a particular displaying site and a MVPL (which represent the distance, that male Great Bustards minimally keep from MVPLs during displaying site selection, i.e. the width of totally rejected zone surrounding MVPLs)
- the portion of the displaying sites located within 500 m from the closest MVPL (it can be regarded as a critical distance for the Great Bustards in Central Hungary, since individuals almost never move further when a person or a car appears in such a distance)
- the minimal distance between displaying sites and MVPLs kept by 75% of locations
- the minimal distance between displaying sites and MVPLs kept by 95% of locations

'Method II' was used for comparison of the distribution of real (occupied) displaying sites and random points in overlapping belts with increasing width surrounding MVPLs. This method was used to determine the width of piece of land surrounding MVPLs where significant negative effect can be observed. Regarding this method the following consecutive steps were performed:

a) Overlapping concentric polygons were created which represented the surroundings of the MVPLs with width of 400, 800, 1500, 3000, 3500, 4000 m, respectively.

b) As preliminary data analyses revealed the number of observed displaying sites (which was 221, see the results section) 200 random points were placed in the study area within the frames of a Monte Carlo simulation (the RND function of MS Excel was used to create the coordinates of random points).

c) The probability of occurrence of a displaying site within a particular belt was calculated as the ratio between the number of displaying sites located in the certain belt and the total number of observed displaying sites.

d) The probability of occurrence of a random point within a particular belt was calculated as the ratio between the number of

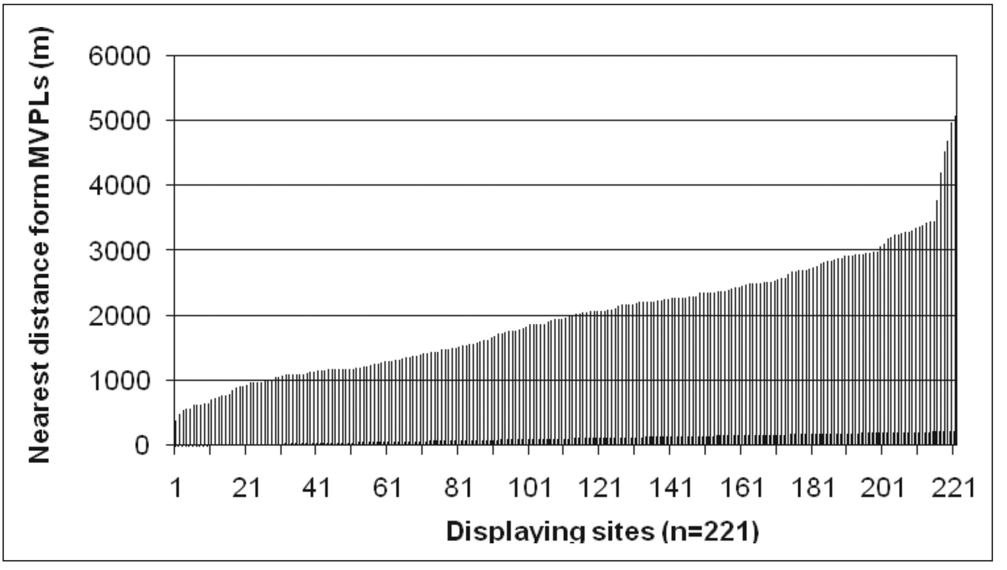

Figure 1. Nearest distances between displaying sites and above-ground MVPLs
1. ábra A dürgőhelyek távolsága a legközelebbi középfeszültségű légvezetéktől

random points located in the certain belt and the total number of points.

e) Welch-test was used for comparison of these probabilities.

Results

The spatial distribution of displaying sites with respect to the distance from above-ground MVPLs

The distribution of distances between above-ground MVPLs and observed displaying sites (n=221) is shown at *Figure 1*.

There were no birds showing displaying behaviour within the 383 meters surroundings of MVPLs, which can be interpreted as the distance of total rejection of a particular location as a displaying site by the Great Bustards. Within the 500 meters buffer of MVPLs only 2 displaying sites were observed. Ninety-five percent of displaying sites were located at a distance of 740 meters or more from above-ground MVPLs. Seventy-five percent of displaying sites were located at least 1240 meters far from MVPLs *(Table 1)*.

In the case of random points there were 86 points within the 500 meters buffer zone around MVPLs. Ninety-five percent of random points were at least 42 meters far from MVPLs. Seventy-five percent of random points were at least 225 meters far from MVPLs *(Table 1)*.

The distribution of real displaying sites and random points located in particular discrete sized belts around the above ground medium voltage power lines is shown in *Figure 2*.

The distance from above-ground medium voltage power lines at which Great Bustards show rejection during display

The results of Welch-tests show that even at a distance of 3000 meters statistical difference can be detected between the probability of observation of Great Bustard display-

	Minimal distance from MVPLs (m)	Portion of points located within 500m distance from MVPLs	The minimal distance from MVPLs kept by 95% of displaying males (m)	The minimal distance from MVPLs kept by 75% of displaying males (m)
Random points	N.A.*	43.0%	42	225
Occupied displaying sites	383	0.90 %	740	1240

Table 1. Comparison of distances measured from MVPLs and the spatial distribution of points in the case of random points and occupied displaying sites. * this measure has not been calculated since it has no biological meaning

1. táblázat A Monte-Carlo szimulációval előállított random pontok és a valóságban elfoglalt lekek távolsága és térbeli eloszlása. * ez az érték nem bír biológiai jelentéssel, így nem lett megadva

ing sites and the probability of occurrence of random points in the surroundings of MVPLs *(Table 2)*.

Data show that the rejection effect of MVPLs ceases between 3000 and 3500 meters. Between these two values linear interpolation of ts values was applied. Accordingly, the distance where statistical significance changes from high (p=0.01) to low (p=0.05) was calculated as 3324 meters, and the distance where statistically there is no difference between the real and random points was calculated as 3480 meters.

Discussion

The negative effects of above ground wires (power lines, optical cables etc.) has been

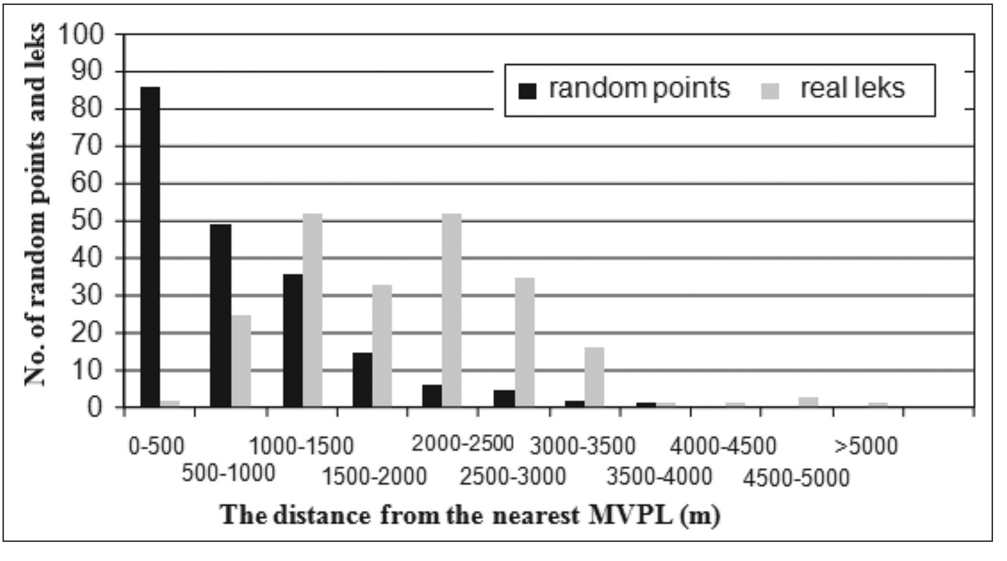

Figure 2. Distribution of the numbers of real displaying sites and random points according to distances from MVPLs

2. ábra A valós lekek és a random pontok térbeli eloszlása és száma a középfeszültségű légvezetékektől mért távolság függvényében

		400m	800m	1500m	3000m	3500m	4000m	4500m
Probability of presence of a random point	**Average**	**0.380**	**0.595**	**0.855**	**0.985**	**0.995**	**0.999**	**0.999**
	Standard deviation	0.487	0.492	0.353	0.122	0.061	0.000	0.000
	Standard error of the mean	0.034	0.035	0.025	0.009	0.004	0.000	0.000
Probability of presence of observed displaying sites	**Average**	**0.005**	**0.072**	**0.357**	**0.900**	**0.973**	**0.992**	**0.995**
	Standard deviation	0.067	0.260	0.480	0.300	0.163	0.087	0.068
	Standard error of the mean	0.005	0.017	0.032	0.020	0.011	0.006	0.005
	ts	**10.819****	**13.421****	**12.186****	**3.852****	**1.880**	**1.092**	**0.735**
	df	**205.887**	**295.018**	**402.464**	**296.596**	**286.284**	**220.000**	**220.000**

Table 2. Comparison of the probabilities of presence of random points and observed displaying sites in the surroundings of above ground medium voltage power lines (represented as belts of particular width) by Welch-tests. **indicates high level (p=0.01) of significance

2. táblázat A random pontok és a valós lekek előfordulási valószínűségének összehasonlítása Welch-próbával a középfeszültségű vezetékek meghatározott szélességű környezetében. **erősen szignifikáns különbség (p=0,01)

reported in several studies (as examples, see Bevanger 1998, Lehman *et al.* 2007). Usually, electrocution (Lehman *et al.* 2007) and collision with wires (Martin & Shawn 2010) are regarded as killing factors for birds, including individuals of species with endangered or vulnerable status. However, considering that the presence of above ground power lines can potentially reduce the extent of suitable (or preferred) feeding/breeding/resting grounds of birds, until recently surprisingly few studies has focused on the potential negative effects of power lines on habitat selection or habitat use of birds (e.g. Ballasus & Sossinka 1996).

Our results revealed that male Great Bustards totally reject the sites located within 350-400 m or closer to medium voltage power lines as displaying sites. This distance is roughly equivalent with the observed safety distance usually kept by Great Bustards, i.e. these birds take wing when noticing potential threatening factors (unknown vehicles, persons etc.) within this distance.

Furthermore, potential displaying sites located at a distance between 500 and 1000 m far from MVPLs are underrepresented as real displaying sites, indicating the relative rejection of these potential displaying sites.

Based on the comparison with random points, occupied (used) displaying sites are overrepresented in the belt located in a distance between 1000 and 3500 m far from MVPLs, indicating the shift of displaying site selection from locations closer to MVPLs toward the more distant locations. However, the rejection of location closer (within 1000 m) to MVPLs is so expressed, that the portion of real displaying sites located at a distance within 3500 m from MVPLs is still smaller than the expected value (based on the results of the Monte Carlo simulation). Accordingly, the overall negative effects influence much larger part of the potential displaying grounds.

The above mentioned phenomena appoint on the fact that MVPLs reduce the extent of suitable displaying sites of the Great Bustards in the Upper-Kiskunság region. Accordingly, installation of new above-ground power lines (and other kind of wires, such as high voltage power lines, optical cables, etc.) would further reduce the extent of suitable displaying sites. Presumably, the installation of new power lines could fragment the traditional displaying grounds, which could easily lead to the total rejection of those fragments of the potential displaying grounds which are characterized with suitable landscape structure but are too small in extent as the Great Bustard prefers large open areas as displaying sites.

It has been previously revealed that the Great Bustards are quite conservative in choosing displaying sites. While breeding females are reported to (re)occur at those locations where no breeding has been observed for decades as the population grows, new displaying grounds has not been reported. Accordingly, the sustenance of traditional displaying grounds forms one of the basic conditions for the preservation of core populations of the Great Bustard.

As the chance for the formation of new displaying sites is low due to the density of MVPLs, it would be reasonable to underground existing above ground cables at potential displaying sites.

Also, taking into consideration of the fact that there is another well known negative effect of power lines, i.e. collision of birds with wires, which represents a major killing factor for the Great Bustard (Reiter 2000), it would be reasonable to underground the existing above ground cables (i.e. replace those with underground cables). Although there are some solutions for reducing the risk of collision, such as the application of flight diverters on wires (Alonso *et al.* 1994), undergrounding of power lines would be the ultimate solution (Raab *et al.* 2011, Raab *et al.* 2012).

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Habitat preference of Great-spotted Woodpecker (*Dendrocopos major* Linnaeus, 1758) and Lesser-spotted Woodpecker (*Dendrocopos minor* Linnaeus, 1758) in the presence of invasive plant species – preliminary study

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Gábor Ónodi & Tibor Csörgő 2014. Habitat preference of Great-spotted Woodpecker (*Dendrocopos major* Linnaeus, 1758) and Lesser-spotted Woodpecker (*Dendrocopos minor* Linnaeus, 1758) in the presence of invasive plant species – preliminary study. – Ornis Hungarica 22(2): 50–64.

Abstract This study was carried out in Hungary, in an old, unmanaged, riparian poplar-willow forest, where two invasive tree species, the green ash and the boxelder maple are presented and reproduce more effectively therefore are more abundant than the native species in the study area. There are also invasive hybrid wild grapes to be found. These invasive plants cause widespread problems in floodplain forests in Central Europe. We studied Great-spotted and Lesser-spotted Woodpeckers. We investigated the following questions: Which tree species are preferred by the foraging birds? How are the foraging birds distributed spatially between the microhabitats? Are there any differences in terms of foraging niche utilization between the two studied species? We gathered our data through weekly standard observations throughout two whole years. Based on our findings we could determine that both species preferred the less abundant native trees rather than the invasive ash and maple trees, though Lesser-spotted Woodpeckers preferred hybrid wild grapes the most. Great-spotted Woodpeckers preferred the middle heights of the trees, they also moved mainly on trunks. Lesser-spotted Woodpeckers used the thinnest branches in the canopy. Based on our results we predict that the decrease of the native tree species may create a suboptimal habitat compared to the current situation. As the studied species are the major cavity excavators, the above mentioned changes will probably have significant effects on numerous cavity dependent species.

Keywords: woodpecker ecology, foraging preference, floodplain forest, invasive arboreal species, conservation

Összefoglalás A vizsgálatot a Közép-Tiszai Tájvédelmi Körzetben, egy 60-70 éves, kezeletlen fűz-nyár ártéri erdőben végeztük. A területen két invazív fafaj fordul elő, az amerikai kőris és a zöld juhar. E két fafaj terjedése jelentős környezeti problémát jelent Közép-Európa szerte. Másodlagos lombkorona szintet alkotva leárnyékolják az őshonos fák újulatát, allelopatikumaikkal meggátolják az őshonos fűz és nyár csemeték fejlődését. A területen szintén előforduló, invazív, hibrid szőlőfaj szintén problémát jelent. Két harkályfajt, a nagy és a kis fakopáncsot vizsgáltuk. A következő kérdésekre kerestük a választ: A táplálkozó-pihenő madarak mely fafajokat preferálják? Az egyedek milyen téreloszlásban vannak jelen a fákon? A fafaj preferenciák vizsgálatához felmértük az egyes fásszárú fajok gyakoriságát. Az adatokat egy teljes éven át, heti rendszerességgel gyűjtöttük. Az amerikai kőrist és a zöld juhart egyik vizsgált faj sem preferálta. A nagy fakopáncsok legjobban a fűzfákat, a kis fakopáncsok a hibrid szőlőket részesítették előnyben. A nagy fakopáncsok a fákon főként a felsőbb régiókban, a törzsön, a kis fakopáncsok a lombsátor legvékonyabb ágain mozogtak. A jelenlegi állapothoz képest az őshonos fafajok állománycsökkenése a két harkály faj számára szuboptimális élőhely kialakulásához vezet. Mivel ezen élőhely típusban a vizsgált fajok a fő odúkészítők, az említett változások más odúlakó állatfajok helyzetét is befolyásolhatják.

Kulcsszavak: harkály ökológia, táplálék preferencia, ártéri erdő, invazív fásszárú fajok, természetvédelem

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Introduction

There are 216 species in the family of woodpeckers (Picidae). Nine of 10 European species are native in Hungary (del Hoyo 2002, Gorman 2004). These species live in woody habitats and feed mainly on arthropods. Cavity-excavator species can breed only in such habitats, where trees are old and thick enough to make a cavity in (von Boltzheim & Bauer 1980, Cramp 1985).

The picids play a key role in forest ecosystems (keystone species) (Johnsson 1993, Gorman 2011). Cavity-excavator species provide nesting cavities for other cavity-dweller species. Numerous species depend on tree cavities all around the world. Cavity-dweller invertebrates include numerous species of wasps (Hymenoptera), and butterflies (Lepidoptera) etc. Among vertebrates, we find secondary cavity-nester birds, such as tits (*Parus* spp.), flycatchers (*Ficedula* spp.), owls (Strigidae), the Goldeneye *(Bucephala clangula)*, the Stock Dove *(Columba oenas)* etc. There are mammalian cavity-dweller species as well, for example wood mice (*Apodemus spp.*), dormice (Gliridae), squirrels (Sciuridae) and bats (Chiroptera) (del Hoyo 2002, Bai 2005). For the protection of cavity-dweller species, it is crucial to protect their cavity-excavators as well. Woodpecker species are considered umbrella species, as with their protection one could protect other species as well (Cramp 1985, Carlson *et al.* 1998, Martin & Eadie 1999, Martin *et al.* 2004, Kosiński & Ksit 2006, Kosiński *et al.* 2006, Smith 2006, Kosiński & Kempa 2007, Roberge *et al.* 2008a,b, Edman *et al.* 2011, Gorman 2011, Shurulinkov *et al.* 2012).

For the protection of cavity-excavator species, it is crucial to protect their habitats, and so, one should study the ecological needs of the specific species. This requires studies on habitat preference. Every woodpecker species has its preferences, according to their needs. For co-existing species – and different sexes – the interspecific, intraspecific and intrasexual competition is minimized by spatial segregation, so their realised niche differ from their fundamental niche (Peters & Grubb 1983, Pettersson 1983, Török & Csorba 1986, Székely 1987, Török 1990, Hogstad 1971, Olsson *et al.* 1992, Osiejuk 1998, Stenberg & Hogstad 2004, Pierson *et al*. 2010).

Our study species were the Great-spotted and Lesser-spotted Woodpeckers. The Great-spotted Woodpecker *(Dendrocopos major)* is a generalist species, which can inhabit nearly every kind of woody habitat in Hungary, from closed, montane forests to urban parks. This species mainly feeds on arthropods on trunks and thicker branches but will also eat seeds, fruits and small vertebrates, including bird nestlings. Depending on the species composition of competing birds, this species can use various microhabitats (Hogstad 1971, Alatalo 1978, Török & Csorba 1986, Török 1990, Stenberg & Hogstad 1992, del Hoyo 2002, Gorman 2004).

The Lesser-spotted Woodpecker *(D. minor)* breeds only in old, closed forests, with snags. This species needs snags both for foraging and nesting. The specimens mainly forage on twigs of the canopy, and prefer dead substrates for cavity excavation (Alatalo 1978, Török 1990, del Hoyo 2002, Gorman 2004, Charman *et al*. 2010).

As a cosequence of forestry management and agricultural practices, in Hungary the only forest types that remain in lowland landscapes in a nearly natural state are riparian forests. There are two main types of riparian forests, the one close to the river bed soft wood riparian gallery forests composed of poplar and willow species, while the other one further from the river bed hard wood gallery oak-ash-elm forests. Most of the latter are disappearing, as a result of river control, placing them on the other side of the dams or clearing them, for agriculture. Most of Hungary's riparian forests now consist of poplar and willow species, like white poplar *(Populus alba)*, black poplar *(P. nigra)*, white willow (*Salix alba*) and crack willow *(S. fragilis)*. As the range of aspen *(P. tremula)* and the range of white poplar are overlapping in Hungary, according to the high genetic similarity between aspen and white poplar, one can only find the hybrids of these two species *(P. × canescens)* in the riparian woods. Due to the large extent of planted hybrid poplar *(P. × euramericana)*, most black poplars in these forests nowadays could be hybrids with the planted poplars as well (Gencsi & Vancsura 2002).

There are several non-native tree species in almost every riparian forest of Hungary (and in Central Europe as well). Among them, there are two invasive species, the green ash *(Fraxinus pennsylvanica)* and the boxelder maple *(Acer negundo)*. These two species reproduce faster and are much more abundant than the native species in the study area. They influence the chemical traits of the soil and also develop a second canopy layer under the native specimens' canopy and thus increasingly shade the ground preventing the saplings of the autochtonous trees from growing properly. As a result there are very few saplings of the native species in the study area (Mihály & Botta-Dukát 2004, Erfmeier *et al.* 2011).

In the late 19th and early 20th centuries a North-American pest was introduced. This was the grape phylloxera (*Daktulosphaira vitifoliae* – Phylloxeridae, Hemiptera) – which can cause lethal damage to the neck of the root of grapes. Because of that, more than two third of European vineyards died out. As a solution, some American grape species were introduced – like river bank grape *(Vitis riparia)* and fox grape *(V. labrusca)* – which were adapted to this insect species. People in Europe grafted their native breeds onto the rootstocks of these introduced plant species, so our grape breeds could survive (Laguna 2004, Arrigo & Arnold 2007). These American grape species ran wild and hybridized with our native wild grape species, *(V. sylvestris)*. This hybrid form spread quickly in the riparian woods, mainly in sparse vegetation, in clearings and forest edges. As it grows, it climbs up the trees, and can cover the whole canopy with their leaves, so the tree can die as a result of insufficient sunlight. This hybrid grape is also a widespread problem in the riparian forests in Hungary (Botta-Dukát & Mihály 2006).

Very little is known about this relatively new habitat (though it's a widespread problem in Central Europe so far), its processes, as well as its cavity-nesting community. As the Great-spotted Woodpecker is the most generalist woodpecker species of the Western Palaearctic region, its role would be crucial for the cavity-nesting fauna of this transforming habitat. For the proper future treatments, it is important to study the habitat preferences of this well-known species (Cramp 1985, Gorman 2004, Erfmeier *et al.* 2011, Ónodi & Csörgő 2012, 2013).

The questions of our study were: Which tree species are preferred by the foraging birds? How are the foraging birds distributed spatially between the microhabitats? Are there any differences in terms of foraging niche utilization between the two studied species?

Our hypothesis suggested that the studied species do not prefer the non-native arboreal species for foraging as these species have few wood-dwelling arthropod species that could be the prey for the woodpeckers. According to the different ecological needs of the two woodpecker species, we predicted that the two species utilize different microhabitats.

Material and methods

Our study area was a 60-70-year old unmanaged riparian poplar-willow forest (cc. 35 ha) (N 47°04' E 20°11'–N 47°02' E 20°11') situated in the Central-Tisza Landscape Protection Area, which belongs to the Hortobágy National Park, in the floodplain area of the river Tisza. The following native tree species were recorded: white poplar, black poplar, white willow, crack willow. Among the overstorey species, there are some introduced arboreal species in the area: green ash, boxelder maple, white mulberry *(Morus alba)*, common hackberry *(Celtis occidentalis)* and a hybrid wild grape *(Vitis × spp.)*. Among them, the green ash, the boxelder maple and the hybrid wild grape known to be invasive plants as well. The midstorey consisted mainly of the saplings of the above mentioned invasive species. The other scrub layer species are European dewberry *(Rubus caesius)*, and at the edges, the North-American bastard indigobush *(Amorpha fruticosa)*.

Four of the nine Hungarian woodpecker species breed in the area: Great-spotted, Lesser-spotted, Green and Black Woodpecker (*Picus viridis* and *Dryocopus martius*). Our study species were the Great-spotted and Lesser-spotted Woodpecker. Previously we counted the used nesting cavities for each woodpecker species as we followed the begging calls of the nestlings. According to that examination, the two studied species had eleven and two breeding pairs respectively, and both of the Green and Black Woodpeckers had one breeding pair in the study period.

We gathered our data in the whole year of 2012 and from the autumn of 2013 until the autumn of 2014, through a weekly standard 2.5 km long transect line. We registered the following variables on each position where the specimens occurred in a 5 minute observation period (according to the protocols in similar studies (Hogstad 1971, Pettersson 1983, Török & Csorba 1986, Török 1990, Osiejuk 1998): arboreal species used, tree condition, tree height, foraging height, relative distance from trunk, branch thickness, foraging technique and substrate condition.

We recorded the arboreal species of the study area in the following categories: willow species (W.), black poplar and its hybrids (Pb.), white poplar and its hybrids (Pw.), green ash (A.), boxelder maple (M.), white mulberry (Mb.), common hackberry (H.) and hybrid wild grape (G.).

All willow species were listed in one single category due to the very similar architecture and bark structure of the above mentioned species making it difficult to identify exact species when the branches are covered with snow. White poplar often hybridize with aspen, black poplar hybridize with hybrid American planted poplar. The white poplar and its hybrids have smoother bark and consequently have fewer prey species than the black poplar hybrids have in their more rough bark (Gencsi & Vancsura 2002).

We recorded the frequency of each arboreal plant types among plants thicker than 3 cm diameter at breast height (minimum diameter of trees that support prey species of our study species) in 0.05 ha plots (12.62 m radius) situated on a 100 m by 100 m grid.

To estimate the condition of the trees which were utilized by the foraging specimens, we assigned them to one of three categories: living trees (less than half of their branches are decayed), decaying trees (more than half of their branches are decayed, but still have living branches), snags (all of the branches are dead or branchless). During the observations, we measured the height of trees with a Christen height meter, and assigned each to one of six categories: <5.1 m, 5.1-10 m, 10.1-15 m, 15.1-20 m, 20.1-25 m, 25 m<. We made five equal height sections to record the foraging height, and five equal sections according to the length of the branch, to register the relative distance of the given bird from trunk. In this foraging dimension, we also registered if the specimen occurred on the trunk. The thickness of the utilized branch was assigned to one of six categories: <10.1 cm, 10.1-20 cm, 20.1-30 cm, 30.1-40 cm, 40.1-50 cm, 50 cm<. We estimated the thickness of the branch relative to the biometric measures of the study species (length 21-23 cm, wingspan 34-39 cm, Cramp 1985). We made three categories for foraging techniques. 'Searching' refers to those instances, when the specimen was clinging to a certain position on a tree and examined the bark surface. 'Probing' refers to a specimen that searches for prey by pecking the surface without deep blows. 'Excavating' refers to the activity when specimens peck deep into the wood. As the vegetation is very dense in the vegetation period, due to the dense lower canopy layers of the invasive trees and the upper canopy layers of the native trees, we have not studied other behaviours. It is hard to see if the birds search for their prey among the leaves or if they hunt for it above the canopies in the open air, like flycatchers (Muscicapidae). To study foraging techniques in this habitat type is therefore better suited for representing foraging techniques that occurred on the trunks or the branches, or that occurred with any sounds. We gathered data on the condition of the used substrate in two categories: "Living" and "Dead". To avoid multiple encounters with the specimens in one day, we only registered data of same sexes that occurred at least 200 m apart from each other (Hogstad 1971, Pettersson 1983, Török & Csorba 1986, Morrison & With 1987, Török 1990, Aulén & Lundberg 1991, Suhonen & Kuitonen 1991, Engstrom & Sanders 1997, Osiejuk 1998, Imbeau & Desrochers 2002, Pechacek 2006, Hogstad 2009, Czeszczewik 2010).

We gathered 572 records on Great-spotted and 45 records on Lesser-spotted Woodpeckers. We calculated the frequency distribution of each species according to all above mentioned foraging dimensions. We made Mann-Whitney tests to reveal if these distributions differ between the two species. As the frequencies of each category of tree type, tree condition and tree height is known through the previous vegetation survey, we calculated the Jacobs' preference index values for the distributions of foraging occasions of the above mentioned foraging dimension for both species. This index represents a –1, +1 scale from avoidance to preference respectively (Loehle & Rittenhouse 1982, Swamidoss *et al.* 2012).We made Mann-Whitney tests to reveal if these distributions differ between the two species. We calculated the values of the Levin's niche breadth formula for all of the studied variables, to see if one species more specialist than the other. To compare the values of the two species we made two-sample t test, to determine if there are any significant differences between the two species. We carried out the analyses with PAST 2.17c and the tables with Microsoft Office Excel 2007 software (Hammer *et al.* 2001).

Results

The most utilized tree type by Great-spotted Woodpeckers was the black poplar hybrids, the second was the willow, the third was the white poplar hybrids, the fourth was the green ash, the fifth was the boxelder maple, the sixth was the white mulberry and the least utilized was the common hackberry, this species did not utilize the hybrid grapes. Lesser-spotted Woodpecker utilized mostly the willow trees, the second utilized was the black poplar hybrids, the third was the grape, the fourth was the white poplar hybrids, the fifth was the green ash, the sixth was the boxelder maple and this species did not utilize the white mulberry and the common hackberry *(Table 1a)*. The Mann-Whitney test revealed significant differences between the study species *(Table 2)*.

Both species utilized living trees the most and snags the least *(Table 1b)*. The Mann-Whitney test did not reveal significant differences between the two species *(Table 2)*.

Great-spotted Woodpeckers utilized mainly the middle and Lesser-spotted Woodpeckers utilized the fourth (from the bottom) foraging height region. The not mentioned regions were represented less by both of the studied species *(Table 1c)*. The Mann-Whitney test did not reveal any significant differences between the two species *(Table 2)*.

Both species utilized the medium-size and the highest trees the most, Great-spotted Woodpeckers used the highest trees more exclusively. The other categories were represented less and less *(Table 1d)*. The Mann-Whitney test revealed significant differences between the two species *(Table 2)*.

Great-spotted Woodpeckers mainly utilized the trunks the most and the distal categories were represented less and less. The Lesser-spotted Woodpeckers used the tip of the branches the most. Additionally, this species also utilized the trunk and the middle section of the branches with lower frequencies *(Table 1e)*. The Mann-Whitney test revealed significant differences between the two species *(Table 2)*.

Both species mainly utilized the branches thinner than 10 cm. The thicker branches were represented less and less, but Lesser-spotted Woodpeckers utilized the thinnest branches more exclusively *(Table 1f)*. The Mann-Whitney test revealed significant differences between the two species *(Table 2)*.

Both species mainly showed probing behaviour. The excavating and searching behaviour were represented less *(Table 1g)*. The Mann-Whitney test did not reveal any significant differences between the two species groups *(Table 2)*.

Both species mainly foraged on living substrates *(Table 1h)*. The Mann-Whitney test did not reveal any significant differences between the two species *(Table 2)*.

The frequency order of tree types from the most to the least frequent (among trees thicker than 3 cm) is the following: boxelder maple (M.), green ash (A.), white poplar hybrids (Pw.), black poplar hybrids (Pb.), willow (W.), white mulberry (Mb.), hybrid wild grape (G.) and common hackberry (H.) *(Table 3a)*. The order of Jacobs' preference indices of tree types from the highest to the lowest values in the case of Great-spotted Woodpeckers is the following: willow, black poplar hybrids, white mulberry, white poplar hybrids, common a

Tree species	GSW (572)	LSW (45)
W.	28%	36%
Pb.	36%	24%
Pw.	14%	11%
Mb.	4%	0%
A.	9%	11%
M.	8%	4%
H.	0%	0%
G.	0%	13%

b

Tree condition	GSW (572)	LSW (45)
Living (1)	72%	78%
Decaying (2)	23%	20%
Dead (3)	5%	2%
Mean	1.33	1.24
SD	0.57	0.49

c

Foraging height	GSW (572)	LSW (45)
5th (5)	19%	21%
4th (4)	29%	35%
3rd (3)	36%	23%
2nd (2)	10%	16%
1st (1)	6%	5%
Mean	3.45	5.26
SD	1.09	1.14

d

Tree height	GSW (572)	LSW (45)
<5.01 m (1)	4%	18%
5.01-10 m (2)	12%	18%
10.01-15 m (3)	24%	30%
15.01-20 m (4)	15%	9%
20 m < (5)	45%	25%
Mean	3.84	3.05
SD	1.27	1.43

e

Relative distance from trunk	GSW (572)	LSW (45)
trunk (0)	49%	24%
1st (1)	13%	3%
2nd (2)	11%	3%
3rd (3)	14%	27%
4th (4)	7%	0%
5th (5)	6%	43%
Mean	1.34	4.05
SD	1.62	2.04

f

Branch thickness	GSW (572)	LSW (45)
<10.1 cm (1)	48%	81%
10.1-20 cm (2)	19%	7%
20.1-30 cm (3)	16%	5%
30.1-40 cm (4)	9%	2%
40.1-50 cm (5)	4%	2%
50 cm < (6)	3%	2%
Mean	2.13	2.44
SD	1.39	1.12

g

Foraging technique	GSW (572)	LSW (69)
Searching (1)	17%	26%
Probing (2)	45%	39%
Excavating (3)	38%	35%
Mean	2.22	1.09
SD	0.71	0.78

h

Substrate condition	GSW (572)	LSW (45)
Living (0)	84%	84%
Dead (1)	16%	16%
Mean	0.16	0.16
SD	0.36	0.37

Table 1. Distributions of utilizations in the studied foraging dimensions (a-h). Parentheses in upper lines includes the number of cases. Parentheses next to each categories include the score of the given category

1. táblázat Hasznosítási eloszlások a vizsgált táplálkozási dimenzióban a két vizsgált harkályfaj esetében (a-h). A kategóriák melletti zárójelben az adott kategória pontszáma található

Foraging dimensions	P values
Tree species	**0.0438**
Tree condition	0.4186
Foraging height	0.6089
Tree height	**2.3740E-4**
Relative distance from trunk	**4.2750E-7**
Branch thickness	**8.6910E-5**
Foraging technique	0.1785
Substrate condition	0.9777

Table 2. P values of Mann-Whitney analyses in each foraging dimension. Bold numbers represent significant differences

2. táblázat Mann-Whitney teszt p értékei minden táplálkozási dimenzióra. A szignifikáns eltérések félkövérrel szedettek

Availability

a

Tree species (1022)	
W.	8%
Pb.	10%
Pw.	12%
Mb.	3%
A.	26%
M.	39%
H.	1%
G.	2%

Jacobs' preference

b

Tree species	GSW (572)	LSW (45)
W.	0.6561	0.7222
Pb.	0.6485	0.4887
Pw.	0.0849	-0.0398
Mb.	0.1512	-1.0000
H.	-0.1518	-0.4725
A.	-0.4997	-0.8620
M.	-0.7914	-1.0000
G	-1.0000	0.7946

c

Tree condition (1022)	
Living (1)	38%
Decaying (2)	54%
Dead (3)	8%
Mean	1.70
SD	0.60

d

Tree condition	GSW (572)	LSW (45)
Living (1)	0.6138	0.7050
Decaying (2)	-0.5968	-0.6030
Dead (3)	-0.2249	-0.7008
Mean	-0.0693	-0.1996
SD	0.6201	0.7849

e

Tree height (1022)	
<5.01 m (1)	27%
5.01-10 m (2)	40%
10.01-15 m (3)	17%
15.01-20 m (4)	9%
20 m < (5)	6%
Mean	2.28
SD	1.33

f

Tree height	GSW (572)	LSW (45)
<5.01 m (1)	-0.7907	-0.2495
5.01-10 m (2)	-0.6559	-0.5034
10.01-15 m (3)	0.2100	0.3490
15.01-20 m (4)	0.2680	-0.0237
20 m < (5)	0.8418	0.6568
Mean	-0.0254	0.0459
SD	0.6850	0.4634

Table 3. The availability of each tree species (a), tree condition (c) and tree height (e) categories and the Jacobs' preference values of each category by the two species (b, d, f)

3. táblázat A különböző fásszárú fajok (a), a különböző kondíciójú fák (c) és a különböző magasságú fák (e) gyakoriság eloszlásai, illetve ezek Jacobs-féle preferencia értékei a két vizsgált faj esetében (b, d, f)

hackberry, green ash, boxelder maple, hybrid wild grape. The observed specimens showed avoidance to the latter four species. Lesser-spotted Woodpeckers preferred the grapes the most, the second most preferred was the willow. The rest of the arboreal types were avoided by this woodpecker species. The order of avoidance from the least to the most is the following: white poplar hybrids, common hackberry, green ash, white mulberry and boxelder maple *(Table 3b)*. The Mann-Whitney test did not reveal any significant differences between the two species.

The frequency order of tree condition types from the most to the least frequent (among trees thicker than 3 cm) is the following: decaying trees, living trees, dead trees *(Table 3c)*. Both studied species preferred living trees and avoided decaying trees and snags, though Great-spotted Woodpeckers avoided snags the most and the other species avoided snags the most *(Table 3d)*. The Mann-Whitney test did not reveal any significant differences between the two species.

In the case of tree height, the 5.01-10 m high trees were the most frequent ones among the trees thicker than 3 cm, the second most frequent trees were lower than 5.01 m. The higher trees were represented less and less *(Table 3e)*. Both woodpecker species preferred the highest trees the most, though Lesser-spotted Woodpeckers showed slight avoidance to the second highest category. The lower tree categories were represented less and less, as the two species showed avoidance to the two lowest tree categories *(Table 3f)*. The Mann-Whitney test did not reveal any significant differences between the two species.

Great-spotted Woodpecker showed higher niche-breadth values in terms of tree condition, relative distance from trunk, branch thickness and substrate condition. Lesser-spotted Woodpecker showed higher niche-breadth values in terms of tree species, foraging height, tree height and foraging technique. Although Great-spotted Woodpecker showed higher mean niche-breadth value, the two-sampled t test did not reveal any significant differences between the two species.

Discussion

Although the studied species are among the most common woodpecker species, very few researchers studied the foraging preferences of these species and moreover no one did survey these woodpecker species in the presence of these invasive arboreal species. For proper conservation efforts, we have found it crucial that more researchers should study these new habitat types.

In the study area Great-spotted Woodpeckers foraged mainly on native trees, in the upper regions, on branches and trunks thinner than 10 cm. The birds preferred living trees. It is a common phenomenon, that Great-spotted Woodpeckers use living branches of living trees for foraging, while other species prefer decaying or dead trees and dead substrates (Török 1990, Smith 2007, Lõhmus *et al.* 2010). Compared to other *Dendrocopos* species, the Great-spotted Woodpecker prefers living trees the most. The White-backed Woodpecker *(Dendrocopos leucotos)* for instance is a dead wood specialist. Although its body size and bill length is significantly greater than the study species', White-backed Woodpecker forages exclusively on softer dead wood. According to Aulén and Lundberg (1991), the Great-spotted Woodpecker's shorter but stronger bill seems to be a more efficient tool for excavating fresh/hard substrates, than the White-backed Woodpecker's longer and less robust bill.

As the Great-spotted Woodpecker is a generalist species, it can forage in various microhabitats according to the architecture of the habitat, the distribution of prey species and the spatial distribution of the competitor species etc. In a similar paper in poplar-willow forest patches, where the same four woodpecker species bred and the above mentioned invasive arboreal species were present only in the midstorey, we have found similar preferences, as the Great-spotted Woodpeckers preferred the poplar and willow trees, and used the same microhabitats, the upper parts of the trunk (Ónodi & Csörgő 2012, 2013). In another work in Hungary, which took place in a middle-aged oak forest Great-spotted Woodpeckers used the upper parts of trees too, in the presence of Middle-spotted Woodpeckers (Török & Csorba 1986). In another oak forest, where the Middle- and Lesser-spotted Woodpeckers were the competitors, the Great-spotted Woodpeckers used the lower regions of the trunk in the breeding season, as the other species moved mainly in the upper regions. More precisely, the Middle-spotted Woodpeckers used the thicker and Lesser-spotted Woodpeckers used the thinner branches (Török 1990). The smaller species like the Middle- and Lesser-spotted Woodpeckers are more agile than Great-spotted Woodpeckers, so in habitats, where the above-mentioned species were both present, Great-spotted Woodpeckers did not use the uppermost regions and the thinnest branches. In our study area, there are not any Middle-spotted Woodpeckers, so Great-spotted Woodpeckers could mainly use the thinner trunk in the upper regions. In a pine forest in Finland, the Great-spotted Woodpeckers coexisted with Lesser-spotted, Black and Grey-headed Woodpeckers. In that study, the Great-spotted Woodpecker used mainly the upper regions, more precisely the thicker branches. The Black and the Grey-headed Woodpeckers were weak competitors for Great-spotted Woodpeckers as they foraged mainly on the ground and on the lower parts of the trunk for ants. As the Lesser-spotted Woodpecker is the smallest European woodpecker species, it makes common sense, that this species is more specialist, than the Great-spotted Woodpecker as the Lesser-spotted Woodpeckers use the upper parts of trees, they forage in the canopy, on the thinnest branches (Alatalo 1978, Török 1990, Charman *et al.* 2010).

As the bark structure of the tree species living in the study area is so different and some of those species could have rich food supply underneath the bark, the specimens showed mostly probing behaviour, when the birds gather their food without subcambial excavations. There are subcambial prey items as well in the wood of the native trees. As native trees are less frequent than the invasive species this situation could be the cause of that the birds showed the excavating behaviour less frequently than the probing behaviour. Great-spotted Woodpeckers showed the probing behaviour most frequently in other studies as well, like in the above mentioned study of Török (1990), where this species used almost exclusively oak trees, which have rough bark structure as well, with more arthropods. As in other studies, Lesser-spotted Woodpeckers used the probing technique the most among the three studied foraging techniques as well as the other species. The frequent utilization of the probing behaviour could be due to the woodpeckers trying to optimise the costs and benefits of foraging activities as it could be the most energy saving and still effective foraging behaviour. On the other hand it could be due to that most prey species lives closer to the surface underneath the bark. Both suggestions need further studies. According to other studies, both species use the gleaning technique mainly in the breeding season, and Lesser-spotted Woodpecker uses it more exclusively. This study is not suited for the examination of neither seasonal differences (due to the low amount of data on Lesser-spotted Woodpecker) and nor the use of gleaning technique (due to the highly stratified architecture of the studied habitat in vegetation periods (Alatalo 1978, Török 1990, Smith 2007, Böhm *et al.* 2009, Charman *et al.* 2010).

The arboreal species preferences of the studied birds were similar in terms of native trees as they preferred the rough-barked willow trees and black poplar hybrids the most. Among the native trees, the third preferred species was the white poplar hybrids. Only the white poplar hybrids' bark is smooth among the native trees, so fewer prey species could inhabit their bark. The black poplar hybrids are the oldest and biggest trees in the study area, therefore their wood could be rotten in larger volumes, providing suitable microhabitats for numerous wood-boring insect species. These trees could have more arthropods in and underneath the bark of their trunks, in their decaying and dead limbs and even in their living branches. These characteristics can make the living, but internally decaying branches the most utilized substrate type for both of the studied species. These woodpecker species may prefer wood-dwelling arthropods which live in living or partially decayed branches in the study area. This requires future entomological studies.

White mulberry trees prefer dryer soils. They don't tolerate the 2-3 year floods well, so most mulberry trees in this habitat type are decaying with numerous partially dead or dead branches providing suitable habitat for woodpecker prey species. This could be the result of the high preference shown for them by the Great-spotted Woodpecker, despite the low abundance of this tree species (Mihály & Botta-Dukát 2004).

In North America, the green ash and the boxelder maple occupy the midstorey and the lower canopy layer of the willow-poplar riparian forests as mid-successional species supporting diverse bird communities (Hodorff & Hull Sieg 1986, Rumble & Gobeille 1998). These species survive more successfully in the shade and grow better at the clearings of the source-rich European riparian forests, than the European willow and poplar species (Saccone *et al.* 2010, Porté *et al.* 2011). Both non-native species have secondary metabolic products that prevent herbivory and wood boring insects inhabiting their inner tissues. These species also produce allelopathic chemicals that can prevent the saplings of native species from developing properly (Csiszár 2009, Csiszár *et al.* 2013). Green ash supports very few wood boring insect species. Among them, the most common one is the ash bark beetle *Leperesinus fraxini* (Scolytidae), which lives in the bark of the trees. Only Great-spotted Woodpeckers pecked the bark of this tree species. According to the literature, there are not any known wood boring insect species in the living wood of boxelder maple in Europe. Among the few records (n=46), that were gathered at boxelder maples, the birds showed excavating behaviour near as frequent as probing or searching. That suggested that some arthropod species could have inhabited the wood of the maple trees. This problem needs further entomological surveys. Although in early spring in the study area one could find boxelder maples 'ringed' by Great-spotted Woodpeckers (they made horizontal rows of little holes, so that they can feed on the sap that percolates from the phloem), but in the study period, we've never collected any records on this kind of behaviour as the frequency of this activity is much lower comparing to the other foraging behaviours that were represented (Gencsi &

Vancsura 2002, Gorman 2004, Mihály & Botta-Dukát 2004).

As the green ash and the boxelder maple are the two most avoided tree species in our study, we can confidently predict that the population decrease of the native tree species will probably lead to a suboptimal habitat compared to the current situation. Under these conditions the size of the woodpecker territories is predicted to increase, resulting in lower densities. As the most common cavity excavators, the studied woodpecker species play key role in alluvial forest communities, the above mentioned changes would have significant effects on the population dynamics of numerous cavity-dependent species. Though the Great-spotted Woodpecker could be a serious nest predator for cavity-nesting bird species, and so some species avoid nesting in woodpecker cavities (Wesolowski 2007), this species is the main excavator in the study area. Some species avoid the holes of the studied species, instead they nest in naturally decayed cavities. In many cases, the decaying processes are initiated by the excavating work of foraging woodpeckers, as they can inoculate wood-decaying fungi into wood. Woodpecker-excavated foraging holes could be nesting cavities through decaying processes a couple of decades later. As the invasive tree species have harder wood, these trees decay slower than the native willow and poplar trees, the importance of woodpecker-made foraging and nesting cavities will surely increase (Farris *et al.* 2004, Jackson & Jackson 2004).

These invasive arboreal species have been present in Hungary and across Europe for more than a century and so they are widespread nowadays. These species transformed their new habitats, forming entirely new ecosystems that never existed before. The restoration of these highly transformed habitats would be very source-intensive, if even possible, the managements could mean too much harm to the habitat. South-African and Australian authors termed these transformed ecosystems as ‘emerging’ or ‘novel’ ecosystems. They considered that adaptive management strategies could be the most successful ways to secure the current processes of these ecosystems while trying to preserve the native vegetation as much as possible (Milton 2003, Hobbs *et al.* 2006, Lindenmayer *et al.* 2008, Hobbs *et al.* 2013).

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Fossil and subfossil bird remains and faunas from the Carpathian Basin

Jenő (Eugen) Kessler

Jenő (Eugen) Kessler 2014. Fossil and subfossil bird remains and faunas from the Carpathian Basin. – Ornis Hungarica 22(2): 65–125.

Abstract The author summarizes the knowledge of fossil and subfossil bird life from the Carpathian Basin, of all geological ages, site by site. After a historical overview, he presents the Mesozoic, Tertiary and Quaternary bird fauna, based on a holistic reference material consisting of 196 titles indicated in the bibliography, including papers in English (64), Hungarian (50), German (46), Romanian (26), Croatian (9) and Polish (1) languages. The text is supplemented with maps of fossiliferous sites from different ages and a list from 341 paleontological and archaeological sites on species of the Carpathian Basin, respectively. The number of taxa reaches 845, including 189 extinct taxa (two orders, four families, nine genera – five ichnotaxa of which (154 species, five ichnotaxa and 10 subspecies) were described from the Carpathian Basin, primarily. Most significant records include the Mesozoic taxa *(Eurolimnornis, Palaeocursornis, Elopteryx)*, the new Neogene songbirds species and the presence of predecessors of recent European grouses, Bustards and Corvidae species from the Pliocene and Early Pleistocene in the Carpathian Basin.

Keywords: Carpathian Basin, paleo-ornithological studies, fossil sites, evolution

Összefoglalás A szerző összefoglalja a Kárpát-medence fosszilis és szubfosszilis madárvilágáról szóló ismereteket, mind koronként, mind lelőhelyenként. A történelmi visszatekintés után ismerteti a mezozoikumi, a harmad- és negyedidőszaki lelőhelyek madárfaunáját egy teljességre törekvő, angol (64), magyar (50), német (46), román (26), horvát (9) és lengyel (1) nyelvű, 196 tételből álló hivatkozáslista alapján. A kréta és harmadidőszaki, a kora- és középső-pleisztocén, a késő-pleisztocén, valamint a késő-glaciális és holocén kori lelőhelyek térképei, valamint (mellékletként) a meghatározott taxonok rendszertani és időrendbeli táblázata egészíti ki a tanulmány szövegét. A Kárpát-medencéből 341 őslénytani és régészeti lelőhelyről ismerünk fosszilis és szubfosszilis madármaradványokat. A taxonok száma eléri a 845-öt. Ebből 189 kihalt taxon (két rend, négy család, kilenc genus – ebből öt ichnotaxon (154 faj, öt ichnotaxonnal és 10 alfaj) először a Kárpát-medencéből került leírásra. Legjelentősebb leletek a mezozoikumiak *(Eurolimnornis, Palaeocursornis, Elopteryx)*, de igen fontos a neogen kori énekesek és a recens európai fajdok, túzokok és varjúfélék fosszilis elődjei jelenlétének kimutatása is a Kárpát-medence pliocénjében és kora-pleisztocénjében.

Kulcsszavak: Kárpát-medence, madárőslénytani kutatások, madárfossziliák, evolúció, fosszília-lelőhelyek

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Introduction

The paleogeographic conditions in the Carpathian Basin's ancient area (the tectonic plates which constitute the actual territory were not necessarily on their present-day place all the time) are believed to have provided adequate conditions for bird life, presumably, in the time when they appeared on the Earth. The area was covered by more or less widespread masses of water (lakes, inland and open seas) from the Triassic to the Neogene period, but sometimes it had vast littoral zones with lagoons and archipelagos as well. We have a lot of evidence of continental life already from the Triassic for both the plant and animal kingdoms. There are well-known plant marks and relics developed in the Mecsek and Királyerdő Mountains (Munţii Pădurea Craiului) from the Early Jurassic. However, animal remains such as footprints of dinosaurs in Mecsek, nothosaurs described in the Báród Basin, a sea-protocrocodile skeleton in Gerecse, Early Cretaceous remains of vertebrates of Cornet in Királyerdő, fossils of dinosaurs, crocodiles, lizards but even Mammalia from the Late Cretaceous in Erdély (Transylvania) and in the Bakony. As a consequence of paleogeographic conditions, terrestrial life forms are poorly represented (e.g. there are fewer bird fossils).

This is plausible because the Carpathian Basin did not even exist at that time. It was represented by islands or microcontinents located on three tectonic plates between Europe and Africa. Plant fossils indicate that climate was warmer than in the rest of Europe, but their area has limited both the variety of forms of life and the possibilities of fossilization. From the Neogene and especially after the formation of the basin in the present-day location, during and following the uprising of the ring of mountains and the formation of the internal sea which later became a lake, in many places, there appeared adequate conditions for fossilization. As a consequence, in many places, even bones of birds could be found. From the beginning of the Quaternary, the life forms in the Carpathian Basin became more and more similar to the present-day ones. This flora and fauna had many similarities to those described in other parts of Europe but also had a lot of endemic species. From the Mesozoic, even the occurrence of dwarfism, a characteristic of archipelagos, is demonstrated.

In this region, another characteristic of that 200 million years long period between the Triassic and the Quaternary was a warmer climate. This can be seen from the composition of both the flora and vertebrate fauna. For example, several vertebrates, which today are characteristic to the tropics (primeval reptiles, crocodiles, turtles, birds and even mammals), lived here. The diverse and lush vegetation with its insects, as well as the fauna of the vast aquatic surroundings, provided rich food sources for many, including birds, allowing them to exist. Their presence is indicated by findings already from the Mesozoic, but we have plentiful fossils from the Tertiary and especially from the Neogene. As a consequence of the extensive karstification, in numerous caves, rich bird fossils from the Quaternary were discovered. These fossils allow us to easily trace the changes of the avifauna during the succeeding glacial and interglacial periods, up to the present situation.

We discuss in this paper the evolution of this avifauna based on the available literature and the bird fossils examined and determined by us.

List of collections:

GIB = Geological Institute Bucureşti, Romania

IPUW = Institute of Paleontology, University of Wien, Austria

EMNH = Eötvös Museum of Natural History, Eötvös Loránd University, Budapest, Hungary

LPUB = Laboratory of Paleontology, University București, Romania

MÁFI = Magyar Állami Földtani Intézet (Geological Institute of Hungary, new Geological and Geophysical Institute of Hungary: GGIH, Budapest, Hungary)

MEMEK = Museum 'Erdélyi Múzeum Egylet' Kolozsvár, Romania

MMB = Moravian Museum Brno, Czech Republic
MMP = Museum Municipal Pásztó, Hungary
MPUBBC = Museum of Paleontology University 'Babeș-Bolyai' Cluj – Kolozsvár, Romania
MTM = Magyar Természettudományi Múzeum (Department of Paleontology and Geology of the Hungarian Natural History Museum, Budapest, Hungary – HNHM)
MȚCO = Museum 'Țării Crișurilor Oradea', Nagyvárad, Romania
NHML = Natural History Museum, London, England
NHMW = Natural History Museum Wien, Austria

The short history of avian paleontology in the Carpathian Basin

According to the earliest known data (Neugeboren 1850), Michael Ackner collected songbird remains around the middle of the nineteenth century from the Popláka chasm near Sibiu in Transylvania. The next finding, an imprint of a feather, was reported from the Miocene of Oltszakadát and Brașov in 1855 (Andrae 1855). Hermann von Meyer described a finch *(Fringilla radobojensis)* from the Miocene of Radoboj, Croatia (von Meyer 1865). A few years later, Samu Róth excavated caves I. and III. of Novi Hill in Szepes (Spiš) County, Slovakia, and Antal Cave in Ružín (1879-1880). The remains found were classified and published by Alfred Nehring (Nehring 1880, 1881). In the second half of the nineteenth century, Gábor Téglás, an archeologist from Déva, gathered material from the Hátszeg (Haţeg) Basin and Apuseni Mountains, both in Transylvania. He mentioned several species while identifying the findings from the Nándori Cave (Téglás 1880). With paleontological research making rapid headway in the late ninetieth-early twentieth century, the year 1904 was a significant one regarding avian paleontology, when Mihály Tóth discovered the site on the southwest versant of Somló Hill near Oradea. Excavation of the remains of the cave system formerly known as Püspökfürdő, then as Betfia, was initiated by Tivadar Kormos. He was also the one to publish the avian fossils' preliminary classification (Kormos 1911, 1913). In-depth classification was made by Waclav Čapek Czech osteologist (Čapek 1917). In 1905, Zoltán Szilády gathered material (avian bones among others) from the Lucsia Cave near Aranyos-Szohodol in Transylvania. These remains have only been found in 2000 in the collection of the Department of Geology and Paleontology of the Hungarian Natural History Museum by Erika Gál and identified recently (Gál 2002a). Bones found in the cavern of Dealul Şprenghi in Brașov were classified by Ferenc Toula (Toula 1909). A few years later, Gyula Éhik studied the same site (Éhik 1913). In 1915, Ottokár Kadić gathered material from Zoltán Cave in Băile Herculane, Romania. Findings of the latter two excavations mentioned were also classified by Erika Gál (Gál 2002a). Several fossils collected in the meantime have been transported to foreign museums. From the material purchased from Ferenc Nopcsa and originating from the Late Cretaceous layers of the Hátszeg Basin, Charles William Andrews English paleontologist identified a much-debated ibis-like species (*Elopteryx nopcsai* Andrews, 1913) (Andrews 1913, Lambrecht 1933). Between 1911 and 1917, Tivadar Kormos and Ottokár Kadić gathered rich findings from numerous sites in Transylvania, North Hungary, Croatia and Hungary, classified and published by Kálmán Lambrecht (Lambrecht 1912a,b, 1913, 1915, 1916a), including the avian fossils found in the bituminous sand of Tataros in Partium (Lambrecht 1916b). This became possible because he had established the comparative collection in the Ornithological Centre in Budapest, consisting of more than 1400 skeletons. Due to his role during the Soviet regime, Lambrecht could not continue his researches in Hungary until 1926, when he became a librarian under Ferenc Nopcsa in the Hungarian Geological Institute. He presented material gathered after World War I. on the XXVIII. Ornithological World Congress held in Budapest (Lambrecht 1929). Finally, in Berlin in 1933, Lambrecht's major comprehensive work, referred to and used to this day, the 'Handbuch der Palaeornithologie' was published, summarizing the paleornithological literature of the day, along with findings in foreign collections examined and classified by Lambrecht himself. Sadly, fate did not give him much more time to work thereafter, and in 1936, Kálmán Lambrecht, one of the most significant figures of Hungarian and international avian paleontology, died. Findings and descriptions following his death were sparse. From the 1930's, Mária Mottl collected and classified inter alia bird fossils from Hungarian, Transylvanian and, later, Austrian caves. From the late thirties, Miklós Kretzoi got engaged in avian paleontology. From 1941, he gathered bird remains from several Transylvanian and North Hungarian sites, such as from older and more recent parts of Püspökfürdő. He registered a few species in his preliminary report (Kretzoi 1941). The new name of the site, Betfia, can also be credited to him. As a result of his study of ample small mammal findings, he established the Biharian stage and the Betfian faunal level. From 1951 to 1960, Kretzoi has classified and published avian bones from sites at Csákvár, Kisláng, Southern Baranya and from newer sites of Betfia (Kretzoi 1961-1962). In 1953, the first work of Dénes Jánossy regarding avian paleontology was published, describing material from the cave of Istállóskő. Until the end of the 90's he wrote papers one after the other not only on Hungarian, but also on Slovakian, Transylvanian and German sites. In 1985, László Kordos published his work on footprints (on birds' prints, among others) found at Ipolytarnóc. In later essays (working either with Jánossy or alone), he published lists of species from cavernous sites from the Quaternary of Hungary. Meanwhile, from 1961, Mirko and Vesna Malez classified and published the bird fauna of states of former Yugoslavia in numerous works. At the same time, in the former Czechoslovakia, Ian Horáček, Oldřich Fejfar, Robert Musil, Petr Svec, then in the last decade mainly Jirí Mlikovskỳ, reported several avian findings from Slovakia, Austria and Croatia. In Austria, at the same time Otto Wettstein, Elsbeth Soergel, Johann Nepomuk Woldrich, Franz Bachmayer, Ursula Göhlich, Gernot Rabeder and others have collected and classified remains, but Kálmán Lambrecht, Dénes Jánossy and Jíri Mlikovskỳ also had a significant role in the classification of the material. The Kessler's first work on the history of avian paleontological research in Romania was published in 1973 in Romania in cooperation with Tibor Jurcsák. This was followed by the classification and publication of material found in Romanian collections by himself and also with co-authors (note that only Erika Gál and Tibor Jurcsák have made effective avian paleontological research, other co-authors only described either the geological features of the sites or other fossil remains in their works). Tibor Jurcsák paleontologist, who had laid the foundation of paleornithological research in the 'Ţara Crişurilor' Museum (collecting fossils, creating a comparative bone collection, obtaining literature), passed away in 1992. The author, having become a professor of the 'Babeș-Bolyai' University of Cluj-Napoca, began working with Erika Gál in 1994, who in her PhD thesis (Gál 2002a) discussed the Pleistocene avian fauna of Romania. Since 2002, they both continued their research in Hungary. In the last decade with the retirement of Miklós Kretzoi and Dénes Jánossy, and their death in 2005, a very significant and fertile era of Hungarian paleontology has ended. However, with the moving of the Hungarian Natural History Museum's Department of Paleontology and Geology, the creation of suitable research conditions could begin. Ever since the Late Pleistocene, the presence of man has on the one hand influenced the very existence of birds (being responsible for the lapsing and even the extinction of many species), but on the other hand with storing up uneaten bones around their habitats, they contributed to the remains' going down to posterity. Even material from Palaeolith sites is considerable, but mainly bones from the Holocene Mesolithic, Neolithic, Metal Age and historical times indicate human customs of hunting and breeding birds. Since parts undigested by predators (found mainly in caves) have been piled up in parallel with bones in the cesspool of humans, their classification, which is a task of zooarchaelogy, provides information on the avifauna of the past few thousand years. Experts of zooarchaeology were mainly those mentioned in the field of Paleornithology. This also indicates the peculiarity of classifying avian remains. It was Gábor Téglás who reported archaeozoological bird fossils from the area of the Carpathian Basin from the second half of the 19th century, followed by Kálmán Lambrecht, Mária Mottl and the above-mentioned Austrian researchers between the two World Wars. In the second half of the twentieth century, Sándor Bökönyi, István Vörös and László Bartosiewitz registered bird findings in Hungary, but most of them have been classified by Dénes Jánossy. In Romania, Erika Gál and the author did the same and the former has continued her activity in Hungary as well. There are far more than a hundred zooarchaeology sites in Hungary, Austria, Romania, Serbia, and Slovakia, providing numerous remains of wild fowl species. It can be noted in the light of the description above that as of yet no avian fossils or subfossils are known from sites in the Carpathian regions of Slovenia and Ukraine (Kessler 2013a).

The mesozoic bird life of the Carpathian Basin

Among vertebrates of the Upper Triassic – Lower Jurassic living in shallow coastal lagoons, the reptiles ruled. This is evidenced by the *Notosaurus* and *Tanystropheus* from the Upper Triassic of Bárod Basin in Transylvania, the dinosaur footprints from the Lower Jurassic of Mecsek Mountains, and the sea crocodilian skeleton from Gerecse Hill. Ancestral bird remains are not found, but their presence can not be excluded. Nevertheless, they are only known from the Cretaceous. The Cretaceous sites from the Carpathian Basin are clustered in three areas:

1. The oldest (Berriasian, Lower Cretaceous, 145 million years) is a Transylvanian Cornet bauxite mine in the Királyerdő Mountains. These fossils were collected in 1978-1980, together with several dinosaurs and pterosaurs remains. Between 1982 and

1986, the author and Tibor Jurcsák identified three bird taxa here: – aff. *Archaeopteryx* sp., *Eurolimnornis corneti* Kessler and Jurcsák, 1984 (new ordo, family, genus and species) and *Palaeocursornis biharicus* Kessler and Jurcsák, 1986 (also new ordo, family, genus and species). Their true bird character was much doubted (Benton *et al.* 1997, Feduccia 1999 and other authors). Based on the recently completed revision (Dyke *et al.* 2010): 'Aside from their phylogenetic affinities, these unique Romanian fossils are also important because of their age; in particular, very few birds are known globally from the earliest Cretaceous. Reexamination of collections in Oradea (Nagyvárad) confirms the presence of both birds and pterosaurs in the Cornet bauxite: although the fragmentary bird remains are mostly indeterminate, one record of a hesperornithiform is confirmed. These records are extremely significant because of the age of the Cornet deposit. The fossil birds from this site are just a few million years younger than *Archaeopteryx* (Aves) from the Late Jurassic of Germany.' On the one hand, it was proved that they are among the oldest bird remains; on the other hand, erroneously was treated as '*nomina dubia*' Deposited in MȚCO.

2. Iharkút opencast bauxite mine, Bakony Mountains, Hungary (Upper Cretaceous, Santonian, Csehbánya Formation, 80 million years). The sites were identified by Attila Ősi in the previous decade and furnished many turtle, lizard, crocodile, dinosaur and pterosaur remains. Next to them were Enantiornithes bones as well. A new genus and species: *Bauxitornis mindszentyae* was described here (Dyke & Ősi 2010). In addition, Enantiornithes indet and Aves indet were also recorded. Deposited in HNHM.

3. Szentpéterfalva (Sînpetru), Hátszeg (Haţeg) Basin, Romania (Upper Cretaceous, Maastrichtian, 65 million years). In 1904, Baron Ferenc Nopcsa began the collection in this site. Besides dinosaur remains, he also discovered avian bones. These were identified by Charles William Andrews in 1913 as the new bird taxon *Elopteryx nopcsai.* This resulted in much discussion, but in 2005, at the same site, a new bone was discovered, which confirmed the previous determination (Kessler *et al.* 2005). Deposited in NHML and LPUB.

4. Valiora (Vălioarea). Hátszeg (Haţeg) Basin, Romania (Upper Cretaceous, Maastrichtian, 65 million years). Here in 1990, D. Grigorescu discovered problematic bird bones, which were published as Ornithurinae birds (Wang *et al.* 2011), but in my opinion, they are Enantiornithes. Deposited in LPUB.

5. Szászsebes (Sebeș), Alba County, Romania (Upper Cretaceous, Maastrichtian, 65 million years). In 2011 Mátyás Vremir discovered an entire nesting colony (with eggs and embryos). After Gareth Dyke, these are derived from Enantiornithes. Deposited in MEMEK.

Tertiary avian remains and localities of the Carpathian Basin:

After the extinction of the Theropods and Sauriurae birds, the Ornithurae bird fauna underwent an explosive development. However, the numbers of Paleogene fossils are not too many in the Carpathian Basin due to paleogeographic reasons. In contrast, the number found in Neogene sites is much higher.

A. Paleogene localities:

1. Kolozsmonostor (Cluj-Mănăștur), Romania (Middle Eocene, MP 13). Was discovered by Antal Koch and described by Kálmán Lambrecht as *Eostega lebedinskyi* Lambrecht, 1929, based on a partial mandible. The genus and species was described in

the new family Elopterygidae (Lambrecht 1929), but it appears that it is in fact a typical member of the modern family Sulidae (Mlikovskỳ 2007). Deposited in NHMW.

2. Kolozsvár – Fellegvár (Cluj-Cetăţuie), Romania (Lower Oligocene, MP 24).

– *Rallicrex kolozsvariensis* Lambrecht, 1933, based on the partial skeleton of a new rail genus and species (Lambrecht 1933). It was discovered by János Tulogdy. Deposited in MÁFI.

– Anseridarum gen. et sp. indet. based on a partial lower limb imprint; was discovered by Mátyás Vremir (Kessler *et al.* 1998). Deposited in MPUBBC.

3. Budapest – Újhely Clay Open pit mine in Szépvölgy, Hungary (Lower Oligocene, MP 24; Kiscell Clay Formation). The discovery of an almost complete wing skeleton, assigned to the petrel-like new fossil bird *Diomedeoides harmathi* Kessler, 2009. The slab including the fossil specimen was collected by István Harmat in 1923. This is the oldest modern bird species (Ornithurine) found in the present-day territory of Hungary. The presence of this aquatic bird belonging to the order of Procellariformes is in accordance with presumed deep-sea conditions in the Carpathian Basin during the Miocene (Kessler 2009c). Deposited in HNHM.

4. Petrozsény (Petroșani) – Câmpul lui Neag, Romania (Upper Oligocene, MP 25). Footprints of *Charadriipedia limosa* Radan et Brustur, 1993 (Rădan & Brustur 1993). Deposited in GIB.

5. Máriahalom – Hungary (Upper Oligocene, MP 25, Mány Formation). The remains were discovered by Zoltán Evanics and partially determined by the authors as: aff. *Gavia* sp., aff. *Grallavis edwardsi* (Lydekker 1891) *Mionetta robusta* (Milne-Edwards 1868), *Pandion* sp. foss., aff. *Balearica excelsa* (Milne-Edwards 1868), Aves indet. (Kessler & Rabi manuscript). The bird fauna indicates a freshwater environment. Deposited in EMNH.

B. Neogene localities:

The Neogene avifauna of the Carpathian Basin is incomparably richer than the Paleogene one. Footprints, feather imprints, eggshell pieces and, of course, primarily bones occur. Almost all geological periods are represented.

Miocene:

a) Lower Miocene

MN 1-4:

1. Erősd (Ariușd), Romania – with problematic? *Haliaeetus* sp. (Lambrecht 1929). Its whereabouts are unknown.

2. Ipolytarnóc, Hungary – footprints discovered in 1900. László Kordos described, in 1983, four birds, ichnotaxa: *Avidactyla media* Kordos, 1983, *Ornithotarnocia lambrechti* Kordos, 1983, *Passeripedia ipolyensis* Kordos, 1987, *Tetraornithopedia tasnadii* Kordos, 1983 (Kordos 1985, 1987). Deposited in MÁFI.

3. Piski (Simeria), Romania – unidentified feather imprints were collected by János Mallász (Lambrecht 1929). Their location is unknown.

MN 3-4:

4. Limberg, Austria – the partial skeleton imprint and feather imprints were collected in the XIX. century and identified as: *Prosybris antiqua* (Milne-Edwards 1863) by Jiri Mlíkovskỳ (Bachmayer 1980, Mlikovskỳ 2002). Deposited in NHMW.

MN 4:

5. Grund – Molasse Basin, Austria – the bird remains were determined by Ursula Göhlich as: *Microsula pygmaea* (Milne-Edwards 1874); *Phalacrocorax intermedius* (Milne-Edwards 1867); cf. *Palaeortyx*

intermedia Ballmann, 1969; Laridae indet.; Aves indet. (Göhlich 2003). Deposited in NHMW.

6. Oberdorf, Austria – the few fragments were collected from a coal mine of Graz Basin and determined by Jiri Mlikovskỳ as: Anatidae gen. et sp. indet. and Passeriformes fam. indet. (Mlikovskỳ 1998b). Deposited in NHMW.

MN 5:

7. Borosd (Weingraben), Austria – the feather imprints attributed to the Podicipedidae, Phalacrocoracidae, Ardeidae and Anatidae from Burgenland are signalled by Bachmayer (1964) and Mlikovskỳ (1996). Deposited in NHMW.

8. Litke 2, Hungary – discovered in 1998 by János Hír, the fossiliferous site furnished a rich bird bone material, determined by the author as: *Cygnopterus neogradensis* Kessler and Hír, 2009; *Palaeortyx* aff. *Phasianoide*;, *Palaeortyx gallica*; *Rallicrex litkensis* Kessler and Hír, 2012; *Corvus* sp. indet.; *Galerida cserhatensis* Kessler and Hír, 2012; *Cinclus major* Kessler andt Hír, 2012; *Turdicus minor* Kessler and Hír, 2012; *Luscinia praeluscinia* Kessler and Hír, 2012; *Bombycilla hamori* Kessler ande Hír, 2012; *Emberiza bartkoi* Kessler and Hír, 2012; Passeriformes indet. (Kessler & Hír 2009, 2012a,b). Deposited in MMP.

b) Middle Miocene

MN 6-8:

1. Brassó (Brașov), Romania – unindentified feather imprint (Lambrecht 1933, Andrae 1955). Its location is unknown.

2. Dévényújfalú (Devinska Nová Ves, Neudorf), Slovakia – bone fragments of the Phasianidae as *Miogallus altus* (Milne-Edwards 1869) and unidentified passerines (Švec 1986, Kordos 1987, Mlikovskỳ 1996). Deposited in MMB.

3. Egerszólát-Ádám Valley, Hungary – the site was discovered by János Hír in 2005. A few materials (two claw bones) can be attributed to cf. *Palaeortyx* sp. indet. (Kessler & Hír 2012a). Deposited in MMP.

4. Felménes (Minișul de Sus), Romania – the only bone fragment was collected by Vlad Codrea and identified by the author as: *Anser* sp. indet. (Kessler & Codrea 1996). Deposited in MPUBBC.

5. Felsőtárkány, Hungary – the fossil material was collected by János Hír in 2000 and was determined by the author and Erika Gál as: *Miophasianus (Miogallus)* sp.; *Praealauda hevesensis* Kessler and Hír, 2012; *Anthus antecedens* Kessler and Hír, 2012; *Phylloscopus miocaenicus* Kessler and Hír, 2012; *Bombycilla hamori* Kessler and Hír, 2012; Passeriformes indet. (Hír *et al*. 2001, Kessler & Hír 2012b). Deposited in MMP.

6. Felsőtárkány-Felnémet 2/3 and 2/7, Hungary – the fossil material was collected by János Hír in 2002-2003 and was determined by the author as: Ardeidae gen. et sp. indet.; Ciconiidae gen. et sp. indet.; cf. *Miogallus altus; Rallicrex litkaensis* Kessler and Hír, 2012; Strigidae gen. et sp. indet.; *Muscicapa leganyii* Kessler and Hír, 2012*;* *Lanius schreteri* Kessler and Hír, 2012; Passeriformes indet.; Aves indet. (Kessler & Hír 2012a,b). Deposited in MMP.

7. Kőalja 2. (Subpiatra 2), Romania – the site was discovered by János Hír and Márton Venczel in 2004. The fossiliferous site furnished rich rodent and bird material. The bird bones were determined by the author as: *Proardeola walkeri* Harrison, 1979; *Anas albae* Jánossy, 1979; *Palaeortyx gallica* Milne-Edwards, 1869; Perdicidae gen. et sp. indet., Gruidae gen. et sp. indet., Rallidae gen. et sp. indet., Meropidae gen. et sp. indet., Sittidae gen. et sp. indet., Certhidae

gen. et sp. indet., *Luscinia jurcsaki* Kessler and Venczel, 2011, Sylviidae gen. et sp. indet., Laniidae gen, et sp. indet., Passeriformes indet. (Kessler & Venczel 2009, 2011). Deposited in MȚCO.

8. Mátraszőlős 1, Hungary – situated in Nógrád County the site had been discovered in 1940, but vertebrate remains were collected by János Hír in 1998. The bird material was determined by Kessler and Gál (2001, 2009, 2012) as: aff. *Anhinga* sp.; *Phalacrocorax* sp. indet.; *Bucephala* aff. c*ereti* Boef et Mourer-Chauviré, 1991; *Anas* cf. *velox* Milne-Edwards, 1868; *Clangula matraensis* Kessler and Hír, 2012; *Mergus minor* Kessler, 2009; *Palaeortyx* cf. *gallica* Milne-Edwards, 1869; *Rallicrex litkensis* Kessler and Hír, 2012; *Porzana* aff. *estramosi* Jánossy, 1979; *Porzana matraensis* Kessler, 2009; *Gallinago* cf. *veterior* Jánossy, 1979; Cuculidae g. et sp. indet.; *Galerida cserhatensis* Kessler and Hír, 2012; *Lullula neogradensis* Kessler and Hír, 2012; *Motacilla* sp. indet.; *Erithacus bartkoi* Kessler and Hír, 2012; Passeriformes indet. (Gál *et al.* 1998-1999; Kessler 2009a,b, Kessler & Hír 2012a,b). Deposited in MMP.

9. Mátraszőlős 2, Hungary – discovered by János Hír in 1999, also provided avian fossils, determined by the author and Erika Gál as: *Proardeola walkeri* Harrison, 1979; Ardeidae gen. et sp. indet.; *Megapaleolodus goliath* Miller, 1944; *Mionetta consobrina* Milne-Edwards, 1867; cf. *Miogallus altus* Milne-Edwards, 1869; Columbidae gen. et sp. indet.; *Turdicus minor* Kessler and Hír, 2012; Passeriformes indet.; Aves indet. (Gál *et al.* 2000, Kessler 2009b, Kessler & Hír 2012b). Deposited in MMP.

10. Mátraszőlős 3, Hungary – the new site lays about 20 m south-east to the site Mátraszőlős 2. It was discovered in 2008 by János Hír. The avian material was determined by the author as: *Cygnopterus neogradensis* Kessler and Hír, 2009; *Paleolodus ambiguus/crassipes* Milne-Edwards, 1863; *Tadorna minor* Kessler and Hír, 2012; Anatidae gen. et sp. indet., *Miocorvus larteti* (Milne-Edwards 1871); *Turdicus minor* Kessler and Hír, 2012; Aves indet. (Kessler & Hír 2009, 2012a,b). Deposited in MMP.

11. Oltszakadát (Săcădate), Romania – unidentified feather imprint (Andrae 1855, Lambrecht 1933). Its location is unknown.

12. Radoboj, Croatia – situated near Zagreb, from the site a partial skeleton was identified, formerly thought to be a passerine bird (*Fringilla radobojensis* Meyer, 1865). Subsequently, it was re-defined as *Merops radobojensis* Mlikovskỳ, 1997 (Mlikovskỳ 1997a). Deposited in NHMW.

13. Szentmargitbánya (Sankt Margarethen), Austria – the fossiliferous site in Burgenland provided a partial skeleton of *Gavia schultzi* Mlikovskỳ, 1998 (Mlikovskỳ 2002). Deposited in NHMW.

14. Tasádfő – Drágcséka (Tășad), Romania – the site was discovered by János Hír and Márton Venczel in 1999. The avian material was determined and published by the author and Erika Gál as: *Miocorvus larteti* (Milne-Edwards 1871) (Gál & Kessler 2006, Kessler 2010a). Deposited in MȚCO.

c) Upper Miocene

MN 9:

1. Atzelsdorf, Austria – the *Anas sansanensis* Milne-Edwards, 1868 has been indicated here by Ursula Göhlich (Göhlich 2009). Deposited in NHMW.

2. Heiligenstadt – Wien, Austria – an unidentified eggshell was mentioned by Kálmán Lambrecht (Lambrecht 1933). Deposited in NHMW.

3. Rudabánya, Hungary – rich avian material was determined and published by Dénes Jánossy and Eugen Kessler as: *Anas* aff. *velox* Milne-Edwards, 1868; *Anas* sp*., Falco* sp*., Miogallus* cf. *altus* (Milne-Edwards 1869); *Palaeortyx phasianoides* Milne-Edwards, 1869; *P. gallica* Milne-Edwards, 1869; *P. brevipes* Milne-Edwards, 1868; *Miorallus major* Milne-Edwards, 1868; *Strix intermedia* Jánossy, 1972; *Athene* sp*., Tringa* sp,. *Merops radobojensis* Mlikovsky, 1997; *Miocorvus larteti* Milne-Edwards, 1871; *Certhia janossyi* Kessler and Hír, 2012, *Sturnus kretzoii* Kessler and Hír, 2012 (Jánossy 1993, Kessler 2009a,b, Kessler & Hír 2012b). Deposited in MÁFI.

MN 10:

4. Götzendorf, Austria – the bone of *Anhinga pannonica* Lambrecht, 1916 and *Dendroness* sp. was signaled by Jíri Mlikovskỳ (Mlikovskỳ 1992). Deposited in NHMW.

5. Gyepűfüzes (Kohfidisch), Austria – bird bones identified and published by Jíri Mlikovskỳ as: *Pogonolius* sp., *Crex* sp., *Tyto sanctialbani* Lydekker, 1893 (Mlikovskỳ 2002). Deposited in NHMW.

6. Tataros (Derna-Tătăruș, Brusturi), Romania – bones were collected from bituminous sand and identified by Kálmán Lambrecht as: *Anhinga pannonica* Lambrecht, 1916 (Lambrecht 1916). Deposited in MÁFI and NHMW.

7. Vösendorf, Austria – bones of Phaethontidae and Phasianidae were identified and published by Jíri Mlikovskỳ as: *Heliadornis paratethydicus* Mlikovsky, 1997; *Palaeortyx* sp. (Mlikovskỳ 1997b). Deposited in NHMW and IPUW.

MN 11-13:

8. Csákvár (Esterházy Cave), Hungary – avian material was collected, identified and published by Kálmán Lambrecht and later by Miklós Kretzoi as: *Cygnanser csákvárensis* Lambrecht, 1931; *Grus pentelici* Gaudry, 1872; *Bubo florianae* Kretzoi, 1957 (Lambrecht 1931, Kretzoi 1957). Deposited in MÁFI.

9. Korond (Corund), Romania – unidentified feather imprints (Gheorghiu *et al.* 1965). Their locations are unknown.

10. Rátka, Hungary – the almost complete skeleton in slab was identified by the author as: *Palaeocryptonix hungaricus* Jánossy, 1991 (Kessler 2009b). Deposited in a private museum at Tállya.

11. Sümeg, Hungary – a few bones of the Heliornithidae, Phasianidae and Apodidae were identified and published by Dénes Jánossy and Eugen Kessler as: *Chaetura bacconica* Jánossy, 1977; *Palaeortyx* aff. *grivensis* Lydekker, 1893; (Jánossy 1976b, 1977), *Heliornis sümeghensis* Kessler, 2009 (Kessler 2009b). Deposited in MÁFI.

12. Tardosbánya, Hungary – bones of the Phasianidae, identified by Dénes Jánossy as: *Palaeortyx* aff. *grivensis* (Jánossy 1976b). Deposited in HNHM.

MN 13:

13. Polgárdi, Hungary – in the vicinity of the town Polgárdi the limestone quarry at Somlyó Hill and Kőszár Hill (226 m alt.) contained several karst fissures with vertebrate remains. Among them, the Polgárdi 2, 4 and 5 localities furnished bird bones. Polgárdi 2 had been quarried in two excavation campaigns in 1910 by Tivadar Kormos. The bird remains were identified by Waclav Čapek and were published by Kálmán Lambrecht (Lambrecht 1912b, 1933). Polgardi 4 was discovered in 1984-1985 by László Kordos. This locality yielded a rich mammal and bird assemblage. The bird fauna was identified and published by Dénes Jánossy (Jánossy 1991). Polgárdi 5 was discovered in the NE part of the quarry system in 1988 by László Kordos and the bird

fauna was published by Dénes Jánossy (Jánossy 1991). Based on revision of the whole material and on determination of the unidentified material, the author identified and published the following taxa: *Egretta polgardiensis* Kessler, 2009; *Anas denesi* Kessler, 2013; Anatidae indet.; *Anas albae* Jánossy, 1979; *Buteo* sp.; *Falco* cf. *cherrug; Falco tinnunculus atavus* Jánossy, 1972; *Palaeortyx gallica* Milne-Edwards,1869; *P. brevipes* Milne-Edwards,1869; *Palaeocryptonyx hungaricus* Jánossy, 1991; *Pavo archiaci* Gaudry, 1862; Galliformes indet.; *Porzana estramosi* Jánossy, 1979; *Porzana kretzoii* Kessler, 2009; *Rallicrex polgardensis* Jánossy, 1991; *Otis kalmani* Jánossy, 1980; *Otis* aff. *khosiatzkyi* Bochenski & Kurochkin, 1987; *Gallinago* sp., *Cursorius* sp., *Calidris janossyi* Kessler, 2009; *Gallinago veterior* Jánossy, 1979; *Charadrius lambrechti* Kessler, 2009; *Limosa* sp. (5), *Tringa* sp. (4), *Tyto campiterrea* Jánossy, 1991; *Athene noctua veta* Jánossy, 1992; *Surnia robusta* Jánossy, 1977; *Cuculus pannonicus* Kessler, 2009; *Apus baranensis* Jánossy, 1977; *Chaetura* aff. *baconica* Jánossy, 1977; *Alauda tivadari* Kessler, 2013; *Calandrella gali* Kessler, 2013; *Lullula minor* Kessler, 2013; *Hirundo gracilis* Kessler, 2013; *Delichon polgardiensis* Kessler, 2013; *Riparia major* Kessler, 2013; *Motacilla intermedia* Kessler, 2013; *Anthus hiri* Kessler, 2013; *Bombycilla brevia* Kessler, 2013; *Cinclus gaspariki* Kessler, 2013; *Troglodytes robustus* Kessler, 2013; *Turdus polgardiensis* Kessler, 2013; *T. miocaenicus* Kessler, 2013; *T. pannonicus* Kessler, 2013; *Prunella freudenthali* Kessler, 2013; *Oenanthe kormosi* Kessler, 2013; *Saxicola lambrechti* Kessler, 2013; *Muscicapa miklosi* Kessler, 2013; *Luscinia denesi* Kessler, 2013; *Tichodroma capeki* Kessler, 2013; *Sylvia intermedia* Kessler, 2013; *Hippolais veterior* Kessler, 2013; *Acrocephalus major* Kessler, 2013; *A. minor* Kessler, 2013; *Cettia janossyi* Kessler, 2013; *Locustella kordosi* Kessler, 2013; *Phylloscopus venczeli* Kessler, 2013; *Aegithalos gaspariki* Kessler, 2013; *Sitta gracilis* Kessler, 2013; *Lanius capeki* Kessler, 2013; *Sturnus brevis* Kessler, 2013; *Passer hiri* Kessler, 2013; *Fringilla kormosi* Kessler, 2013; *Carduelis kretzoii* Kessler, 2013; *C. lambrechti* Kessler, 2013; *Pyrrhula gali* Kessler, 2013; *Emberiza pannonica* Kessler, 2013; *E. polgardiensis* Kessler, 2013; *Plectrophenax veterior* Kessler, 2013; Passeriformes indet.; Aves indet. (Jánossy 1977, 1979a,b,c, 1991, 1995, Kessler 2009 b, 2010a, 2013a,b). Deposited in MÁFI.

Pliocene

The fossil bird material indicates the environmental conditions at the end of the Miocene and after the sedimentation of the Lake Pannon.

a) Lower and Middle Pliocene:

MN 14

1. Osztramos 1, Hungary – the localities lie on the hill Osztramos in NE Hungary. The fossil material was collected by Miklós Kretzoi in 1955 and Dénes Jánossy between 1965 and 1975 (inclusive in Osztramos 9). The bird remains were determined and published by Jánossy as: ?*Palaeortyx intermedia* (redetermined as *Palaeortyx grivensis* Lydekker, 1893 in Kessler 2009b); *Accipiter* sp., *Turdoides borealis* Jánossy, 1979; Passeriformes indet. (Jánossy 1972, 1979a,b,c). Deposited in HNHM.

2. Osztramos 9, Hungary – this site contained the following bird material: Galliformes indet. *Porzana estramosi* Jánossy, 1979 (Jánossy 1979b). Deposited in HNHM.

MN 15:

3. Gérce, Hungary – among the plant remains collected from this site two feather imprints were discovered (Fischer & Hably 1991). Deposited in HNHM.

MN 15-16:

4. Beremend 5, Hungary – Szőlő Hill of Beremend (174 m altitude) is located aproximately 9 km south around Villány village. It made up the flat and has covered Lower Cretaceous limestone (Nagyharsány Limestone Formation). The limestone was mined for over a hundred years and each year there were more and more discovered karst cavities and fissures containing bones. In 1910, 1916 and in the 1930's Tivadar Kormos collected in the sites No. 4-10. In 1953 Miklós Kretzoi and Dénes Jánossy continued to collect in the mine. The bird remains were determined and published by Dénes Jánossy (1976b, 1977, 1979b,c) and by Jenő Kessler (2009b) as: *Falco* sp. *Gallus beremendensis* Jánossy, 1976; *Francolinus capeki* Lambrecht, 1933; Perdicidae indet., *Otis kalmani* Jánossy, 1980; *Upupa phoeniculoides* Jánossy, 1974; *Apus baranensis* Jánossy, 1977; Passeriformes indet. Deposited in MÁFI.

5. Beremend 26, Hungary – Dénes Jánossy and Endre Krolopp ply the research and excavation since 1973 (sites No. 11-17) and with László Kordos (Jánossy 1979a, Kordos 2001). From 1993, László Pongrácz investigated the new sites (No. 18-39) and collected the fossil remains. The bird remains from Beremend 26. were identified and published by the author (Kessler 2009a,b,c; 2013a,b) as: *Podiceps* sp.; *Egretta* sp.; *Accipiter* sp.; *Falco tinnunculus atavus* Jánossy, 1972; *Falco* sp., *Tetrao praeurogallus* Jánossy, 1969; *Tetrao partium* Kretzoi, 1962; *Gallus beremendensis* Jánossy, 1976; *Francolinus capeki* Lambrecht, 1933; *Palaeocryptonix hungaricus* Jánossy, 1991; *Perdix perdix jurcsaki* Jánossy, 1976; *Rallus polgardensis* Jánossy, 1991; *Miorallus major* (Milne-Edwards 1869); *Porzana* sp., *Otis kalmani* Jánossy, 1972; *O. lambrechti* Kretzoi, 1941; *Chlidonias* sp., *Tringa* sp., *Columba* sp., *Glaucidium baranensis* Kessler, 2010; *Athene noctua veta* Jánossy, 1992; *Strix intermedia* Jánossy, 1972; *Picus pliocaenicus* Kessler, 2012; *Dendrocopos praemedius* Jánossy, 1974; *Melanocorypha minor* Kessler, 2013; *Galerida pannonica* Kessler, 2013; *Lullula parva* Kessler, 2013; *Lullula minuscula* Kessler, 2013; *Delichon major* Kessler, 2013; *Parus robostus* Kessler, 2013; *Parus medius* Kessler, 2013; *Sitta villanyensis* Kessler, 2013; *Muscicapa petényii* Kessler, 2013; *Erithacus minor* Kessler, 2013; *Luscinia pliocaenica* Kessler, 2013; *Saxicola baranensis* Kessler, 2013; *Saxicola magna* Kessler, 2013; *Monticola pongraczi* Kessler, 2013; *Phoenicurus baranensis* Kessler, 2013; *Oenanthe pongraczi* Kessler, 2013; *Turdus major* Kessler, 2013; *Turdus medius* Kessler, 2013; *Turdus minor* Kessler, 2013; *Oriolus beremendensis* Kessler, 2013; *Acrocephalus kretzoii* Kessler, 2013; *Sylvia pusilla* Kessler, 2013; *Locustella magna* Kessler, 2013; *Locustella janossyi* Kessler, 2013; *Regulus pliocaenicus* Kessler, 2013; *Motacilla minor* Kessler, 2013; *Motacilla robusta* Kessler, 2013; *Bombycilla kubinyii* Kessler, 2013; *Prunella kormosi* Kessler, 2013; *Lanius major* Kessler, 2013; *Lanius intermedius* Kessler, 2013; *Sturnus pliocaenicus* Kessler, 2013; *Sturnus baranensis* Kessler, 2013; *Passer pannonicus* Kessler, 2013; *Coccothraustes major* Kessler, 2013; *Loxia csarnotanus* Kessler, 2013; *Emberiza gaspariki* Kessler, 2013. Deposited in a private collection (László Pongrácz).

6. Bodvavendégi (Hostovce 2), Slovakia – only unspecified bird bones have signaled

from this site (Mlikovskỳ 1996). Deposited in a private collection (Jan Horáček).

7. Csarnóta 2, Hungary – Tivadar Kormos began collecting bone material from the columns of red clay deposited in the clefts of the disused stone quarry on the flat top of Cserhegy Hill near the village of Csarnóta in the western part of the Villány Mountains between 1910 and 1930 (marking the site as the 'upper quarries'). Between 1954-1959 Miklós Kretzoi and Dénes Jánossy regularly collected material there. Of the four sites, Sites 2 and 4 yielded bird material. The Csarnóta 2 list of species is as follows: *Podiceps csarnotanus* Kessler, 2009; *Anas albae* Jánossy, 1979; *Falco tinnunculus atavus* Jánossy, 1972; *Palaeortyx brevipes* Milne-Edwards, 1869; *Francolinus capeki* Lambrecht, 1933; *Gallus beremendensis* Jánossy, 1976; *Tetrao praeurogallus* Jánossy, 1969; *Otis kalmani* Jánossy, 1972; *Rallicrex polgardensis* Jánossy, 1991; *Porzana kretzoii* Kessler, 2009; *Gallinago veterior* Jánossy, 1979; *Cuculus csarnotanus* Jánossy, 1979; *Bubo bubo, Aegolius* sp.; *Glaucidium baranensis* Kessler, 2009; *Athene noctua veta* Jánossy, 1992; *Apus baranensis* Jánossy, 1992; *Garrulus glandarius, Pyrrhocorax graculus vetus* Kretzoi, 1962; *Corvus harkanyensis* Kessler, 2009; *Miocorvus larteti* Milne-Edwards, 1871; *Pica pica major* Jánossy, 1979; *Turdoides borealis* Jánossy, 1979 (Kretzoi 1962, Jánossy 1976a,b, 1977, 1979a,b,c, Kessler 2009a,b). Over recent years, the author has identified and defined the species below from the surviving unclassified songbird material as: *Galerida pannonica* Kessler, 2013; *Lullula parva* Kessler, 2013; *Hirundo major* Kessler, 2013; *Delichon pusillus* Kessler, 2013; *Aegithalos congruis* Kessler, 2013; *Parus robustus* Kessler, 2013; *Paru parvulus* Kessler, 2013; *Sitta pusilla* Kessler, 2013; *Certhia immensa* Kessler, 2013; *Saxicola baranensis* Kessler, 2013; *Saxicola parva* Kessler, 2013; *Phoenicurus erikai* Kessler, 2013; *Oenanthe pongraczi* Kessler, 2013; *Turdus major* Kessler, 2013; *Turdus medius* Kessler, 2013; *Turdus minor* Kessler, 2013; *Cettia kalmani* Kessler, 2013; *Acrocephalus kretzoii* Kessler, 2013; *Acrocephalus kordosi* Kessler, 2013; *Sylvia pusilla* Kessler, 2013; *Locustella janossyi* Kessler, 2013; *Phylloscopus pliocaenicus* Kessler, 2013; *Anthus baranensis* Kessler, 2013; *Cinclus minor* Kessler, 2013; *Prunella kormosi* Kessler, 2013; *Lanius hungaricus* Kessler, 2013; *Passer minusculus* Kessler, 2013; *Carduelis parvulus* Kessler, 2013; *Carduelis medius* Kessler, 2013; *Pyrrhula minor* Kessler, 2013; *Fringilla petényii* Kessler, 2013; *Loxia csarnotanus* Kessler, 2013; *Pinicola kubinyii* Kessler, 2013; *Emberiza media* Kessler, 2013; *Emberiza parva* Kessler, 2013 (Kessler 2013a,b). Deposited in MÁFI.

8. Csarnóta 4, Hungary – from Csarnóta 4 in the last years, there were bones of *Tetrao partium* collected by Kretzoi (1962) and determined by Kessler (2009a). Deposited in a private collection (László Pongrácz).

9. Ivánháza (Ivanovce I), Slovakia – situated in West Slovakia, the site furnished a few bones of birds, as: *Alectoris donnezani* (Deperet 1892); *Hirundo rustica, Turdus* sp. (Mlikovskỳ 2002). Deposited in a private collection (Oldřich Fejfar).

b) Upper Pliocene

MN 16:

10. Ajnácskő (Hajnačka), Slovakia – a single bone identified and published by Petr Švec as *Mergus* sp. (Švec in Fejfar & Heinrich 1985), deposited in a private collection. Later, other remains were identified in museum collections and determined by

the author, as *Alectoris donnezani* (Deperet 1892); *Heliadornis minor* Kessler, 2009 (Kessler 2009a,b). Deposited in HNHM.

11. Beremend 11, Hungary – with *Francolinus capeki* Lambrecht, 1933; *Falco* sp.; Passeriformes indet. Collected in 1973 by Dénes Jánossy and Endre Krolopp, and determined by Jánossy (1976b, 1979b,c). Deposited in HNHM.

12. Beremend 15, Hungary – The site was discovered in 1981 and the rich micro- and macrofauna was determined by Dénes Jánossy. From the bird remains, he identified the following taxa: *Ciconia stehlini* Jánossy, 1992; *Anas crecca percrecca* Jánossy, 1992; *Falco tinnunculus atavus* Jánossy, 1972; *Otis khozatzkii beremendensis* Jánossy, 1992; *Numenius* cf. *arquata*, *Anthus* sp., *Serinus* sp., *Corvus pliocaenus* (Portis 1889) (Jánossy 1987, 1991, 1992, 1996b,c) and *Cuculus pannonicus* Kessler, 2010 identified by the author (Kessler 2010a). Deposited in HNHM.

13. Beremend 18, Hungary – collected by László Pongrácz, the bird remains were determined by the author as: *Pelecanus* sp., *Egretta* sp. (*E. alba* size), *Tetrao partium* Kretzoi, 1962; *Palaeocryptonyx hungaricus* Jánossy, 1991; *Francolinus capeki* Lambrecht, 1933; *Perdix perdix jurcsaki* Jánossy, 1976; *Corvus pliocaenus* (Portis 1889) (Kessler 2009a,b, 2010a). Deposited in a private collection (László Pongrácz).

14. Beremend 38, Hungary – collected by László Pongrácz, the bird remains were determined by the author as: *Otis kalmani* Jánossy, 1972; *Upupa phoeniculoides* Jánossy, 1974; Passeriformes indet. (Kessler 2009b). Deposited in a private collection (László Pongrácz).

15. Beremend 39, Hungary – collected by László Pongrácz, the bird remains were determined by the author as: *Miorallus major* (Milne-Edwards 1869-1871); *Gallinula* sp. (Kessler 2009b). Deposited in a private collection (László Pongrácz).

16. Osztramos 7, Hungary – the bird remains were determined and published by Dénes Jánossy as: *Tetrao praeurogallus* Jánossy, 1969; *Francolinus capeki* Lambrecht, 1933; *Bubo* sp., *A. noctua veta* Jánossy, 1992; *Surnia robusta* Jánossy, 1977; Passeriformes indet. (Jánossy 1973, 1976a,b, 1979a,b,c). Deposited in MÁFI.

MN 16-17:

17. Beremend 1-4, Hungary – the bird remains were determined and published by Dénes Jánossy as: *Francolinus capeki* Lambrecht, 1933; (1-3), *Surnia robusta* Jánossy, 1977; (4), (Jánossy 1974, 1976b, 1977). Deposited in HNHM.

18. Betfia 13, Romania – the Betfia localities are among the most important Plio-Pleistocene sites in Europe. They were discovered in 1904 by Mihály Tóth. Since then, numerous investigations have been conducted here. Between 1904 and 1917, Tivadar Kormos, in 1941, Miklós Kretzoi, and from 1951, specialists from the Municipal Museum of Oradea and from the Speological Institute 'Emil Racovitza' of București conducted excavations, and discovered new sites. The number of sites raised to 13 in 1971-1972 following work by Elena Terzea and Tibor Jurcsák. The bird remains were determined by the author and Erika Gál as: *Anser* sp., *Anas querquedula, Anas crecca*, Anatidae indet., *Falco vespertinus, Francolinus capeki* Lambrecht, 1933, cf. *Crex crex, Vanellus vanellus, Tringa erythropus, Tringa* cf. *ochropus, Sterna hirundo, Asio* cf. *otus, Columba palumbus, Lanius collurio, Turdus merula* (Kessler 1975, Gál 2002a). Deposited in MȚCO.

19. Kisláng, Hungary – eggshell fragments and bones of the *Struthio pannoni-*

cus (Kretzoi 1954) and remains of *Anas* sp. They were collected, determined and published by Miklós Kretzoi (1954a, 1955). Deposited in MÁFI.

20. Villány 3, Hungary – the quarry from Templomhegy, Villány-Kalkberg was discovered by Károly Hofmann in 1874. Here Tivadar Kormos (between 1910 and 1939), Miklós Kretzoi, and Dénes Jánossy (after 1950) collected fossil materials for decades. The bird remains were determined and published by Dénes Jánossy and by the author, as: *Anas platyrhynchos submajor* (Jánossy 1979); *Anas albae* Jánossy, 1979; Anatidae sp. indet., *Aquila* cf. *chrysaetos, Pandion haliaetus, Falco* sp., *Francolinus capeki* Lambrecht, 1933; *Gallus beremendensis* Jánossy, 1976; *Lyrurus* cf. *partium* Kretzoi, 1962; *Bubo bubo, Strix intermedia* Jánossy, 1972; *Asio otus, Surnia robusta* Jánossy, 1977; *Corvus* sp., *Pyrrhocorax pyrrhocorax* Aves indet. (Jánossy 1976a,b, 1977, 1979a; Kessler 2009a,b, 2010a). Deposited in MÁFI.

Quaternary avian remains and localities of the Carpathian Basin:

The bird fauna of the last 1.8 MY represents the recent avifauna and the majority of recent taxa. There are fossil taxa from the Early and Middle Pleistocene, but in the Late Pleistocene, they almost disappeared. A feature of the period is the alternating cold and mild phases, resulting in bird migration.

During the Holocene, the human impact is becoming stronger in birdlife. This is shown by the large number of zooarcheological sites with fossil and subfossil bird remains. In addition, the role of owls in fossilization of bird bones was of great importance, mostly in cave sediments.

a) Phase I.: Lower Pleistocene (1 800 000 – 800 000 years ago)

MN 17-18: Pliocene-Pleistocene limit: Kolon 2. (Kolinany 2), **Slovakia**.

Q1: Villányian–Lower Biharian: Németóvár 2C, 4B (Deutsch-Altenburg) – **Austria**; Betfia 2, 7/1, 9 – **Romania**; Villány 5; Győrújfalu; Kőröshegy; Nagyharsányhegy 2; Osztramos 2,5,8,20; Somssich-hegy 1; – all **Hungary**.

Q1-2. Betfia 'Aven', 7 – **Romania**.

With species: *Podiceps nigricollis,* cf. *Ixobrychus minutus, Pelargosteon tothi, Ciconia* cf. *stehlini, Anas clypeata, Anas crecca, Anas querquedula, Anas strepera, Aythia nyroca, Anas* sp., Anatidae sp. indet., *Accipiter nisus, Aquila* cf. *clanga, Buteo* cf. *buteo, Buteo lagopus, Circus* sp., *Falco vespertinus, Falco tinnunculus atavus, Falco subbuteo, Falco columbarius, Falco cherrug, Falco* sp., *Tetrao partium, Perdix perdix jurcsaki, Perdix* sp., *Francolinus capeki, Alectoris donnezani, Rallus aquaticus, Crex crex, Porzana porzana, Porzana pusilla/P. parva, Porzana pusilla, Otis lambrechti, Otis kalmani, Limosa limosa, Gallinago* cf. *gallinago, Gallinago media, Recurvirostra* sp. foss. indet., cf. *Tringa erythropus, Tringa* cf. *ochropus, Tringa* cf. *nebularia, Tringa hypoleuca/T. glareola, Tringa* sp., cf. *Philomachus pugnax, Scolopax rusticola, Chlidonias nigra,* Charadriiformes indet., *Tyto* cf. *alba, Bubo bubo, Asio otus, Asio flammeus, Otus scops, Glaucidium passerinum, Aegolius funereus, Athene noctua veta*, *Caprimulgus capeki, Eurystomus* sp. foss., *Merops* sp., *Dendrocopos major, Dendrocopos medius, Dendrocopos minor, Picus viridis, Jynx torquilla, Garrulus glandarius, Corvus pliocaenicus, Corvus hungaricus, Corvus monedula, Pica pica, Pyrrhocorax* cf. *graculus vetus,* Corvidae indet., *Galerida cristata*, cf. *Melanocorypha calandra, Alauda arvensis, Lullula arborea,* Alaudidae gen. et sp. indet., *Hirundo rustica, Delichon urbica, Riparia riparia, Lanius minor, Lanius excubitor, Anthus trivialis, Anthus* sp., *Motacilla alba, Motacilla* cf. *cinerea, Motacilla flava, Bombycilla garrulus, Oriolus oriolus, Sturnus vulgaris, Acrocephalus palustris, Acrocephalus* sp., *Locustella fluviatilis*, cf. *Sylvia communis,* cf. *Sylvia atricapilla, Sylvia* sp., *Certhia familiaris, Sitta europaea, Turdus viscivorus, Turdus pilaris, Turdus merula, Turdus philomelos, Turdus iliacus*, *Turdus* sp., *Saxicola rubetra, Erithacus rubecula, Luscinia luscinia, Luscinia megarhynchos, Muscicapa* cf. *striata, Aegithalos caudatus, Parus major, Parus lugubris, Parus caeruleus, Lanius excubitor, Lanius minor, Cinclus cinclus, Sturnus vulgaris, Passer montanus, Erithacus rubecula, Fringilla coelebs, Fringilla montifringilla, Carduelis chloris, Carduelis carduelis, Carduelis cannabina, Carduelis spinus, Carduelis* sp., *Loxia curvirostra, Coccothraustes coccothraustes, Pyrrhula pyrrhula, Serinus* cf. *serinus, Pinicola* cf. *enucleator,* Fringillidae indet., cf. *Emberiza calandra, Emberiza* cf. *citrinella,* Emberizidae sp. indet., Passeriformes sp. indet., Aves indet. (Kormos 1913, Lambrecht 1916a, 1933, Čapek 1917, Kretzoi 1941, 1961-1962, 1975, Kessler 1975, 1985b, 2009b, 2010a, 2013a, Jánossy & Kordos 1976, 1977, Jánossy 1976a,b, 1979a,b,c, 1981, Horaček 1985, Döppes & Rabeder 1997, Mlíkovskỳ 1998a, 2002, Gál 2002a).

b) Phase II.: Middle Pleistocene (800 000 – 120 000 years ago)

Q2. Upper Biharian*:* Betfia 5,7/2-3; Kiskóh (Chișcău – Bear Cave) – **Romania**; Méhész (Mihỳska, Včelare 3) – **Slovakia**; Beremend 16, 17, 28; Kövesvárad; Nagyharsányhegy 1-4; Somssichhegy 2; Ürömhegy; Villány 6, 8; – all **Hungary**.

Q3/I. Hundsheim – **Austria**; Aranyosszohodol (Sohodol) – Lucia Cave; Betfia 7/4; Brassó-Fortyogóhegy (Brașov) – Gensperger Cave – **Romania**; Gombaszög (Gombasek) – **Slovakia**; Beremend 23; Tarkő 1, 2-16; Várhegy Cave; Vértesszőlős 2 – **Hungary**.

Q3/II. Pilis stage-Solymár substage: Repolusthöhle – **Austria**; Vindija – **Croatia**; Dorog; Hór-völgy; Nagyharsányhegy 6; Solymár; Süttő; Uppony – **Hungary**.

With species: *Podiceps nigricollis, Ardea cinerea,* cf. *Pelargosteon tothi, Branta ruficollis, Anser anser subanser, Tadorna tadorna, Tadorna* sp., *Anas penelope, Anas acuta, Anas platyrhynchos submajor, Anas clypeata, Anas* sp., *Aythya nyroca, Aythya fuligula, Aythya ferina, Aythya* sp., *Mergus connectens, Mergus merganser, Mergus* sp., Anatidae sp. indet., *Accipiter gentilis, Accipiter nisus, Aquila heliaca,* cf. *Haliaetus angustipes, Aegypius monachus, Gyps fulvus, Gyps melitensis, Buteo lagopus, Buteo buteo, Buteo* sp., *Circus aeruginosus, Falco rusticolus, Falco subbuteo, Falco vespertinus, Falco tinnunculus atavus, Falco columbarius, Falco cherrug, Falco* cf. *antiquus, Falco* sp., Accipitriformes sp. indet., *Perdix perdix jurcsaki, Francolinus čapeki, Coturnix coturnix, Alectoris donnezani, Ammoperdix* sp., *Alectoris graeca,* ?*Phasianus* sp., ?*Gallus* sp., *Tetrao partium, Tetrao praeurogallus, Bonasia praebonasia, Lagopus lagopus, Lagopus mutus, Grus grus, Rallus* sp., *Fulica atra, Gallinula chloropus, Rallus aquaticus, Otis lambrechti, Otis kalmani, Otis* sp., *Tringa ochropus, Scolopax rusticola, Gallinago gallinago, Gallinago media, Vanellus vanellus, Recurvirostra avosetta, Limosa limosa, Larus minutus, Larus ridibundus, Larus* sp., *Columba palumbus, Columba* sp., *Cuculus canorus, Tyto alba, Asio otus, Asio flammeus, Bubo bubo, Nyctea scandiaca, Surnia robusta, Athene noctua, Otus scops, Aegolius* *funereus, Glaucidium passerinum, Strix intermedia, Strix aluco, Apus melba submelba, Apus apus palapus, Merops apiaster, Upupa phoeniculoides, Halcyon* sp. foss., *Picus viridis, Dendrocopos major submajor, Dendrocopos praemedius, Alauda arvensis, Galerida cristata, Hirundo rustica, Hirundo* sp., *Turdus iliacus, Turdus merula, Turdus viscivorus, Turdus pilaris, Turdus philomelos, Turdus* sp., *Phoenicurus phoenicurus, Oenanthe oenanthe, Muscicapa striata, Luscinia svecica, Parus major, Parus palustris, Parus ater, Parus* sp., *Anthus cervinus, Anthus campestris/spinoletta, Motacilla* sp., *Sylvia borin, Phylloscopus* sp., *Regulus* sp., *Sitta europaea, Sitta* sp., *Lanius excubitor, Bombycilla garrulus, Oriolus oriolus, Sturnus vulgaris, Garrulus glandarius, Pica pica major, Corvus monedula, Corvus corone, Corvus corax, Corvus hungaricus, Corvus pliocaenus, Pyrrhocorax pyrrhocorax, Pyrrhocorax graculus vetus,* Corvidae gen. et sp. indet., *Passer montanus, Pinicola* sp., *Nucifraga caryocatactes, Fringilla coelebs, Coccothraustes coccothraustes, Emberiza citrinella,* Emberizidae gen. et sp. indet., Passeriformes indet., Aves indet. (Toula 1909, Lambrecht 1916a, 1933, Kretzoi 1941, 1961-1962, 1975, Malez, M. 1961, Jánossy 1962b, 1963, 1969, 1971, 1974b, 1976a,b, 1977, 1978, 1979a,b,c, 1980, 1981a, 1982b, 1983, 1986, 1990, Malez, V. 1973, 1988, 1991, Kessler 1975, 1982, 2009a,b, 2010a, 2013a, Malez & Rukavina 1979, Musil 1980, Horaček 1985, Jurcsák & Kessler 1988, Döppes & Rabeder 1997, Gál 2002a, Mlikovskỳ 2002, 2009).

c) Phase III.: Upper Pleistocene (120 000 – 15 000 years ago)

Q4/I. Pilis stage – Szántó substage: Grosse Badlhöhle; Hundsteig bei Krems; Luegloch; Merkenstein; Mixnitz–Drachenhöhle; Schwarzgrabenhöhle – **Austria**; Krapina (Husnjakovo Brdo); Velika Pecina; Velika pec na Lipi; Veternica – **Croatia**; Barcarozsnyó-Gura Cheii Cave (Râşnov); Esküllő (Aștileu) – Igric Cave; Hidegszamos (Someșul Rece) – Csontos Cave; Homoródalmás (Vârghiș) – Orbán Balázs Cave, – Medve Cave; Kőrösmart (Râpa); Magura-Valea Coacăzei Cave; Nándor (Nandru) – Nándori Cave; Ohábaponor – Bordu Mare Cave (Ohaba Ponor); Oláhszászka (Sasca Română) – Néravölgyi Cave; Rév (Vadu Crișului) – Kecske Cave, – Pince Cave, – Vizes Cave; Szamosfalva (Someșeni); Szegyestel (Sighiștel) – Magura Cave, – Tibocoaia Cave; Tordai Gorge (Cheile Turzii) – Binder Cave – **Romania**; Detrekőszentmiklós – Pálffy Cave (Dzeráva Skála – Plavecky Mikulas); Galgóc (Hlohovec); Gánócz (Ganovce); Lándzsásötfalu (Hôrka-Ondrej); Liszkófalva (Lisková) – Baráthegyi Cave; Novi I, III; Óruzsin (Oruzer) – Antal Cave; – Nagy Cave; Porács (Porač) – **Slovakia**; Bajót – Cave no. 3., – Baits Cave, Hóman Cave, Jankovich Cave, – Öregkő Cave; Barcarozsnyó; Budapest – Remete Cave, Remetehegyi Cave; Buják, Csákvár – Eszterházy Cave; Cserépfalu – Subalyuk; Csobánka – Kiskevély; Diósgyőr – Tapolcai Cave; Érd; Felsőtárkány – Peskő Cave, Gencsapáti, Hámor-Herman Ottó Cave; Puskaporos-kőfülke, – Szeleta Cave; Hollókő; Jósvafő – Porlyuk Cave; Kecskésgalya; Kesztölc – Bivak Cave; Kőszeg; Lovas; Mérk, Nagyvisnyó – Háromkúti Cave; Ölyveskőér; Pilisszántói Cave; Répáshuta – Balla Cave; Ballavölgyi-Cave, Poroslyuk; Sály; Szárazgerence; Szilvásvárad – Istállóskő; Tata; Tatabánya – Kálváriahegy Cave No.4., – Szelim Cave; Tokod-Nagyberek; Varbó – Lambrecht Kálmán Cave; Vaskapu – **Hungary**.

With species: *Podiceps auritus, Ardea cinerea, Ciconia ciconia, Plegadis falcinel-*

lus, Anser anser, Anser albifrons, Anser fabalis, Anser sp.*, Branta ruficollis, Tadorna ferruginea, Cygnus olor, Anas crecca, Anas platyrhynchos, Anas penelope, Anas strepera, Anas querquedula, Anas clypeata, Anas acuta, Anas* sp.*, Melanitta nigra, Aythya nyroca, Aythya fuligula, Aythya ferina, Mergus merganser, Mergus albellus, Bucephala clangula, Gypaetus barbatus*, *Aegypius monachus, Gyps fulvus, Aquila chrysaetos, Aquila clanga, Aquila heliaca, Halliaeetus albicilla, Buteo buteo, Buteo lagopus, Buteo rufinus, Pernis apivorus, Circus cyaneus, Circus macrourus, Accipiter nisus, Accipiter gentilis, Falco peregrinus, Falco cherrug, Falco rusticolus, Falco tinnunculus, Falco columbarius, Falco vespertinus, Falco subbuteo, Perdix perdix, Coturnix coturnix, Alectoris graeca, Tetrao urogallus, Tetrao tetrix, Bonasa bonasia, Lagopus lagopus, Lagopus mutus,* Galliformes sp. indet., *Grus grus, Rallus aquaticus, Crex crex, Porzana porzana, Otis tarda, Otis tetrax, Gallinago gallinago, Gallinago media, Tringa erythropus, Tringa totanus, Tringa* sp.*, Scolopax rusticola, Vanellus vanellus, Himantopus himantopus, Calidris alpina, Calidris ferruginea, Charadrius* sp.*, Limosa limosa, Pluvialis squatarola, Numenius arquata, Numenius phaeopus, Numenius phaepus/N. tenuirostris, Numenius* sp.*, Philomachus pugnax, Larus ridibundus, Larus canus, Sterna hirundo, Chlidonias* sp.*, Syrrhaptes paradoxus, Columba palumbus, Columba oenas, Columba livia, Cuculus canorus, Asio otus, Asio flammeus, Nyctea scandiaca, Athene noctua, Aegolius funereus, Surnia ulula, Strix aluco, Strix uralensis, Strix nebulosa, Glaucidium passerinum, Apus apus, Apus melba, Caprimulgus europaeus, Dendrocopos major, Dendrocopos medius, Dendrocopos leucotos, Picus canus, Picus* sp.*, Jynx torquilla, Galerida cristata, Alauda arvensis, Eremophila alpestris, Hirundo rustica, Delichon urbica, Riparia rupestris, Perisoreus infaustus, Pica pica, Pyrrhocorax pyrrhocorax, Pyrrhocorax graculus, Garrulus glandarius, Nucifraga caryocatactes, Corvus monedula, Corvus corone, Corvus frugilegus, Corvus corax, Parus major, Parus palustris, Parus caeruleus, Parus cristatus, Parus montanus, Parus* sp.*, Anthus pratensis, Anthus trivialis, Anthus* sp.*, Motacilla alba, Motacilla flava, Oriolus oriolus, Turdus pilaris, Turdus iliacus, Turdus torquatus, Turdus philomelos, Turdus viscivorus, Turdus* sp.*, Monticola saxatilis, Saxicola torquata, Erithacus rubecula, Cinclus cinclus, Lanius collurio, Lanius senator, Lanius excubitor, Lanius* sp.*, Sylvia curruca, Sylvia borin, Prunella modularis, Sturnus vulgaris, Pastor roseus, Troglodytes troglodytes, Fringilla coelebs, Fringilla montifringilla, Pyrrhula pyrrhula, Coccothraustes coccothraustes, Carduelis cannabina, Carduelis chloris, Carduelis carduelis, Carduelis flammea, Pinicola enucleator, Loxia curvirostra, Passer montanus, Passer domesticus, Emberiza schoeniclus, Emberiza calandra, Emberiza cirlus, Emberiza* sp.*, Plectrophenax nivalis*, Passeriformes indet., Aves indet. (Lóczy 1877, Nehring 1880, Téglás 1880, Róth 1881, Fischer & Maurersberger 1989, Lambrecht 1912a,b, 1913, 1915, 1916a, 1933, Kormos 1914a,b, 1916, Mottl 1938, 1941, 1942, 1951, 1953,Wettstein & Mühlhofer 1938. Jánossy 1952, 1954, 1955, 1960, 1962a, 1964, 1965, 1971, 1976a,b, 1977a,b, 1978; 1979a,b,c, 1980, 1981, 1986, Spahni 1954, Wojčic 1966, Jánossy in Hamar & Csák 1969, Malez, V. 1973, 1984, 1988, 1993, Kessler 1974a, 1977a,b,d, 1982, 1985b, 2013a, Kretzoi 1975, Malez-Bačic, V.1979, Musil 1980a,b, Fischer & Stephan 1977, Jurcsák & Kessler 1988, Fladerer 1993, Gál 1998, 2002a, 2003, 2004, 2005, Mlikovskỳ 2000).

d) Phase IV: Holocene (15.000 – the end of the Middle Ages)

Q4/II.: Grosse Offenbergerhöhle; Hohlensteinhöhle; Knochenhöhle; Marchegg; Teufelslucken; Tropfsteinhöhle; Tunnelhöhle – **Austria**; Aranyosmeggyes (Medieșu Aurit); Berettyószéplak (Suplacu de Barcău); Bégakalodva (Cladova); Diószeg (Diosig); Esküllő (Aștileu)-Kis Cave; Érmihályfalva (Valea lui Mihai); Felsőlubkó (Gornea); Gálospetri (Galoșspetreu); Gyulafehérvár (Alba Iulia); Herkulesfürdő (Herculane) – Rabló Cave, – Zoltán Cave; Kalota (Căalăaătea); Kazánszoros (Cazanele Mari) – Climente I. Cave, – Töröklik Cave – Icoana Cave, – Gaura Chindiei Cave; Kisbács (Baciu) – Bácsi-torok; Kovászna (Covasna); Kisderzsida (Dersida); Kőrösbánlaki (Bălnaca) Cave; Nagyvárad (Oradea) – Szálka Hill; Kőrösgyéres (Girisu de Cris); Mezőfény (Foieni); Mezősámsond (Sincai); Ompolymező (Poiana Ampoiului); Parác (Parţa); Peterd (Petrești, Cheiile Turzii) – Tordai Gorge – Magyar Cave; Püspökfürdő (Băile 1 Mai, Cordău) Lake; Radnót (Iernuţ); Remetelórév (Lorău) – Bólyikői Cave; Révi (Vadu Crișului) Cave; Révtizfalui (Zece Hotare – Şuncuiuş) Cave; Szegyestel (Sighiștel) – Drăacoia Cave; Szegyestel völgyi (Valea Sighiștel) Cave; Szilágyzovány (Zăuan); Szind (Săndulești-Cheile Turului) – Túri Gorge; Szkerisóra (Scărișoara) – Coiba Mare Cave, – Sasok Cave; Szalacs (Sălacea); Székelykeresztúr (Cristuru Secuiesc); Vargyasi szorosi (Vârgiş) Cave; Vársonkolyos (Şuncuiuș) – Kismagyar Cave, – Izbindis Cave; Vaskóh (Vașcău); Vizakna (Ocna Sibiului) – **Romania**; Ludas – Budzsák; Nosza – Gyöngypart; Padina; Starcevo; Szabadka – Palics (Palić-Subotica); Vlassać – **Serbia**; Érsekújvár (Nové Zámszky); Jászó (Jasov) – Takács Menyhért Cave; Kisvárad (Nitriansky Hrádok) – **Slovakia**; Ács – Vaspuszta; Aggtelek; Alattyán – Tulát; Bajcsa – Vár; Bakonynána; Balatonboglár – Berekre-dülő; Balatonkeresztúr – Réti-dülő; Balatonlele – Kenderföldek; Balatonszemes – Bagódomb; Berettyószentmárton; Berettyóújfalu – Herpály; Békés –Városerdő; Bélmegyer; Bodajk – Rigólyuk; Budapest – Aquincum, – Francia-barlang – Gellért-hegy; Csákvár – Esterházy Cave; Csapástető; Csév Cave; Csobánka – Csontos Cave; Debrecen – Nyulas; Dunaújváros – Intrecisa – Koszider; Ecsegfalva; Endrőd 3/6, 39, 119; Esztergom – Alsó sziget; Felnémet – Berva Cave; Felsőnyék – Várhegy; Felsőtárkány – Petényi Cave; Folyás-Szilmeg; Füzesabony; Gyula – Castle; Hillebrand Cave (Bükk); Hosszúhegy (Pilis); Jánoshida; Jósvafő – Musztáng-Cave; Kardoskút – Hatablak; Kevélynyergi Pit; Kisköre – Szingegát; Kötelek – Huszársarok; Legény Cave; Maroslele – Pana; Mélyföld; Mezőkomárom; Mezőlak-Szélmező; Mezőzombor – Cemetery; Mélyvölgy (Mecsek); Miskolc – Felső forrás Cave; – Névtelen Cave; Nagykörü; Nagysomlyói Furow; Neszmély – Tekeres Creek; Ordacsehi – Kistöltés; Ószentiván – Tiszasziget; Paks – Dunakömlőd; Pilismarót – Malom Creek; Polgár-Folyás, – Csőszhalom; Pomáz-Zravlyák; Répáshuta – Rejteki Pit; Rezi; Röszke-Ludvár; Szajol – Felsőföld; Szegvár – Tűzköves; Szendrő; Szentkirály; Szerencs – Taktaföldvár; Székesfehérvár; Szolnok-Szanda; Tatabánya – Denevér Cave; Tatabánya alsó – Törekvés Cave; Tác-Fövénypuszta, – Gorsium; Tápiószele-Tűzköves; Tiszalök-Rázom; Tiszaluc – Danka domb, – Sarkad; Tiszapolgár-Csőszhalom; Tiszaszőlős-Gomaháza-Puszta; Tiszavalk-Négyesi Boundary, – Tetes; Tiszavasvári-Deákhalmi Boundary, – Keresztfal; Tokod – Erzsébetakna; Tószeg – Laposhalom; Turkeve – Móricz; Tűzköves Cave; Visegrád Castle – Alsóvár; Zalaszentistván – **Hungary**.

With species: *Gavia arctica, Gavia stellata, Podiceps griseigena, Podiceps cristatus, Podiceps auritus, Tachybaptus ruficollis, Pelecanus onocrotalus, Pelecanus* sp.*, Phalacrocorax carbo, Platalea leucorodia, Ardea purpurea, Ardea cinerea, Botaurus stellaris, Nycticorax nycticorax, Egretta alba, Egretta garzetta, Ciconia ciconia, Ciconia nigra, Cygnus cygnus, Cygnus olor, Cygnus* sp.*, Anser erythropus, Anser anser, Anser fabalis, Anser* sp.*, Tadorna tadorna, Tadorna ferruginea, Branta* sp.*, Anas platyrhynchos, Anas crecca, Anas penelope, Anas strepera, Anas acuta, Anas querquedula, Anas clypeata, Anas* sp.*, Aythya ferina, Aythya nyroca, Aythya fuligula, Aythya marila, Mergus merganser, Mergus serrator, Accipiter gentilis, Accipiter nisus, Circus aeruginosus, Circus* sp.*, Buteo buteo, Buteo lagopus, Circaetus gallicus*, *Hieraetus pennatus, Milvus migrans, Milvus* sp.*, Gyps fulvus, Aquila chrysaetos, Aquila rapax, Aquila clanga, Aquila pomarina*, *Aquila* sp.*, Haliaeetus albicilla, Falco cherrug, Falco columbarius, Falco tinnunculus, Falco subbuteo, Perdix perdix, Coturnix coturnix, Alectoris graeca, Gallus* sp.*, Phasianus* sp.*, Numida meleagris, Tetrao tetrix, Tetrao urogallus, Bonasa bonasia, Lagopus lagopus, Lagopus mutus, Grus grus, Rallus aquaticus, Crex crex, Porzana porzana, Gallinula chloropus, Fulica atra, Otis tarda, Otis tetrax, Gallinago gallinago, Gallinago media, Lymnocryptes minimus, Vanellus vanellus, Arenaria interpres, Tringa totanus, Tringa hypoleucos,Tringa* sp.*, Scolopax rusticola, Limosa limosa, Numenius arquata, Numenius phaeopus, Charadrius hiaticula, Larus argentatus, Columba palumbus, Columba oenas, Columba livia, Columba* sp.*, Streptopelia turtur, Nyctea scandiaca, Bubo bubo, Strix uralensis, Strix aluco, Asio otus, Asio flammeus, Athene noctua, Aegolius funereus, Coracias garrulus, Upupa epops, Apus apus, Picus viridis, Picus canus, Dendrocopos major, D. leucotos, Galerida cristata, Alauda arvensis, Eremophila alpestris, Hirundo rustica, Delichon urbica, Cinclus cinclus, Garrulus glandarius, Nucifraga caryocatactes, Corvus frugilegus, Corvus corone, Corvus monedula, Corvus corax, Pyrrhocorax graculus, Pyrrhocorax pyrrhocorax, Pica pica, Turdus merula, Turdus philomelos, Turdus viscivorus, Turdus pilaris, Turdus torquatus, Turdus iliacus, Parus major, Luscinia megarhynchos, Anthus trivialis, Motacilla alba, Motacilla cinerea, Muscicapa striata, Phoenicurus ochrurus,* cf. *Oenanthe oenanthe, Erithacus rubecula, Saxicola rubetra, Acrocephalus arundinaceus, Acrocephalus* sp.*, Regulus* sp.*, Oriolus oriolus, Sitta europaea, Prunella collaris, Lanius ecubitor, Lanius minor, Sturnus vulgaris, Passer montanus, Passer domesticus, Fringilla coelebs, Fringilla montifringilla, Montifringilla nivalis, Pinicola enucleator, Pyrrhula pyrrhula, Coccothraustes coccothraustes, Loxia curvirostra, Carduelis chloris, Emberiza citrinella, Emberiza calandra, Emberiza* sp.*,* Passeriformes sp. indet., Aves indet. (Kormos 1915, Lambrecht 1933, Jánossy 1962c, 1976a,b, 1977, 1978, 1979a,b,c, 1985, 1986, Bökönyi 1964, 1974, 1984, Bökönyi & Jánossy 1965, Soergel 1966, Jurcsák & Kessler 1973, 1986, 1988, Kessler 1974b,c, 1977c,d, 1980-81, 1982, 1985a,b, 2009a,b, 2010a, Kretzoi 1975, Jánossy & Kordos 1976b, Fischer & Stephan 1977, Kordos 1981, 1984, Krolopp & Vörös 1982, Bartosiewicz 1991, 1997, Körösi 1991, Rabeder 1992, Fladerer 1993, Bochenski & Tomek 1994, Döppes & Rabeder 1997, Kessler & Gál 1997, 1998, Gál 2002b, 2004, 2005, 2007a,b, 2008, Pike-Tay *et al.* 2004, Tassi 2006, Bindea 2008).

Results and Conclusions

In the area of the Carpathian Basin, fossil and subfossil bird remains are known from 341 paleontological and archaeological sites. The number of taxa reaches 845. In the list, 24 orders, 65 families, 193 genera (five ichnotaxa), 430 species (five ichnotaxa), 10 subspecies and two problematic taxa can be found. Of these, five orders, eight families, 30 genera, 188 species and 10 subspecies have become extinct, while 71 taxa (two orders, 19 families and 50 genera) are thought to be extinct taxa. One hundred and eighty-nine extinct taxa (two orders, four families, nine genera – five ichnotaxa – 154 species – five ichnotaxa – and 10 subspecies) were described primarily from the Carpathian Basin. Besides these, 58 known extinct taxa (three orders, five families, 17 genera and 33 species) have been identified. In addition, more knowledge is gathered from feather imprints (seven cases), eggshells (two cases) and urocoprolits (in one case).

The Mesozoic (Cretaceous) bird fauna is represented from four sites with 20 taxa (five orders, families, genera and species), all extinct taxa, except for one present ordo (Pelicaniformes).

The Paleogene bird fauna is represented from five sites with 46 taxa (nine orders and families, eight genera and ten species – one ichnotaxa – + Aves indet.), with one extinct family, five extinct genera and ten extinct species.

The Neogene bird fauna is represented from 60 sites.

The Miocene sites furnish 193 taxa (12 orders, 34 families, 66 genera and 81 species), of which 76 are extinct (2 families, 15 genera and 59 species).

The Pliocene sites furnish 229 taxa (18 orders, 38 families, 59 genera and 116 species), of which 45 are extinct (6 genera and 39 species).

The Quaternary bird fauna is represented from 272 sites (119 sites from Pleistocene and 153 sites from Finiglaciale-Holocene) and furnish 452 taxa (15 orders, 41 families, 130 genera and 266 species).

The 13 Lower Pleistocene sites furnish 119 species (with 10 extinct species and 3 extinct subspecies);

The 29 Middle Pleistocene sites furnish 120 species (with 10 extinct species and 15 extinct subspecies);

The 77 Upper Pleistocene sites furnish 177 species.

The 153 Finiglaciale and Holocene sites furnish 171 species.

Each of the three ancient Mesozoic bird types (Sauriurae: Archaeornithinae and Enantiornithinae; as well as Ornithurae) is represented in the fossil bird fauna of the Carpathian Basin.

In the Cenozoic, the Sauriurae and Hesperonithidae birds no longer exist. Only Ornithurae (Neornithes) remained alive.

All identified taxa from the Paleogene are typical to water and a humid habitats. Six of them are specifically deep waters feeding species. Four species (*Eostega, Diomedeoides, Rallicrex* and *Charadriipedia*) and two genera representative *(Gavia, Pandion)* are endemic for the area. Three taxa are known from the Western European sites (*Grallavis, Mionetta* and *Balearica*). Only one taxon was described by footprint *(Charadriipedia)*.

The Late Miocene avifauna is represented by coastal wildlife and that of the archipelago by deep sea or waterfront species (*Mic-*

rosula, Phalacrocorax, Cygnopterus, Haliaeetus, Anatidae and Laridae). However, the representative species of forest-grassland areas appear independent from the aquatic environment *(Palaeortyx, Prosybris,* Passeriformes, *Tetraornithopedia)*. The avifauna still has many similarities with the western sites, four such taxa were described from Carpathian Basin *(Microsula, Phalacrocorax, Palaeortyx, Prosybris)*. Eight extinct species *(Cygnopterus neogradensis, Rallicrex litkaensis, Galerida cserhatensis, Cinclus major, Turdicus minor, Luscinia praeluscinia, Bombycilla hamori, Emberiza bartkoi)* and four ichnotaxa *(Avidactyla, Ornithotarnocia, Passeripedia, Tetraornithopedia)* are considered to be endemic.

The Middle Miocene avifauna changed significantly. This is not only a significant increase in the number of taxa, but it also refers to the composition of the species list. The remaining water-covered environment reflects a significant representation of these types of areas (18 taxa), including open water species (*Gavia, Anhinga, Paleolodus, Phalacrocorax, Cygnopterus, Anas, Bucephala, Clangula, Mergus* spp*.*) and humid environment species (*Anser, Proardeola,* Gruidae, *Rallicrex, Porzana*, Rallidae, *Gallinago* taxa). However, there was a significant increase in the number of representatives of forest grassy open areas' (*Palaeortyx, Miogallus,* Perdicidae, Pteroclidae, Cuculidae, *Merops*), and also in the number of songbirds (17 taxa). Twelve of the 42 taxa are endemic species (*Cygnopterus, Anas albae, Clangula, Mergus, Rallicrex, Porzana estramosi* and *P. matraensis, Merops, Galerida cserhatensis, Lullula neogradensis, Luscinia jurcsaki, Erithacus bartkoi*). The representatives of the Western European type species are present in a large number *(Proardeola, Paleolodus, Anas velox, Mionetta, Bucephala, Miogallus, Miocorvus)*, and are typically mostly aquatic. Of particular interest is the presence of two flamingo species *(Megapaleolodus, Paleolodus)* as indication of the brackish water in the north coast (Mátraszőlős).

The avifauna of the Lake Pannon seems to have been significantly richer than that in the previous periods. The previously dominating marine bird life – was only represented by a tropical bird species (Fam. Phaethontidae: *Heliadornis*). There remains, however, a significantly rich aquatic bird species community (23 taxa), including a special, at present time tropical *Heliornis* species (resembling Grebe and has a similar lifestyle). Another, even more interesting, phenomenon is the presence of *Anhinga pannonica*. Since the aforementioned three genera today are represented only by species living in the tropics, this is also a reference to Lake Pannon's climatic conditions. From the Late Miocene, 65 extinct species and two extinct subspecies were described, which are considered to be endemic (plus also 14 fossil taxa in the family and genus level determined). The Western European Miocene fauna is represented primarily with gallinaceous species (*Palaeortyx, Miophasianus, Pavo* spp.), and perhaps also a duck *(Anas velox)*, crane *(Grus pentelici)*, rail *(Miorallus major)*, owls *(Tyto sanctialbani, Intulula brevis)*, and crows *(Corvus pliocaenus, Miocorvus larteti)*. The ordo Passeriformes are extraordinarily richly represented (44 species).

By analyzing the species list, it becomes clear that almost all ecotypes are represented in the Lake Pannon bird fauna.

The sedimentation of Lake Pannon and the inherent impact of environmental change are both reflected in the Early Pliocene birdlife. Due to disappearing sea types, reduction of water and humid environment types (only 6 species), the forest-grassland-open habitat-dwelling bird types became significantly dominant. Most of the extinct taxa are endemic (50 species and four subspecies) and we encountered only four extinct species described from other parts of Europe (representative of the genera: *Palaeortyx, Allectoris, Miocorvus*).

The Middle and Late Pliocene avifauna already was much richer and more diverse than the Early Pliocene. Number of taxa increases (42), so does the extent of the aquatic environment. Among them quite interesting is the *Heliadornis minor*, being a pelagic bird, probably represents a vagrant specimen. Also interesting in other respects are the ostrich remains from Kisláng *(Pachystruthio pannonicus)*, which are regarded as the westernmost occurrence of the genus in Europe. A significant number of endemic taxa are described (22 species and 6 subspecies), of which, only six were described from other parts of Europe. In the genus level, the defined taxa represent a large number (39), more than half of which are songbirds (20 taxa).

In the Early Pleistocene bird fauna, the extinct taxa are still represented (with 11 endemic species and subspecies), which is about 10% of the total taxa. By studying the species list, it can be observed that the specifically tropical-subtropical bird fauna is represented by only one taxon (*Eurystomus* sp.). But likewise, the arctic and alpine types are poorly represented (with only *Nyctea, Bombycilla* and *Pyrrhocorax graculus vetus* taxa) and the seabirds are also missing. Thus, we can conclude that bird migration was not common. Other taxa in the species list can be found in the recent bird fauna. In summary, a significant part of recent avifauna of the Carpathian Basin has developed in the Early Pleistocene and only its prevalence changed in the glacials and after.

The Middle Pleistocene bird fauna is more poorly represented than that of the Early and Late Pleistocene. Twenty-two of 142 taxa have been determined to ordo, family and genus level. One of them (*Halcyon* sp.) probably represents a new extinct species. In 120 species level taxa were found fifteen extinct species and 10 extinct subspecies the majority (11 species and 10 subspecies) became first described in the Carpathian Basin area. Six species (*Tetrao* sp., *Bonasa, Otis* sp., *Corvus hungaricus*) and all subspecies are considered predecessors of present taxa. The bird fauna was dominated by the stationary species and the northern guests. The number of warmer-climate species has been considerably reduced (only *Merops, Apus, Cuculus, Upupa, Oriolus, Hirundo, Sylvia, Phylloscopus* sp.), which also indicates the initial stage of migration.

The Late Pleistocene was represented by a rich avifauna in the Carpathian Basin. The direct descendants of extinct species and subspecies from the previous eras can be found. The composition of the species list already reflects the development of seasonal migration patterns. This is confirmed by the number of species which are here only in the summer (their share exceeds 20%, similar rates can be found in today's winter guests). This suggests that summers created suitable conditions for them to feed and breed during the glacial period. It is also possible that today's winter visitors will become summer guest or could overwinter. The northern areas in the Carpathian Basin provided poor survival conditions for them, typically lacking the open sea and coastal bird fauna and the tropical via subtropical species.

The avifauna of the last 15,000 years is showing an image of current bird life. In the post-glacial warming for over 10,000–12,000 years, the bird fauna was constantly changing, species disappeared and new ones appeared in the Carpathian Basin. The migration routes finally formed. Many already nesting species appeared just as winter guests or migrants. Some summer visitors have become all-year residents. The coastal species reappeared as winter guests. Surprising is the complete lack of some species (e.g. *Phalacrocorax pygmaeus* and *Neophron percnopterus*), which were not uncommon in the past. The capercaillie, the black grouse and the rock partridge moved to the edges of the Carpathian Basin. At the same time, many new species appeared and settled in the area (e.g. Eurasian Collared Dove, Syrian Woodpecker etc.). From the 171 identified taxa, 157 have been determined to species level, representing all recent species.

As it was shown, the evolution of birds in the Carpathian Basin can be tracked from the Jurassic-Cretaceous boundary on the basis of the known remains. Eight fauna exchange stages can be separated based on these data. The first three have been in the Mesozoic. The first one is still hypothetical, because it lacks physical evidence. This is the interval between the Upper-Triassic and Lower Cretaceous. It corresponds to the origin of birds and the different phases of development. The second stage corresponds to the Lower Cretaceous. Despite the poor material, it can be shown, that all ancient bird taxa (types) were already valid (Sauriurae with *Archaeopteryx bavarica*, Ornithurae with *Eurolimnornis corneti, Palaeocursornis biharicus* and one representative of Hesperornithidae). The presence of valid species also makes it apparent that evolution of mentioned taxa has been done, which is important for two reasons. First, it confirms that the Sauriurae were contemporaries of the true birds and therefore could not have been their ancestors. Second, the first true birds lived in aquatic environments. This fact is confirmed by other Lower Cretaceous fossil remains. The third phase is represented by Upper Cretaceous dispersed materials (Enanitornithidae and problematic Ornithurae). They provide less data and inference opportunities.

Since the Paleogene, we know of only true birds. Here, two fauna stages can be distinguished. The first between the Paleocene and the end of Eocene, and the second between the start of the Lower Oligocene and the end of Lower Miocene to the development of the Pannon Lake. All known deposits from the Paleogene indicate that bird types lived in an aquatic environment, with open marine and coastal species. Afterwards, at the beginning of the Miocene, bird species typical to terrestrial environments appeared (including Galliformes, predators and songbirds).

The next phase includes the Lake Pannon avifauna. It reflects a change in the ratio of the water – shore area of the Carpathian Basin, with are typical warm-climate indicator species. Besides typical aqueous environment species, the forest and open land bird fauna were already very rich. The present genera were dominant and many extinct species are to be considered predecessors of the present ones.

Disappearance of the Pannon Lake induced a new phase in the bird fauna. Composition of the Pliocene and Lower Pleistocene avifauna indicates a still hot, but much drier climate. While in the previous phase, the similarity with the Western European bird fauna is high, by the end of the Neogene and beginning of Quaternary, this situation changes and the endemic species became dominant. A number of present species were already present, while in the Late Pleistocene, the proportion of fossil species barely reached 10-15%.

From the Middle Pleistocene due to the cold and increasingly continental climatic conditions, the last representatives of the old types and of warmth-liking species gradually disappeared from the bird fauna. From the Late Pleistocene to the present, could be found only recent species. From the Holocene a growing human impact is perceptible in birdlife. This represents the last great faunal change in the Carpathian Basin birdlife. The archaeozoological data reflects the impact of human activities.

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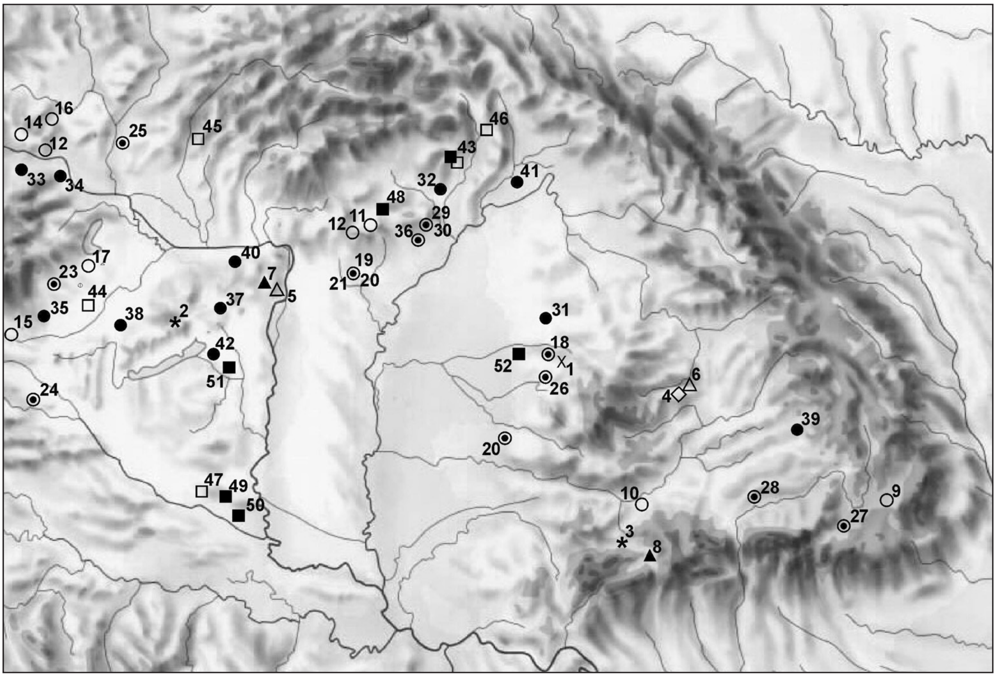
APPENDIX

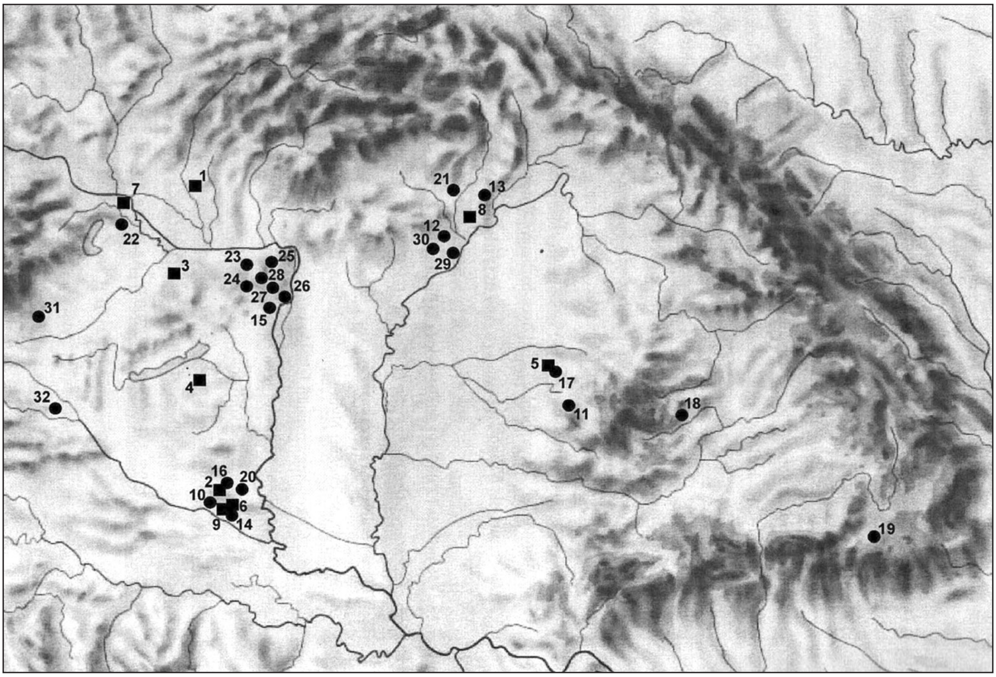


Map 1. Mesozoically and Tertiary sites from Carpathian Basin
1. térkép Mezozoikumi és harmadidőszaki lelőhelyek a Kárpát-medencéből
(After Zentai László 1996. „A Kárpát-medence domborzati alaptérképe". Modified)

Mezozoically sites: 1. Cornet – Lower Creatceous (Berriasian); 2. Iharkút – Upper Cretaceous (Santonian); 3. Hátszeg Basin – Upper Cretaceous (Maastrichtian)

Tertiary – Paleogene sites: 4. Kolozsmonostor – Eocne; 5. Budapest-Szépvölgy; 6. Kolozsvár-Fellegvár – Lower Oligocene; 7. Máriahalom; 8. Petrozsény- Upper Oligocene

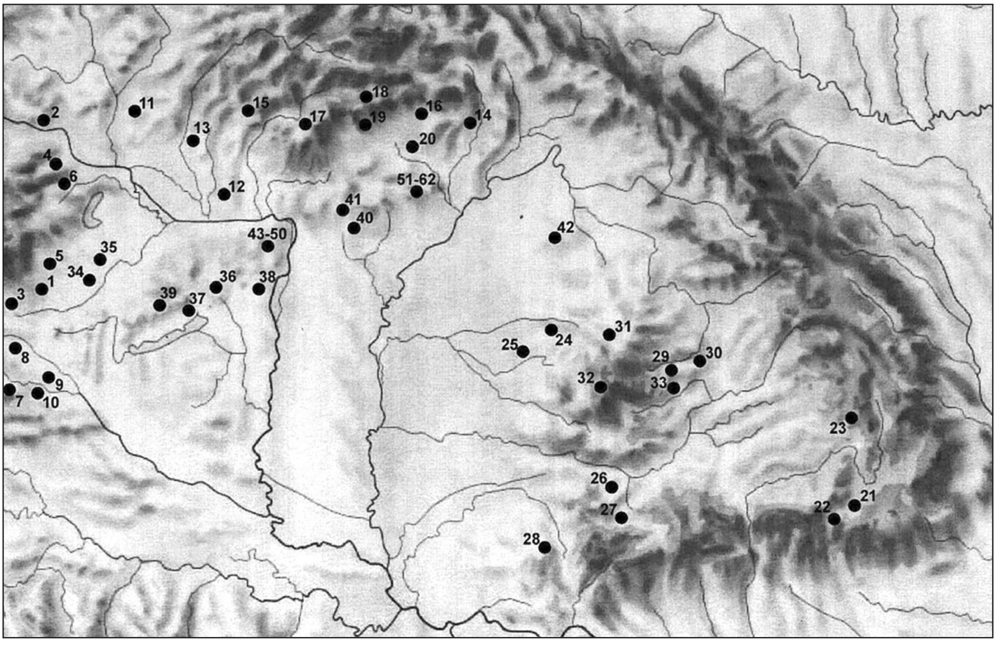
Tertiary – Neogene sites: 9, Erősd; 10. Piski; 11. Ipolytarnóc; 12. Litke 2; 13. Heiligenstadt; 14. Limberg; 15. Oberdorf; 16. Grund; 17. Borosd – Lower Miocene; 18. Kőalja; 19. Mátraszőlős 1; 20. Mátraszőlős 2; 21. Mátraszőlős 3; 22. Dévényújfalu; 23. Felménes; 24. Radoboj; 25. Szentmargitbánya; 26. Tasádfő; 27. Brassó; 28. Oltszakadát; 29. Felsőtárkány; 30. Felsőtárkány-Felnémet; 31. Egerszólát – Middle Miocene; 32. Rudabánya; 33. Vösendorf; 34. Götzendorf; 35. Gyepűfüzes; 36. Tataros; 37. Csákvár; 38. Sümeg; 39. Korond; 40. Tardosbánya; 41. Rátka; 42. Polgárdi – Upper Miocene; 43. Osztramos 1, 7, 9; 44. Gérce; 45. Ivánháza; 46. Bodvavendégi; 47. Csarnóta 1, 2, 4; 48. Ajnácskő; 49. Villány 3; 50. Beremend 1-3, 4-5, 11, 15, 18, 26, 38, 39; 51. Kisláng; 52. Betfia 13 – Pliocene (Lower, Middle and Upper)



Map 2. Lower and Middle Pleistocene sites from Carpathian Basin
2. térkép Alsó- és középső pleisztocén korú lelőhelyek a Kárpát-medencéből
(After Zentai László 1996. „A Kárpát-medence domborzati alaptérképe". Modified)

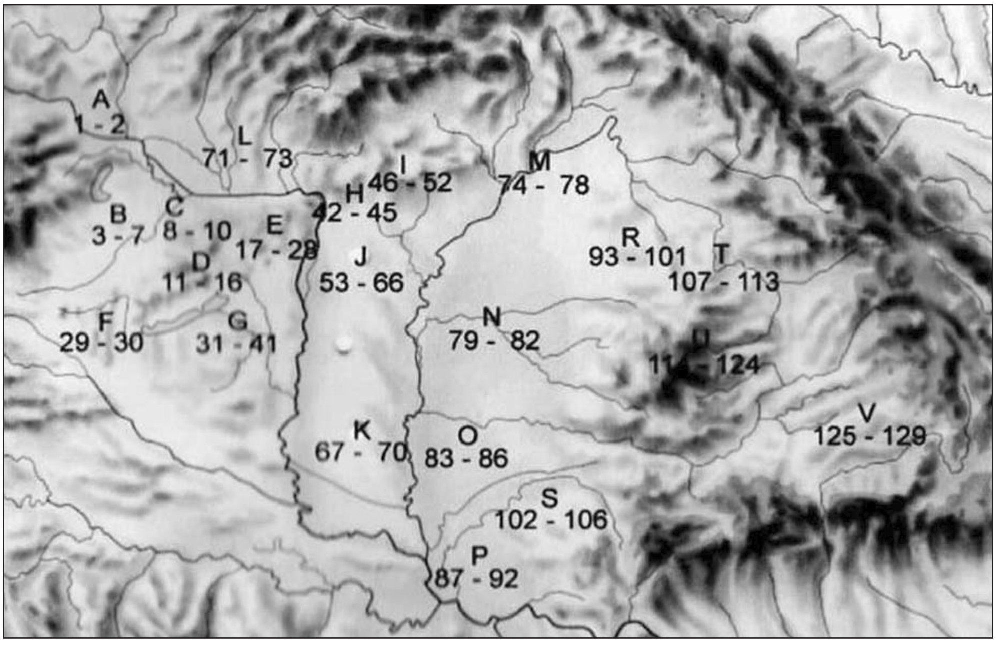
Lower Pleistocene sites: 1. Kolon 2; 2. Villány 5; 3. Győrújfalu; 4. Kőröshegy; 5. Betfia 2, 7/1, 9, 'Aven'; 6. Nagyharsányhegy 2; Beremend 16, 17: 7. Németóvár; 8. Osztramos 2, 5, 8; 9. Somssich-hegy 1

Middle Pleistocene sites: 10. Beremend 28; 11. Kiskóh; 12. Kövesvárad; 13. Méhész 3, 4; 14. Somssich-hegy 2; 15. Ürömhegy16; Villány 6, 8; 17. Betfia 5, 7/2-4; 18. Lucsia-barlang; 19. Brassó-Fortyógóhegy; 20. Nagyharsányhegy 1-4, 6; 21. Gombaszög; 22. Hundsheim; 23. Süttő 1-9; 24. Vértesszőlős 2; 25. Dorog; 26. Budapest-Várhegy; 27. Solymár; 28. Uppony; 29. Hórvölgy; 30.Tarkő 1-16; 31. Repoulust-höhle; 32. Vindija



Map 3. Upper Pleistocene sites from Carpathian Basin
3. *térkép* Felső-pleisztocén korú lelőhelyek a Kárpát-medencéből
(After Zentai László 1996. „A Kárpát-medence domborzati alaptérképe". Modified)

1. Grosse Badhöhle; 2. Hundsteig bei Krems; 3. Luegloch; 4. Merkenstein; 5. Mixnitz –Drachenhöhle; 6. Schwarzgrabenhöhle; 7. Krapina; 8. Velika Pecina; 9. Velika pec na Lipi; 10. Veternica 11; Detrekőszentmiklós; 12. Érsekújvár; 13. Galgóc; 14. Gánócz; 15. Kisvárad; 16. Lándzsásötfalu; 17. Liszkófalva-Baráthegy; 18. Novi I, III.; 19. Óruzsin – Antal- és Nagy-barlang; 20. Porács; 21. Barcarozsnyó; 22. Magura-Valea Coacazai; 23. Homoródalmás-Vargyasi-szoros; 24. Esküllő – Igric-barlang; 25. Kőrösmart; 26. Nándorfalvi barlang; 27. Ohába Ponor; 28. Oláhszászka – Néravölgyi-barlang; 29. Hidegszamos; 30. Szamosfalva; 31. Rév; 32. Szegyestel-völgy; 33. Tordai-hasadék; 34. Gencsapáti; 35. Kőszeg; 36. Csákvár; 37. Lovas; 38. Érd; 39. Szárazgerence; 40. Buják; 41. Hollókő; 42. Mérk; 43-50. Budai-hegység- Gerecse – Pilis (43. Bajót; 44. Budapest; 45.Csobánka; 46. Kesztölc; 47. Pilisszántó; 48. Tata; 49. Tatabánya; 50. Tokod Nagyberek); 51-62. Bükk-hegység (51. Cserépfalu; 52. Diósgyőr; 53. Felsőtárkány; 54. Hámor; 55. Jósvafő; 56. Kecskésgalya; 57. Ölyveskőér; 58. Répáshuta; 59. Sály; 60. Szilvásvárad; 61. Varbó; 62. Vaskapu)



Map 4. Tardiglaciale and Holocene sites from Carpathian Basin
4. térkép Késő-glaciális és holocén korú lelőhelyek a Kárpát-medencéből
(After Zentai László 1996. „A Kárpát-medence domborzati alaptérképe". Modified)

A. Viena Basin: 1. Marchegg, 2.Teufelsluchen; **B. Burgenland:** 3. Grosse Offenber-gerhöhle, 4. Hochlensteinhöhle, 5. Knochenhöhle, 6. Trofsteinhöhle, 7. Tunnelhöhle; **C. Kisalföld:** 8. Ács, 9. Mezőlak; 10. Neszmély; **D. Vértes-Bakony:** 11. Bakonynána, 12. Bodajk, 13. Csákvár, 14. Rezi, 15. Tatabánya, 16. Tűzköves-árok; **E. Buda-Pilis-Gerecse-Visegrád Hills:** 17. Budapest, 18. Csév, 19. Csobánka, 20. Esztergom; 21. Hosszúhegy, 22. Kevélynyereg, 23. Legény-barlang, 24. Nagysomlyó, 25. Pilismarót, 26. Pomáz, 27. Tokod, 28. Visegrád; **F. South Dunántúl**: 29. Bajcsa, 30. Zalaszentistván; **G. Balaton region – Somogy – Tolna – Mecsek:** 31. Balatonboglár, 32. Balatonkeresztúr, 33. Balatonlele, 34. Balatonszemes, 35. Felsőnyék, 36. Mélyvölgy, 37. Mezőkomárom, 38. Orda-csehi, 39. Paks, 40. Székesfehérvár, 41. Tác: **H. Cserhát-Mátra:** 42. Csapástető, 43. Felnémet, 44. Felsőtárkány, 45. Füzesabony; **I. Bükk Hill:** 46. Aggtelek, 47. Cserépfalu, 48. Hilleb-rand-barlang, 49. Jósvafő, 50. Miskolc, 51. Répáshuta, 52. Szendrő; **J. North Alföld:** 53. Alattyán, 54. Folyás, 55. Jánoshida, 56. Kisköre, 57. Kőtelek, 58. Ludas, 59. Nagykörű, 60. Szajol, 61. Szolnok, 62. Tápiószele, 63. Tiszaszőlős, 64. Tiszavalk, 65. Tószeg, 66. Túrkeve; **K. South Alföld:** 67. Maroslele, 68. Röszke, 69. Szegvár, 70. Szentkirály; **L. Slovakia:** 71. Érsekújvár, 72. Jászó, 73. Kisvárad; **M. North Tiszántúl:** 74. Mezőzombor, 75. Polgár, 76. Szerencs; 77. Tiszapolgár, 78.Tiszavasvári; **N. Middle Tiszántúl:** 79. Berettyó-szentmárton, 80. Berettyóújfalú, 81. Bélmegyer, 82. Debrecen; **O. South Tiszántúl:** 83. Békés, 84. Gyula, 85. Kardoskút, 86. Ószentiván; **P. Serbia:** 87.Nosza, 88. Padina, 89. Palics, 90. Szabadka, 91. Starcevo, 92. Vlassac; **R. North Partium (Romania):** 93. Aranyosmeggyes, 94. Berettyószéplak, 95. Diószeg, 96. Érmihályfalva, 97. Gálospetri, 98. Kalota, 99. Nagyvárad, 100. Püspökfürdő, 101. Szalacs; **S. South Partium (Romania):** 102. Bégakalodva, 103. Felsőlubkó, 104. Parác, 105. Herkulesfürdő, 106. Kazánszoros; **T. Middle Transylvania (Romania):** 107. Kisbács, 108. Kisderzsida, 109. Mezőfény, 110. Mezősámsond, 111. Radnót, 112. Szilágyzovány, 113. Vizakna; **U. Apuseni Mountain (Romania):** 114. Körösbánlak, 115. Lórév, 116. Peterd, 117. Révi-szoros, 118. Révtizfalu, 119. Sebeskőrös-völgye, 120. Szind, 121. Szkerisóra, 122. Szegyestel-völgy, 123. Vársonkolyos, 124. Vaskóh; **V. South Transylvania (Romania):** 125. Gyulafehérvár, 126. Homoródalmás, 127. Kovászna, 128. Ompolymező, 129. Székelykeresztúr

List of species (Fajlista)

(**Annotation (Magyarázat):** Me – Mesozoic (Mezozoikum); Eo – Eocene (Eocén); Ol – Oligocene (Oligocén); LM – Lower Miocene (alsó-miocén); MM – Middle Miocene (középső-miocén); UM – Upper Miocene (felső-miocén); LP – Lower Pliocene (alsó-pliocén); UP – Upper Pliocene (felső-pliocén); LQ – Lower Pleistocene (alsó-pleisztocén); MQ – Middle Pleistocene (középső-pleisztocén); UQ – Upper Pleistocene (felső-pleisztocén); Ho – Holocene (Holocén); end. – signaled first from the Carpathian Basin area (először a Kárpát-medencéből leírt taxon); – taxon defined until species level (fajszintig nem meghatározott taxon)l; foss – extinct taxon, signaled first from other area (más területről először jelzett taxon); rec. – recent taxon (recens taxon), sp. – species (faj); ssp. – subspecies (alfaj); g/gen. – genus (genus, nemzetség); f/fam. – family (család); sfam. – subfamily (alcsalád); o/ord. – ordo (rend)).

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Ord. **Archaeopterygiformes**	×												foss.ord.
Fam. **Archaeopterygidae**	×												foss.fam.
Gen. ***Archaeopteryx***	×												foss.gen.
Archaeopteryx bavarica	×												foss.
Ord. **Enantiornithiformes**	×												foss.ord.
Fam. **Enantiornithidae**	×												foss.fam.
Gen. ***Bauxitornis***	×												end.gen.
Bauxitornis mindszentyae	×												end.
Enantiornithidae g. sp. indet.	×												foss.?
Ord. **Palaeocursornithiformes**	×												end.ord.
Fam. **Palaeocursornithidae**	×												end.fam
Gen. ***Palaeocursornis***	×												end.gen.
Palaeocursornis biharicus	×												end.
Ord. **Limnornithiformes**	×												end.ord.
Fam. **Limnornithidae**	×												end.fam.
Gen. ***Eurolimnornis***	×												end.gen.
Eurolimnornis corneti	×												end.
Ornithurinae indet.	×												foss.?
Ord. Hesperornithiformes	×												foss.ord.
Hesperonithidae f. g. sp. indet	×												foss.?
Ord. Struthioniformes								×					rec.ord.
Fam. Struthionidae								×					rec.fam.
Gen. *Struthio (Pachystruthio)*								×					rec.gen.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Struthio pannonicus								×					end.
Ord. Gaviiformes			×		×							×	rec.ord.
Fam. Gaviidae			×		×							×	rec.fam.
Gen. *Gavia*			×		×							×	rec.gen.
Gavia ***schultzi***					×								end.
Gavia **sp. foss. indet.**			×										foss.?
Gavia stellata												×	rec.
Ord.Podicipediformes							×		×		×	×	rec.ord.
Fam. Podicipedidae							×		×		×	×	rec.fam.
Gen. *Podiceps*							×		×		×	×	rec.gen.
Podiceps csarnotanus							×						end.
Podiceps nigricollis									×				rec.
Podiceps griseigena												×	rec.
Podiceps auritus											×		rec.
Podiceps cristatus											×		rec.
Ord.Procellariformes			×										rec.ord.
Fam. **Diomedeoididae**			×										foss.fam.
Gen. **Diomedeoides**			×										foss.gen.
Diomedeoides harmathi			×										end.
Ord. Pelecaniformes	×	×		×	×	×						×	rec.ord.
Fam. **Elopterygidae**	×												end.fam.
Gen. ***Elopteryx***	×												end.gen.
Elopteryx nopcsai	×												end.
Fam. Sulidae		×			×								rec.fam.
Gen. ***Eostega***		×											end.gen.
Eostega lebedynskii		×											end.
Gen. ***Microsula***					×								foss.gen.
Microsula pygmaea					×								foss.
Fam. Anhingidae					×	×							rec.fam.
Gen. *Anhinga*					×	×							rec.gen.
Anhinga ***pannonica***						×							end
Anhinga **sp. foss. indet.**					×								foss.?
Fam.Phalacrocoracidae				×	×								rec.fam.
Gen. *Phalacrocorax*				×	×								rec.gen.
Phalacrocorax ***intermedius***				×									foss.
Phalacrocorax **sp. foss. indet.**					×								foss.?
Phalacrocorax carbo												×	rec.
Fam. Pelecanidae								×				×	rec.fam.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Gen. *Pelecanus*								×				×	rec.gen.
Pelecanus onocrotalus												×	rec.
Pelecanus sp. indet.								×				×	rec.?
Fam. Phaethontidae						×		×					rec.fam.
Gen. ***Heliadornis***						×		×				.	foss.gen.
Heliadornis paratethydicus						×							end.
Heliadornis minor							×						end.
Ord. Ardeiformes					×	×		×	×	×	×	×	rec.ord.
Fam. Ardeidae					×	×		×	×	×		×	rec.fam.
Gen. *Ardea*										×		×	rec.gen.
Ardea cinerea										×		×	rec.
Ardea purpurea												×	rec.
Gen. ***Proardeolla***					×								foss.gen.
Proardeolla walkeri					×								foss.
Gen. *Egretta*						×		×				×	rec.gen.
Egretta **polgardiensis**						×							end.
Egretta **sp. foss. indet.**								×					foss.?
Egretta alba												×	rec.
Egretta garzetta												×	rec.
Gen. *Ixobrychus*												×	rec.gen.
Ixobrychus minutus												×	rec.
Gen. *Botaurus*									×			×	rec.gen.
Botaurus stellaris												×	rec.
Botaurus sp. indet.									×			×	rec.?
Gen. *Nycticorax*									×			×	rec.gen.
Nycticorax nycticorax												×	rec.
Nycticorax sp. indet.									×				rec.?
Fam. Plataleidae											×	×	rec.fam.
Gen. *Plegadis*											×		rec.gen.
Plegadis falcinellus											×		rec.
Gen. *Platalea*												×	rec.gen.
Platalea leucorodia												×	rec.
Fam. Ciconiidae			×		×				×	×		×	rec.fam.
Gen. ***Grallavis***			×										foss.gen.
Grallavis edwardsi			×										foss.
Gen. *Ciconia*								×	×			×	rec.gen.
Ciconia ***stehlini***								×	×				end.
Ciconia ciconia									×			×	rec.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Ciconia nigra												×	rec.
Gen. ***Pelargosteon***									×	×			end.gen.
Pelargosteon tothi									×	×			end.
Ciconiidae **g. et sp. foss. indet.**					×								foss.?
Fam. **Palaelodidae**					×								foss.fam.
Gen. ***Palaelodus***					×								foss.gen.
Palaelodus goliath					×								foss.
Palaelodus ambiguus/crassipes					×								foss.
Ord. Anseriformes			×	×	×	×	×	×	×	×	×	×	rec.ord.
Fam. Anatidae			×	×	×	×	×	×	×	×	×	×	rec.fam.
Sfam. Cygninae					×	×					×	×	rec.sfam.
Gen. *Cygnus*						×					×	×	rec.gen.
Cygnus ***csakvarensis***						×							end.
Cygnus *olor*											×	×	rec.
Cygnus cygnus												×	rec.
Cygnus sp. indet.												×	rec.?
Gen. ***Cygnopterus***				×	×								foss.gen.
Cygnopterus neogradensis				×	×								end.
Sfam. Anserinae			×		×			×	×	×	×	×	rec.sfam.
Gen. *Anser*			×		×			×		×	×	×	rec.gen.
Anser anser ***subanser***										×			end.ssp.
Anser **sp. foss. indet.**			×		×			×					foss.?
Anser anser											×	×	rec.
Anser fabalis											×	×	rec.
Anser albifrons											×	×	rec.
Anser erythropus												×	rec.
Anser sp. indet.											×	×	rec.?
Gen. *Branta*										×	×	×	rec.gen.
Branta ruficollis										×	×		rec.
Branta leucopsis												×	rec.
Branta sp. indet.												×	rec.?
Gen. *Tadorna*					×			×	×		×	×	rec.gen.
Tadorna ***minor***					×								end.
Tadorna tadorna								×	×			×	rec.
Tadorna ferruginea											×	×	rec.
Tadorna sp. indet.									×				rec.?
Sfam. Anatinae			×		×	×	×	×	×	×	×	×	rec.sfam.
Gen. ***Mionetta***			×		×								foss.gen.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Mionetta consobrina					×								foss.
Mionetta robusta			×										foss.
Gen. *Dendronessa*						×							rec.gen.
Dendronessa **sp. foss. indet.**						×							foss.?
Gen. *Anas*					×	×	×	×	×	×	×	×	rec.gen.
Anas ***velox***					×	×							foss.
Anas ***sansanensis***						×							foss.
Anas ***albae***					×	×	×	×					end.
Anas ***denesi***						×							end.
Anas platyrhynchos ***submajor***								×	×	×			end.ssp.
Anas platyrhynchos											×	×	rec.
Anas penelope									×		×	×	rec.
Anas strepera									×		×	×	rec.
Anas crecca ***percrecca***								×	×				end.ssp.
Anas crecca										×	×	×	rec.
Anas acuta									×	×	×	×	rec.
Anas querquedula								×	×	×	×	×	rec.
Anas clypeata									×	×	×	×	rec.
Anas **sp. foss. indet.**					×	×							foss.?
Anas sp. indet.									×	×	×	×	rec.?
Sfam. Aythyinae					×				×	×	×	×	rec.sfam.
Gen. *Aythya*									×	×	×	×	rec.gen.
Aythya nyroca									×	×	×	×	rec.
Aythya fuligula										×	×	×	rec.
Aythya ferina										×	×	×	rec.
Aythya marila												×	rec.
Aythya sp.										×			rec.
Gen. *Clangula*					×								rec.gen.
Clangula ***matraensis***					×								end.
Sfam. Merginae					×				×	×	×	×	rec.sfam.
Gen. *Bucephala*					×						×		rec.gen.
Bucephala ***cereti***					×								foss.
Bucephala clangula											×		rec.
Gen. *Mergus*					×				×	×	×	×	rec.gen.
Mergus ***minor***					×								end.
Mergus ***connectens***									×				foss.
Mergus serrator												×	rec.
Mergus albellus											×		rec.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Mergus merganser										×	×	×	rec.
Mergus **sp. foss. indet.**							×						foss.?
Mergus sp.										×			rec.
Gen. *Melanitta*											×		rec.gen.
Melanitta nigra											×		rec.
Anatidae **g. et sp. foss. indet.**					×	×		×					foss.?
Anatidae gen. et sp. indet.									×				rec.?
Ord. Accipitriformes			×	×		×		×	×	×	×	×	rec.ord.
Fam. Accipitridae			×	×		×	×	×	×	×	×	×	rec.fam.
Gen. *Aegypius*										×	×	×	rec.gen.
Aegypius monachus										×	×	×	rec.
Gen. *Gyps*										×	×	×	rec.gen.
Gyps ***melitensis***										×			foss.
Gyps fulvus										×	×	×	rec.
Gen. *Gypaeetus*											×	×	rec.gen.
Gypaeetus barbatus											×	×	rec.
Gen. *Circus*									×	×	×	×	rec.gen.
Circus macrourus											×		rec.
Circus cyaneus											×		rec.
Circus aeruginosus										×		×	rec.
Circus sp.									×			×	rec.
Gen. *Accipiter*									×	×	×	×	rec.gen.
Accipiter nisus									×	×	×	×	rec.
Accipiter gentilis										×	×	×	rec.
Gen. *Aquila*								×	×	×	×	×	rec.gen.
Aquila chrysaetos								×			×	×	rec.
Aquila heliaca									×	×	×	×	rec.
Aquila clanga									×		×		rec.
Aquila pomarina												×	rec.
Aquila rapax												×	rec.
Aquila sp.										×		×	rec.
Gen. *Haliaeetus*				×					×		×	×	rec.gen.
Haliaeetus ***angustipes***									×				foss.
Haliaeetus albicilla											×	×	rec.
Haliaeetus **sp. foss. indet.**				×?									foss.?
Gen. *Milvus*									×			×	rec.gen.
Milvus ***brachypterus***									×				end.
Milvus migrans												×	rec.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Milvus sp. indet.												×	rec.?
Gen. *Pernis*											×		rec.gen.
Pernis apivorus											×		rec.
Gen. *Buteo*						×			×	×	×	×	rec.gen.
Buteo buteo									×	×	×	×	rec.
Buteo lagopus									×		×	×	rec.
Buteo rufinus											×		rec.
Buteo **sp. foss. indet.**						×							foss.?
Buteo sp.indet.										×			rec.?
Gen. *Hieraetus*												×	rec.gen.
Hieraetus pennatus												×	rec.
Gen. *Circaetus*												×	rec.gen.
Circaetus gallicus												×	rec.
Fam. Pandionidae			×					×					rec.fam.
Gen. *Pandion*			×					×					rec.gen.
Pandion haliaeetus								×					rec.
Pandion **sp. foss. indet.**			×										foss.?
Fam. Falconidae						×	×	×	×	×	×	×	rec.fam.
Gen. *Falco*						×	×	×	×	×	×	×	rec.gen.
Falco aff. ***antiquus***										×			foss.
Falco tinnunculus ***atavus***						×	×	×	×	×			end.ssp.
Falco tinnunculus										×	×	×	rec.
Falco vespertinus								×	×	×	×	×	rec.
Falco subbuteo									×	×	×	×	rec.
Falco cherrug									×	×	×	×	rec.
Falco peregrinus											×		rec.
Falco rusticolus										×	×		rec.
Falco columbarius									×	×	×	×	rec.
Falco **sp. foss. indet.**						×	×						foss.?
Falco sp. indet.									×	×	×	×	rec.
Ord. Galliformes				×	×	×	×	×	×	×	×	×	rec.ord.
Fam. Phasianidae				×	×	×	×	×	×	×	×	×	rec.fam.
Gen. ***Palaeortyx***				×	×	×	×						foss.gen.
Palaeortyx brevipes						×	×						foss.
Palaeortyx gallica				×	×	×							foss.
Palaeortyx phasionides				×		×							foss.
Palaoertyx prisca/phasionides					×								foss.
Gen. ***Palaeocryptonix***						×	×		×				end.gen.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Palaeocryptonix hungaricus						×	×		×				end.
Gen. *Francolinus*							×	×	×				rec.gen.
Francolinus ***capeki***							×	×	×				end.
Gen. *Coturnix*									×	×	×	×	rec.gen.
Coturnix coturnix									×	×	×	×	rec.
Gen. *Alectoris*							×	×	×	×	×	×	rec.gen.
Alectoris ***donnezani***							×	×	×				foss.
Alectoris graeca										×	×	×	rec.
Gen. *Perdix*							×	×	×	×	×	×	rec.gen.
Perdix perdix ***jurcsaki***							×	×	×	×			end.ssp.
Perdix perdix										×	×	×	rec.
Perdix sp. indet.									×				rec.?
Gen. *Ammoperdix*										×			rec.gen.
Ammoperdix sp. indet.										×			rec.?
Gen. ***Miogallus***					×	×							foss.gen.
Miogallus altus					×	×							foss.
Gen. *Gallus*							×	×	×	×	×	×	rec.gen.
Gallus ***beremendensis***							×	×	×				end.
Gallus sp.										×	×	×	rec.
Gen. *Phasianus*										×		×	rec.gen.
Phasianus sp.										×		×	rec.
Gen. *Pavo*						×	×						rec.gen.
Pavo ***bravardi***							×						foss.
Pavo archiaci						×							foss.
Gen. *Numida*												×	rec.gen.
Numida meleagris												×	rec
Perdicidae **g. sp. foss. indet.**					×								foss.?
Perdicidae gen. et sp. indet.											×	×	rec.?
Fam. Tetraonidae						×	×	×	×	×	×	×	rec.fam.
Gen. *Tetrao*						×	×	×	×	×	×	×	rec.gen.
Tetrao ***praeurogallus***							×		×	×			end.
Tetrao urogallus										×	×	×	rec
Tetrao ***partium***						×	×	×	×	×			end.
Tetrao tetrix									×	×	×	×	rec
Tetrao sp. indet.										×	×		rec
Gen. *Bonasa*									×	×	×	×	rec.gen.
Bonasa ***praebonasia***									×	×			end.
Bonasa bonasia											×	×	rec

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Gen. *Lagopus*										×	×	×	rec.gen.
Lagopus lagopus										×	×	×	rec
Lagopus mutus										×	×	×	rec
Galliformes **foss. indet.**						×							foss.?
Ord. Ralliformes			×	×	×	×	×	×	×	×	×	×	rec.ord.
Fam. Heliornithidae						×							rec.fam.
Gen. *Heliornis*						×							rec.gen.
Heliornis ***sumegensis***						×							end.
Fam. Gruidae			×		×	×					×	×	rec.fam.
Gen. *Grus*						×					×	×	rec.gen.
Grus ***pentelici***						×							foss.
Grus grus											×	×	rec.
Gen. *Balearica*			×										rec.gen.
Balearica ***excelsa***			×										foss.
Gruidae **g. et sp. foss. indet.**					×								foss.?
Fam. Otididae						×	×	×	×	×	×	×	rec.fam.
Gen. Otis						×	×	×	×	×	×	×	rec.gen.
Otis ***khozatzki beremendensis***						×		×					end.ssp.
Otis ***kalmani***						×	×	×	×				end.
Otis tetrax										×	×	×	rec.
Otis ***lambrechti***							×	×	×	×			end.
Otis tarda										×	×	×	rec.
Otis sp. indet.									×	×			rec.
Fam. Rallidae			×	×	×	×	×		×		×	×	rec.fam.
Gen. ***Rallicrex***			×	×	×	×	×						end.
Rallicrex kolozsvarensis			×										end.
Rallicrex litkensis				×	×								end.
Rallicrex polgardensis						×	×						end.
Gen. ***Miorallus***						×	×		×				foss.gen.
Miorallus major						×	×		×				foss.
Gen. *Porzana*					×	×	×		×		×	×	rec.gen.
Porzana ***estramosi***					×	×	×						end.
Porzana ***matraensis***					×								end.
Porzana ***kretzoii***						×							end.
Porzana porzana									×		×	×	rec.
Porzana parva									×				rec.
Porzana pusilla									×				rec.
Porzana **sp. foss. indet.**							×						foss.?

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Gen. *Crex*						×			×		×	×	rec.gen.
Crex crex									×		×	×	rec.
Crex **sp. foss. indet.**						×							foss.?
Crex sp. indet.									×				rec.?
Gen. Rallus							×		×	×	×	×	rec.gen.
Rallus aquaticus									×	×	×	×	rec.
Rallus **sp. foss. indet.**							×						foss.?
Rallus sp. indet.									×				rec.?
Gen. *Gallinula*									×	×		×	rec.gen.
Gallinula chloropus									×	×		×	rec.
Gen. *Fulica*									×			×	rec.gen.
Fulica atra									×			×	rec.
Gen. ***Palaeoaramides***									×				foss.gen.
Palaeoaramides beaumonti									×				foss.
Rallidae **gen. et sp. foss. indet.**					×								foss.?
Ord. Charadriiformes					×	×	×	×	×	×	×	×	rec.ord.
Fam. Scolopacidae					×	×	×	×	×	×	×	×	rec.fam.
Gen. *Gallinago*					×	×	×		×	×	×	×	rec.gen.
Gallinago ***veterior***					×	×	×						end.
Gallinago media									×	×	×		rec.
Gallinago gallinago									×	×	×	×	rec.
Gallinago **sp. foss. indet.**						×							foss.?
Gallinago sp. indet.									×				rec.?
Gen. *Lymnocryptes*												×	rec.gen.
Lymnocryptes minimus												×	rec.
Gen. *Limosa*						×			×	×	×	×	rec.gen.
Limosa limosa									×	×	×	×	rec.
Limosa **sp. foss. indet.**						×							foss.?
Gen. *Numenius*								×			×	×	rec.gen.
Numenius arquata											×	×	rec.
Numenius phaeopus											×	×	rec.
Numenius sp. indet.											×		rec.?
Numenius **sp. foss. indet.**								×					foss.?
Gen. *Tringa*						×	×	×	×	×	×	×	rec.gen.
Tringa totanus											×		rec.
Tringa glareola									×				rec.
Tringa erythropus								×	×		×		rec.
Tringa nebularia									×				rec.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Tringa ochropus								×	×	×			rec.
Tringa hypoleucos									×			×	rec.
Tringa **sp. foss. indet.**						×	×		×				foss.?
Tringa sp. indet.											×	×	rec.?
Gen. *Scolopax*							×		×	×	×	×	rec.gen.
Scolopax ***baranensis***							×		×				end.
Scolopax rusticola										×	×	×	rec.
Scolopax sp. indet.											×		rec.?
Gen. *Cursorius*									×				rec.gen.
Cursorius sp. indet.									×				rec.?
Gen. *Arenaria*											×		rec.gen.
Arenaria interpres											×		rec.
Gen. *Phylomachus*									×		×		rec.gen.
Phylomachus pugnax									×		×		rec.
Fam. Charadriidae						×		×	×	×	×	×	rec.fam.
Gen. *Charadrius*						×					×	×	rec.gen.
Charadrius ***lambrechti***						×							end.
Charadrius hiaticula												×	rec.
Charadrius sp. indet.											×		rec.
Gen. *Calidris*						×					×		rec.gen.
Calidris ***janossyi***						×							end.
Calidris alpina											×		rec.
Calidris ferruginea											×		rec.
Gen. *Vanellus*								×	×	×			rec.gen.
Vanellus vanellus								×	×	×			rec.
Gen. *Pluvialis*											×		rec.gen.
Pluvialis squatarola											×		rec.
Fam. Recurvirostridae									×	×	×		rec.fam.
Gen. *Recurvirostra*									×	×			rec.gen.
Recurvirostra avosetta										×			rec.
Recurvirostra **sp. foss. indet.**									×				foss.?
Gen. *Himantopus*											×		rec.gen.
Himantopus himantopus											×		rec.
Fam. Laridae							×	×	×	×	×		rec.fam.
Gen. *Larus*									×	×			rec.gen.
Larus minutus										×			rec.
Larus ridibundus									×	×			rec.
Larus sp. indet.										×			rec.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Gen. *Sterna*								×			×		rec.gen.
Sterna hirundo								×			×		rec.
Gen. *Chlidonias*							×		×		×		rec.gen.
Chlidonias niger									×				rec.
Chlidonias **sp. foss. indet.**							×						foss.?
Chlidonias sp. indet.											×		rec.?
Ord. Columbiformes					×		×	×	×	×	×	×	rec.ord.
Fam. Columbidae					×		×	×	×	×	×	×	rec.fam.
Gen. *Columba*							×	×	×	×	×	×	rec.gen.
Columba livia									×		×	×	rec.
Columba palumbus								×	×	×	×	×	rec.
Columba oenas											×	×	rec.
Columba **sp. foss. indet.**							×						foss.?
Columba sp. indet.												×	rec.?
Gen. *Streptopelia*												×	rec.gen.
Streptopelia turtur												×	rec.
Columbidae **gen. et sp. indet.**					×								foss.?
Fam. Pteroclidae					×						×		rec.fam.
Gen. Syrrhaptes											×		rec.gen.
Syrrhaptes paradoxus											×		rec.
Pteroclidae **g. et sp. foss. indet.**					×								foss.?
Ord. Cuculiformes					×	×	×	×		×	×	×	rec.ord.
Fam. Cuculidae					×	×	×	×		×	×	×	rec.fam.
Gen. *Cuculus*						×	×	×		×	×	×	rec.gen.
Cuculus **csarnotanus**							×						end.
Cuculus ***pannonicus***						×		×					end.
Cuculus canorus										×	×	×	rec.
Cuculidae **g. et sp. foss. indet.**					×								foss.?
Ord. Strigiformes				×	×	×	×	×	×	×	×	×	rec.ord.
Fam. Tytonidae				×		×			×	×			rec.fam.
Gen. ***Prosybris***				×									foss.gen.
Prosybris antiqua				×									foss.
Gen. *Tyto*						×			×	×			rec.gen.
Tyto ***sanctialbani***						×							foss.
Tyto ***campiterrae***						×							end.
Tyto alba									×	×			rec.
Tyto sp. indet.									×				rec.?
Fam. Strigidae					×	×	×	×	×	×	×	×	rec.fam.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Gen. ***Intulula***						×							foss.gen.
Intulula brevis						×							foss.
Gen. *Otus*									×	×	×		rec.gen.
Otus scops									×	×	×		rec.
Gen. *Bubo*						×	×	×	×	×	×	×	rec.gen.
Bubo ***florianae***						×							end.
Bubo bubo									×	×	×	×	rec.
Bubo **sp. foss. indet.**							×	×					foss.?
Gen. *Surnia*						×		×	×		×		rec.gen.
Surnia ***robusta***						×		×	×				end.
Surnia ulula											×		rec.
Gen. *Glaucidium*							×		×	×	×		rec.gen.
Glaucidium ***baranensis***							×						end.
Glaucidium passerinum									×	×	×		rec.
Gen. *Athene*						×	×	×	×		×	×	rec.gen.
Athene ***noctua veta***						×	×	×	×				end.ssp.
Athene noctua											×	×	rec.
Athene **sp. foss. indet.**						×							foss.?
Gen. *Strix*							×	×	×	×	×	×	rec.gen.
Strix ***intermedia***							×	×	×	×			end.
Strix aluco											×	×	rec.
Strix nebulosa											×		rec.
Strix uralensis											×	×	rec.
Gen. *Aegolius*							×	×	×		×	×	rec.gen.
Aegolius funereus									×		×	×	rec.
Aegolius **sp. foss. indet.**							×	×					foss.?
Gen. *Asio*								×	×	×	×	×	rec.gen.
Aso flammeus									×	×	×	×	rec.
Asio otus								×	×	×	×	×	rec.
Asio sp. indet.									×				rec.?
Gen. *Nyctea*										×	×	×	rec.gen.
Nyctea scandiaca										×	×	×	rec.
Strigidae **g. et sp. foss. indet.**					×								foss.?
Strigidae gen. et sp. indet.											×		rec.
Ord. Caprimulgiformes									×		×		rec.ord.
Fam. Caprimulgidae									×		×		rec.fam.
Gen. *Caprimulgus*									×		×		rec.gen.
Caprimulgus europaeus									×		×		rec.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Ord. Apodiformes						×	×	×	×	×	×	×	rec.ord.
Fam. Apodidae						×	×	×	×	×	×	×	rec.fam.
Gen. *Apus*						×	×	×	×	×	×	×	rec.gen.
Apus ***baranensis***						×	×	×					end.
Apus apus									×	×	×	×	rec.
Apus melba										×	×		rec.
Gen. *Chaetura*						×	×						rec.gen.
Chaetura ***baconica***						×	×						end.
Ord. Coraciiformes					×	×	×	×	×	×		×	rec.ord.
Fam. Meropidae					×	×			×	×			rec.fam.
Gen. *Merops*					×	×			×	×			rec.gen.
Merops ***radobojensis***					×	×							end.
Merops apiaster										×			rec.
Merops **sp. foss. indet.**									×				foss.?
Meropidae **g. et sp. foss. indet.**					×								foss.?
Fam. Coraciidae							×		×				rec.fam.
Gen. *Eurystomus*							×		×				rec.gen.
Eurystomus ***beremendensis***							×						end.
Eurystomus **sp. foss. indet.**									×				foss.?
Fam. Upupidae								×		×		×	rec.fam.
Gen. *Upupa*								×		×		×	rec.gen.
Upupa ***phoeniculides***								×		×			end.
Upupa epops												×	rec.
Fam. Alcedinidae										×			rec.fam.
Gen. *Halcyon*										×			rec.gen.
Halcyon **sp. foss. indet.**										×			foss.?
Ord. Piciformes						×	×	×	×	×	×	×	rec.ord.
Fam. Picidae						×	×	×	×	×	×	×	rec.fam.
Gen. *Jynx*									×		×		rec.gen.
Jynx torquilla									×		×		rec.
Gen. *Picus*								×	×	×	×	×	rec.gen.
Picus ***pliocaenicus***								×					end.
Picus viridis									×	×	×	×	rec.
Picus canus											×	×	rec.
Picus sp. indet.											×		rec.?
Gen. *Dendrocopos*							×	×	×	×	×	×	rec.gen.
Dendrocopos major ***submajor***							×		×	×			end.ssp.
Dendrocopos major										×	×	×	rec.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Dendrocopos ***praemedius***							×	×					end.
Dendrocopos medius									×	×	×		rec.
Dendrocopos minor									×				rec.
Dendrocopos leucotos												×	rec.
Gen. *Pogoniulus*						×							rec.gen.
Pogoniulus **sp. foss. indet.**						×							foss.?
Ord. Passeriformes				×	×	×	×	×	×	×	×	×	rec.ord.
Fam. Alaudidae				×	×	×	×		×	×	×	×	rec.fam.
Gen. *Melanocorypha*							×		×				rec.gen.
Melanocorypha ***minor***							×						end.
Melanocorypha calandra									×				rec.
Melanocorypha sp. indet.									×				rec.?
Gen. *Galerida*				×			×		×		×	×	rec.gen.
Galerida ***cserhatensis***				×									end.
Galerida ***pannonica***							×						end.
Galerida cristata									×		×	×	rec.
Galerida sp. indet.									×				rec.?
Gen. ***Praealauda***					×								end.gen.
Praealauda hevesensis					×								end.
Gen. *Alauda*						×			×	×	×	×	rec.gen.
Alauda ***tivadari***						×							end.
Alauda arvensis									×	×	×	×	rec.
Gen. *Lullula*					×	×	×		×				rec.gen.
Lulula ***neogradensis***					×								end.
Lullula ***minor***						×							end.
Lullula ***parva***							×						end.
Lullula ***minuscula***							×						end.
Lullula arborea									×				rec.
Gen. *Calandrella*						×							rec.gen.
Calandrella ***gali***						×							end.
Gen. *Eremophila*											×	×	rec.gen.
Eremophila alpestris											×	×	rec.
Fam. Hirundinidae						×	×		×	×	×	×	rec.fam.
Gen. *Hirundo*						×	×		×	×	×	×	rec.gen.
Hirundo ***gracilis***						×							end.
Hirundo ***major***							×						end.
Hirundo rustica									×	×	×	×	rec.
Hirundo **sp. foss. indet.**							×		×				foss.?

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Hirundo sp. indet.									×	×			rec.?
Gen. *Delichon*						×	×		×		×	×	rec.gen.
Delichon ***polgardiensis***						×							end.
Delichon ***pusillus***							×						end.
Delichon ***major***							×						end.
Delichon urbica									×		×	×	rec.
Gen. *Riparia*						×			×		×		rec.gen.
Riparia ***major***						×							end.
Riparia rupestris											×		rec.
Riparia riparia									×				rec.
Fam. Corvidae						×	×	×	×	×	×	×	rec.fam.
Gen. *Corvus*						×	×	×	×	×	×	×	rec.gen.
Corvus ***pliocaenus***						×	×	×	×	×			foss.
Corvus ***hungaricus***									×				end.
Corvus ***harkanyensis***							×						end.
Corvus monedula									×	×	×	×	rec.
Corvus corax										×	×	×	rec.
Corvus corone cornix										×	×	×	rec.
Corvus frugilegus											×	×	rec.
Corvus **sp. foss. indet.**				×		×	×	×					foss.?
Corvus sp. indet.									×		×	×	rec.?
Gen. ***Miocorvus***					×	×	×						foss.gen.
Miocorvus larteti					×	×	×						foss.
Gen. *Garrulus*									×	×	×	×	rec.gen.
Garrulus glandarius									×	×	×	×	rec.
Gen. *Nucifraga*									×	×	×	×	rec.gen.
Nucifraga caryocatactes									×	×	×	×	rec.
Gen. *Pica*							×		×	×	×	×	rec.gen.
Pica pica ***major***							×		×	×			end.ssp.
Pica pica										×	×	×	rec.
Gen. *Pyrrhocorax*							×	×	×	×	×	×	rec.gen.
Pyrrhocorax graculus ***vetus***							×	×	×	×			end.ssp.
Pyrrhocorax graculus										×	×	×	rec.
Pyrrhocorax pyrrhocorax									×	×	×	×	rec.
Gen. *Perisoreus*											×		rec.gen.
Perisoreus infaustus											×		rec.
Corvidae **g. et sp. foss. indet**							×						foss.?
Corvidae gen. et sp. indet.									×		×		rec.?

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Fam. Paridae						×	×		×	×	×	×	rec.fam.
Gen. *Aegithalos*						×	×		×				rec.gen.
Aegithalos ***gaspariki***						×							end.
Aegithalos ***congruis***							×						end.
Aegithalos caudatus									×				rec.
Gen. *Parus*							×		×	×	×	×	rec.gen.
Parus ***medius***							×						end.
Parus ***robostus***							×						end.
Parus ***parvulus***							×						end.
Parus caeruleus									×		×		rec.
Parus major									×	×	×	×	rec.
Parus lugubris									×				rec.
Parus ater										×			rec.
Parus palustris										×			rec.
Parus montanus											×		rec.
Parus sp. indet.										×	×		rec.
Fam. Sittidae					×	×	×		×		×	×	rec.fam.
Gen. *Sitta*						×	×		×		×	×	rec.gen.
Sitta ***gracilis***						×							end.
Sitta ***pusilla***							×						end.
Sitta ***villanyensis***							×						end.
Sitta europaea									×		×	×	rec.
Sittidae **g. et sp. foss. indet.**					×								foss.?
Fam. Certhiidae					×	×	×		×				rec.fam.
Gen. *Certhia*						×	×		×				rec.gen.
Certhia ***janossyi***						×							end.
Certhia ***imensa***							×						end.
Certhia familiaris									×				rec.
Certhidae **g. et sp. fos. indet.**					×		×						foss.?
Fam. Tichodromidae						×							rec.fam.
Gen. *Tichodroma*						×							rec.gen.
Tichodroma ***capeki***						×							end.
Fam. Muscicapidae					×	×	×		×	×	×	×	rec.fam.
Gen. *Muscicapa*					×	×	×		×	×		×	rec.gen.
Muscicapa ***leganyii***					×								end.
Muscicapa ***miklosi***						×							end.
Muscicapa ***petényii***							×						end.
Muscicapa striata									×	×		×	rec.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Gen. *Erithacus*					×		×		×	×	×	×	rec.gen.
Erithacus ***horusitskyi***					×								end.
Erithacus ***minor***							×						end.
Erithacus rubecula									×	×	×	×	rec.
Erithacus sp. indet.									×				rec.?
Gen. *Luscinia*				×	×	×	×		×	×	×		rec.gen.
Luscinia ***praeluscinia***				×									end.
Luscinia ***jurcsaki***					×								end.
Luscinia ***denesi***						×							end.
Luscinia ***pliocaenica***							×						end.
Luscinia luscinia									×				rec.
Luscinia megarhynchos									×		×		rec.
Luscinia svecica										×			rec.
Luscinia sp. indet.									×				rec.?
Gen. *Saxicola*						×	×		×		×	×	rec.gen.
Saxicola ***lambrechti***						×							end.
Saxicola ***baranensis***							×						end.
Saxicola ***parva***							×						end.
Saxicola ***magna***							×						end.
Saxicola rubetra									×			×	rec.
Saxicola torquata									×		×		rec.
Gen. *Monticola*							×				×		rec.gen.
Monticola ***pongraczi***							×						end.
Monticola saxatilis											×		rec.
Gen. *Phoenicurus*							×			×		×	rec.gen.
Phoenicurus ***erikai***							×						end.
Phoenicurus ***baranensis***							×						end.
Phoenicurus phoenicurus										×			rec.
Phoenicurus ochruros												×	rec.
Gen. *Oenanthe*						×	×			×		×	rec.gen.
Oenanthe ***kormosi***						×							end.
Oenanthe ***pongraczi***							×						end.
Oenanthe oenanthe										×		×	rec.
Muscicapidae **g. et sp. foss. indet.**						×	×						foss.?
Fam. Turdidae				×	×	×	×	×	×	×	×	×	rec.fam.
Gen. ***Turdicus***				×	×	×	×		×				end.gen.
Turdicus matraensis				×	×								end.
Turdicus pannonicus						×							end.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Turdicus tenuis									×				end.
Gen. *Turdoides*							×						rec.gen.
Turdoides ***borealis***							×						end.
Gen. *Turdus*					×	×	×	×	×	×	×	×	rec.gen.
Turdus ***miocaenicus***						×							end.
Turdus **polgardiensis**						×							end.
Turdus ***major***							×						end.
Turdus ***medius***							×						end.
Turdus ***minor***							×						end.
Turdus torquatus									×		×	×	rec.
Turdus merula									×	×	×	×	rec.
Turdus philomelos									×	×	×	×	rec.
Turdus iliacus									×	×	×	×	rec.
Turdus viscivorus									×	×	×	×	rec.
Turdus pilaris									×	×	×	×	rec.
Turdus **sp. foss. indet.**					×	×	×	×					foss.?
Turdus sp. indet.									×	×	×		rec.
Turdidae **g. et sp. foss. indet.**					×								foss.?
Fam. Oriolidae							×		×	×	×	×	rec.fam.
Gen. Oriolus							×		×	×	×	×	rec.gen.
Oriolus ***beremendensis***							×						end.
Oriolus oriolus									×	×	×	×	rec.
Fam. Sylviidae					×	×	×		×	×	×	×	rec.fam.
Gen. *Acrocephalus*						×	×		×			×	rec.gen.
Acrocephalus ***major***						×							end.
Acrocephalus ***minor***						×							end.
Acrocephalus ***kretzoii***							×						end.
Acrocephalus ***kormosi***							×						end.
Acrocephalus palustris									×				rec.
Acrocephalus **sp. foss. indet.**					×		×		×				foss.?
Acrocephalus sp. indet.												×	rec.?
Gen. *Cettia*						×	×						rec.gen.
Cettia ***janossyi***						×							end.
Cettia ***kalmani***							×						end.
Gen. *Hippolais*						×	×		×				rec.gen.
Hippolais ***veterior***						×							end.
Hippolais **sp. foss. indet.**							×		×				foss.?
Gen. *Sylvia*						×	×		×	×	×		rec.gen.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Sylvia ***intermedia***						×							end.
Sylvia ***pusilla***							×						end.
Sylvia *atricapilla*									×				rec.
Sylvia communis									×				rec.
Sylvia borin										×	×		rec.
Sylvia curruca											×		rec.
Sylvia **sp. foss. indet.**						×	×		×				foss.?
Gen. *Locustella*					×	×	×		×				rec.gen.
Locustella ***kordosi***						×							end.
Locustella ***janossyi***							×						end.
Locustella ***magna***							×						end.
Locustella fluviatilis									×				rec.
Locustella **sp. foss. indet.**					×								foss.?
Gen. *Phylloscopus*					×	×	×			×			rec.gen.
Phylloscopus ***miocaenicus***					×								end.
Phylloscopus ***venczeli***						×							end.
Phylloscopus ***pliocaenicus***							×						end.
Phylloscopus sp. indet.										×			rec.?
Gen. *Regulus*							×						rec.gen.
Regulus ***pliocaenicus***							×						end.
Regulus sp. indet.										×		×	rec.?
Sylviidae **g. et sp. foss. indet.**					×								foss.?
Fam. Motacillidae					×	×	×	×	×	×	×	×	rec.fam.
Gen. *Anthus*					×	×	×	×	×	×	×	×	rec.gen.
Anthus ***antecedens***					×								end.
Anthus ***hiri***						×							end.
Anthus ***baranensis***							×						end.
Anthus pratensis											×		rec.
Anthus cervinus										×			rec.
Anthus trivialis									×		×	×	rec.
Anthus spinoletta											×		rec.
Anthus campestris/spinoletta									×				rec.
Anthus **sp. foss. indet.**								×	×				foss.?
Anthus sp. indet.											×		rec.
Gen. *Motacilla*					×	×	×		×	×	×	×	rec.gen.
Motacilla ***intermedia***						×							end.
Motacilla ***minor***							×						end.
Motacilla ***robusta***							×						end.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Motacilla flava									×		×		rec.
Motacilla alba									×		×	×	rec.
Motacilla cinerea									×		×		rec.
Motacilla **sp. foss. indet.**					×	×	×						foss.?
Motacilla sp. indet.										×			rec.?
Fam. Bombycillidae				×	×	×	×		×	×	×		rec.fam.
Gen. *Bombycilla*				×	×	×	×		×	×	×		rec.gen.
Bombycilla ***hamori***				×	×								end.
Bombycilla ***brevia***						×							end.
Bombycilla ***kubinyii***							×						end.
Bombycilla garrulus										×	×		rec.
Bombycilla **sp. foss. indet.**							×		×				foss.?
Fam. Troglodytidae						×					×		rec.fam.
Gen. *Troglodytes*						×					×		rec.gen.
Troglodytes ***robustus***						×							end.
Troglodytes troglodytes											×		rec.
Fam. Cinclidae				×		×	×		×		×	×	rec.fam.
Gen. *Cinclus*				×		×	×		×		×	×	rec.gen.
Cinclus ***major***				×									end.
Cinclus ***medius***						×							end.
Cinclus ***minor***							×						end.
Cinclus cinclus									×		×	×	rec.
Fam. Prunellidae						×	×				×	×	rec.fam.
Gen. *Prunella*						×	×				×	×	rec.gen.
Prunella ***freudenthali***						×							end.
Prunella ***kormosi***							×						end.
Prunella modularis											×		rec.
Prunella collaris												×	rec.
Fam. Laniidae					×	×	×	×	×	×	×	×	rec.fam.
Gen. *Lanius*					×	×	×	×	×	×	×	×	rec.gen.
Lanius ***schreteri***					×								end.
Lanius ***capeki***						×							end.
Lanius ***hungaricus***							×						end.
Lanius ***major***							×						end.
Lanius ***intermedius***							×						end.
Lanius senator											×		rec.
Lanius excubitor									×	×	×	×	rec.
Lanius collurio									×		×		rec.

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Lanius minor									×		×	×	rec.
Lanius **sp. foss. indet.**							×	×					foss.?
Laniidae **g. et sp. foss. indet.**					×								foss.?
Fam. Sturnidae						×	×		×	×	×	×	rec.fam.
Gen. *Sturnus*						×	×		×	×	×	×	rec.gen.
Sturnus ***kretzoii***						×							end.
Sturnus ***brevis***						×							end.
Sturnus ***pliocaenicus***							×						end.
Sturnus ***baranensis***							×						end.
Sturnus vulgaris									×	×	×	×	rec.
Sturnus roseus											×		rec.
Sturnus sp. indet.									×		×		rec.?
Fam. Passeridae						×	×		×	×	×	×	rec.fam.
Gen. *Passer*						×	×		×	×	×	×	rec.gen.
Passer ***hiri***						×							end.
Passer ***minusculus***							×						end.
Passer ***pannonicus***							×						end.
Passer montanus									×	×	×	×	rec.
Passer domesticus											×	×	rec.
Fam. Fringillidae				×	×	×	×	×	×	×	×	×	rec.fam.
Gen. *Serinus*								×			×		rec.gen.
Serinus serinus											×		rec.
Serinus **sp. foss. indet.**								×					foss.?
Gen. Carduelis						×	×		×		×	×	rec.gen.
Carduelis ***kretzoii***						×							end.
Carduelis ***lambrechti***						×							end.
Carduelis ***parvulus***							×						end.
Carduelis ***medius***							×						end.
Carduelis chloris									×		×	×	rec.
Carduelis carduelis									×		×		rec.
Carduelis spinus									×				rec.
Carduelis cannabina									×		×		rec.
Carduelis flammea											×		rec.
Carduelis sp. indet.									×		×		rec.?
Gen. *Pinicola*							×		×	×	×	×	rec.gen.
Pinicola ***kubinyii***							×						end.
Pinicola enucleator									×		×	×	rec.
Pinicola sp. indet.										×			rec.?

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Gen. *Coccothraustes*							×		×	×	×	×	rec.gen.
Coccothraustes ***major***							×						end.
Coccothraustes coccothraustes									×	×	×	×	rec.
Gen. *Pyrrhula*						×	×		×	×	×	×	rec.gen.
Pyrrhula ***gali***						×							end.
Pyrrhula ***minor***							×						end.
Pyrrhula pyrrhula									×	×	×	×	rec.
Pyrrhula **sp. foss. indet.**							×						foss.?
Gen. *Fringilla*				×	×	×	×		×		×	×	rec.gen.
Fringilla ***kormosi***						×							end.
Fringilla ***petenyii***							×						end.
Fringilla montifringilla									×		×	×	rec.
Fringilla coelebs									×		×	×	rec.
Fringilla **sp. foss. indet.**				×	×								foss.?
Gen. *Montifringilla*												×	rec.gen.
Montifringilla nivalis												×	rec.
Gen. *Loxia*							×		×	×	×	×	rec.gen.
Loxia ***csarnotanus***							×						end.
Loxia curvirostra									×	×	×	×	rec.
Loxia sp. indet.											×		rec.?
Fringillidae **g. et sp. foss. indet.**						×	×						foss.?
Fringillidae gen. et sp. indet.											×		rec.?
Fam. Emberizidae				×		×	×		×	×	×	×	rec.fam.
Gen. *Emberiza*				×		×	×		×	×	×	×	rec.gen.
Emberiza ***bartkoi***				×									end.
Emberiza ***pannonica***						×							end.
Emberiza ***media***							×						end.
Emberiza ***parva***							×						end.
Emberiza ***gaspariki***							×						end.
Emberiza cirlus									×				rec.
Emberiza calandra									×		×	×	rec.
Emberiza citrinella									×	×	×	×	rec.
Emberiza schoeniclus											×		rec.
Emberiza sp. indet.									×		×	×	rec.?
Gen. *Plectrophenax*						×							rec.gen.
Plectrophenax ***veterior***						×							end.
Plectrophenax nivalis											×		rec.
Emberizidae gen. et sp. indet										×	×		rec.?

Taxa	Me	Eo	Ol	AM	KM	FM	AP	FP	QA	QK	QF	Ho	character
Passeriformes **foss. indet.**				×	×	×	×	×					foss.?
Passeriformes indet.									×	×	×	×	rec.?
Aves **foss. indet**.			×	×	×	×	×	×					foss.?
Aves indet.									×	×	×	×	rec.?
Ichnotaxa: Gen. ***Charadripedia***			×										end.gen.
Charadriipedia limosa			×										end.
Gen. **Avidactyla**				×									end.gen.
Avidactyla media				×									end.
Gen. ***Ornithotornocia***				×									end.gen.
Ornithotarnocia lambrechti				×									end.
Gen. ***Passeripedia***				×									end.gen.
Passeripedia ipolyensis				×									end.
Gen. **Tetraornithopedia**				×									end.
Tetraornithopedia tasnadii				×									end.
Feather imprints				×	×	×	×			×			foss.
Eggshells				×				×					foss.
Urokoprolits								×					foss.

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DE GRUYTER OPEN

A case of intraspecific killing in passerines: the House Sparrow *(Passer domesticus)*

Guillaume Halliez[1,2*] & Clémence Marie Lucie Becel[2]

Guillaume Halliez & Clémence Marie Lucie Becel 2014. A case of intraspecific killing in passerines: the House Sparrow *(Passer domesticus)*. – Ornis Hungarica 22(2): 126–129.

Abstract Even if intraspecific conflict is a well-known behaviour in birds, intraspecific killing among passerines is very rare in the literature. Cases of intraspecific predation among passerines constitute a very small percentage of published reports, and many of the cases are based on circumstantial evidence. In March 2013, we witnessed a group of House Sparrows *(Passer domesticus)* kill a conspecific male adult in the village of Gonsans (France, Doubs department). During the reproductive season three explanations of others studies (lack of food, weak condition and territorial behaviour during) could be relevant in our case. In conclusion, it appears that our observation is a very rare one and the second one for the House Sparrow.

Keywords: House Sparrow, aggressive event, intraspecific killing, intraspecific competition, passerines

Összefoglalás Míg a fajtársak közötti összetűzés jól ismert viselkedés a madaraknál, a verébalkatúak rendjén belül, a fajtársak megölése az irodalomban ritkán említett jelenség. Ilyen esetben is inkább közvetett bizonyítékok állnak rendelkezésre. 2013 márciusában a franciaországi Gonsans nevű faluban egy kisebb házi verébcsapat *(Passer domesticus)* egy fajtársa megölésének voltunk szemtanúi. Tekintve, hogy ez a téli időszak vége és a szaporodási szezon kezdete, így az élelemhiány, az áldozat rossz fizikai kondíciója és a territoriális viselkedés bármelyike magyarázhatja a történteket. Mindössze egy ilyen jellegű eseményt publikáltak ezelőtt a házi veréb esetén.

Kulcszavak: házi veréb, agresszió, fajtársak közötti gyilkosság, versengés, énekesmadarak

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Introduction

Despite considerable interest in its occurrence or potential occurrence (e.g. Lorenz 1963), both direct and circumstantial evidence of intraspecific killing in adult passerines is rare (Davis 1940, Cottrille 1950, Joslin 1964, Clevenger & Roest 1974, Fisher 1975, Grubbs 1977, Loflin 1982, Cawston 1983, Lombardo 1986, Andersen 2004). Our aim was to contribute to this meagre body of literature with the second observed case of intraspecific killing in adult House Sparrow *(Passer domesticus)*.

Description of the observation and the environmental context

Our study site is the village of Gonsans in France (47°13′58″N, 6°18′04″E). This village is about 545 inhabitants with a surface of 17.29 km² (density of 32 inhabitants per km²) represents a normal size for a village in Franche-Comté area and in France. This village is situated at the beginning of the medium mountain stage (from 500 to 600 meters of elevation). The buildings are composed of old renovated farms in the downtown of the village and new houses in the periphery. The buildings are rarely taller than two floors. Urbanized areas are known to be friendly for the House Sparrow (Bichet *et al.* 2013). In Franche-Comté, the study of the House Sparrow allows us to consider that the density of the species is about 70 individuals per km² (Legay & Weidmann 2005). In the very local urban area where we were (about 10 houses) we observed a maximum of seven different individuals for a number of couple of three. The landscape around the village is composed by grassland and mixed forested areas (Giraudoux *et al.* 1997).

On 7th March 2013 at 9 a.m., we observed an adult male House Sparrow attacked by four others of the species as three adult males and one adult female. We missed the beginning of the combat. We were located 25 meters from the event, which was occurred less than 50 meters from the closest source of food (bakery and bird table) or nesting place. The male was on the ground in the middle of the street and the four other individuals pecked the head of the victim alternatively for almost twenty minutes killing him slowly but certainly. The victim was still alive during the aggressive event (moving slowly) and we examined the corpse after the observation to be sure that the individual was dead and we did not find any clue of an injury by another source (car, predation etc.).

In March, the sparrows were still feeding on pieces of bread from the bakery and sunflower seeds distributed by people situated less than 50 meters from the event. This period (the end of winter/beginning of spring) corresponds to the start of the reproductive season meaning territorial behaviour from potential reproducers and also the existence of differences in body condition between individuals because of the lack of food during winter.

We observed mated pairs starting to build nests in holes below the roofs close to the event (less than 50 meters away). After the aggressive event the four aggressors returned to the building of nests. The victim seemed to be unable to fly or fight off the aggressors.

Considering the fact that we observed the victim alive during the event, was it because of a hurt present before or because of the aggressive event, sickness, our observation cannot bring efficient information to answer.

Discussion

Grubbs (1977) described for the first time for the same species a similar case of intraspecific killing without be able to explain it. One sparrow held the other one by the neck and after a few seconds the struggling victim became still. The attacking sparrow, still on top of the nearly lifeless one, began to hammering on the head of the victim. Several sparrows flew near, then all flew away leaving the motionless body on the ground. Minutes later a sparrow returned, jumped on the dead sparrow and again struck it on the head several times, then flew away. This evidence indicates that House Sparrows are capable of causing mortal wounds on one another.

Kuerzi (1941) presented evidence of intraspecific killing in Tree Swallows *(Tachycineta bicolor)* and reported two fights between a male and a female in brown plumage. During one fight the brown female had the male pinned on the ground, and she pecked at the back of his head until he escaped when Kuerzi approached for a better view. This observation of Kuerzi (1941) is similar to ours with the same 'pecking on the head' behaviour.

In birds, we found additional descriptions of intraspecific killing in avian species including *Egretta sacra*, *Arenaria interpres*, *Passer domesticus*, *Motacilla alba* (Joslin

1964, Grubbs 1977, Crossland 1995, Beckmann 2008). Each time, the attacker(s) killed by pecking on the head of the victim. The potential explanations by those authors are bad body condition or territorial mechanism during reproduction season while the lack of food was never mentioned. During the body inspection of *Arenaria interpres*, Crossland (1995) found the female victim in very poor condition: it weighed only 64.2 grams against a normal average of 100.3 to 170.2 grams (Huston & Barter 1990) while during the body inspection of *Egretta sacra*, Beckmann (2008), it was found that the victim was in poor body condition, and likely starving. In the case of *Motacilla alba*, Joslin (1964) added that there was a new but incomplete nest inside another green house about 50 feet away, where these birds had produced up to three clutches annually for several years. Another common observation of those authors is that there was always more than one attacker (between 2 and 25) and the attackers could be either male or female.

In Passerines (shrikes (Laniidae) excluded), the Great Tit *(Parus major)* is known to be aggressive (until killing by pecking on the head) towards both Passerines (Common Repoll *Carduelis flammea*, Yellowhammer *Emberiza citrinella*, Pied Flycatcher *Ficedula hypoleuca*) and bats (Caris 1958, Barnes 1975, Gosler 1993, Selva *et al.* 2005, Estók *et al.* 2010). This aggressive behaviour of the Great Tit is explained both by lack of food in winter (Drent *et al.* 2003) and territorial mechanism during the reproductive season (Krebs 1982, Drent *et al.* 2003). As we previously explained, we did not observe the beginning of the event and did not see visible injuries on the body of the victim other than the one at the head caused by the aggressive event. Potential contributing factors observed during the event included very localized sources of food (bakery and bird table) and very localized places to nest (roofs). Because of this and considering the period (end of winter and the beginning of the reproductive season), the three explanations of the cited studies (lack of food, bad body condition and territorial mechanism during the reproductive season) could be relevant in our case.

Intraspecific predation is often a function of density. Polis (1981) found 65 reports of increased predation rates due to overcrowding or high densities in birds, fishes and invertebrates (Fox 1975, Polis 1980). There are two possible explanations for this relationship. First, changes in the rate of intraspecific killing occur because predators exhibit density-dependent responses to heterospecific prey as well as for homospecific prey. Second, individuals of many species maintain inter-individual space or territory in which they are intolerant to conspecifics. Crowding caused by the searching for a sexual partner increases the frequency with which conspecifics violate a critical minimum individual distance (intraspecific space) and thus promotes the observed increase in the rate of intraspecific killing. Finally, ethologists have insisted that intraspecific killing and predation in passerines are rare events in the environment. They have stressed that passerine fighting is commonly restrained by ritual, bluff and nonfatal violence (Polis 1981).

In conclusion, it appears that our observation is a very rare one and the second one for the House Sparrow. The literature provides some potential explanations in different cases of intraspecific killing, such as bad body condition, territoriality during reproduction period or lack of food. Considering the period (the end of the winter and the beginning of the reproductive season), all three explanations could be relevant in our case. The lack of knowledge about intraspecific killing in passerines must lead to more specific studies than local observations as ours.

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New species in the Hungarian avifauna in 2013

Tibor Hadarics

Tibor Hadarics 2014. New species in the Hungarian avifauna in 2013. – Ornis Hungarica 22(2): 130–134.

Abstract Three new species appeared in the Hungarian avifauna in 2013: the Black-throated Thrush, the Booted Warbler and the Caspian Plover. A Black-throated Thrush stayed at the Nagyerdő, Debrecen between the 1st and 12th of March. A Booted Warbler was trapped and ringed at the Hortobágy Fishpond on the 25th of May. Finally, a Caspian Plover was observed near Kardoskút on the 15–17th of November. Thus the number of bird species known to occur in Hungary has increased to 409.

Keywords: official bird checklist, Hungarian Checklist and Rarities Committee, Black-throated Thrush, *Turdus atrogularis*, Booted Warbler, *Iduna caligata*, Caspian Plover, *Charadrius asiaticus*

Összefoglalás 2013-ban három faunára új madárfaj bukkant fel Magyarországon: a feketetorkú rigó, a kis geze és a sztyeppi lile. Egy feketetorkú rigó 2013. március 1-től 12-ig tartózkodott a debreceni Nagyerdőben, egy kis gezét 2013. május 25-én gyűrűzés során fogtak a Hortobágyi-halastavon, egy sztyeppi lilét pedig 2013. november 15–17-én figyeltek meg a kardoskúti Fehér-tavon. E fajok előkerülésével a mai Magyarországon bizonyítottan előfordult madárfajok száma 409-re emelkedett.

Kulcsszavak: Magyarország madarainak névjegyzéke, MME Nomenclator Bizottság, feketetorkú rigó, *Turdus atrogularis*, kis geze, *Iduna caligata*, sztyeppi lile, *Charadrius asiaticus*

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In 2013, three bird species were accepted by the Hungarian Checklist and Rarities Committee as new to the Hungarian fauna. These are the Black-throated Thrush (Dezső 2013a), the Booted Warbler (Szilágyi 2013, Dezső 2013b) and the Caspian Plover (Dezső 2014). By these, the number of bird species found in Hungary to date has risen to 409.

Turdus atrogularis Jarocki, 1819
– Black-throated Thrush –

1–12th March, 2013, Debrecen (Hajdú-Bihar County), Nagyerdő, 1 male exemplar (D. Balla and others).

Breeding area of the Black-throated Thrush ranges from the lower Angara and upper Yenisei rivers through the Ob and Irtysh area to the Ural (Clement & Hathway 2000, del Hoyo *et al.* 2005). The distribution area runs into Eastern Europe in a narrow belt where it breeds at the forested foothills of the western part of the Ural Mountains in the coniferous and mixed forests of the middle and northern taiga and the forest-tundra zone (Estafiev *et al.* 1997).

The Eastern European populations are stable, but estimates of population size vary, ranging from 50,000–55,000 (Estafiev *et al.* 1997) to 5000–20,000 (BirdLife International 2004). A northwestwards area expansion is predicted due to climate change (Huntley *et al.* 2007).

Overwintering sites of the Black-throated Thrush are in Iran, Afghanistan, Pakistan and Northern India (del Hoyo *et al.* 2005), evident of a north-southward migration route, thus, Western and Northern European occurrences cannot be explained by reverse migration (Lees & Gilroy 2009). These, however, are the result of some kind of disturbance in the birds` navigation system or of post-breeding random scatter autumn migration (Gilroy & Lees 2003). The apparent increase of West-European occurrences may possibly be explained by the increase of observation intensity.

More than 60 records are reported up until 2007 from the British Isles, mainly from late September to mid November, with a peak in mid October. Records are rarer for the winter period (December–February), and spring occurrences (March–April) are only known since the first half of the 1990's (Slack 2009). Most European occurrences were reported from the northwestern parts of the continent: Sweden >30, Norway >25, Finland >35, with regular sightings also from Denmark and Iceland (Slack 2009). Other data include: France >10, Germany >40, Poland >10, Italy >25, also the Netherlands, Belgium, Bulgaria, Greece and Spain (Lewington *et al.* 1991, Slack 2009). Out of the countries neighbouring Hungary, it was only reported from Austria (nine sightings). More than half of these data are dated to the 19th century. Two cases from Eastern Austria are of particular interest: one specimen at Semmering (Styria) in December 1993 (Mayer 1995), and one immature (2y) male in a garden at Oberpullendorf (Burgenland) in January and February 2003 (Brandner *et al.* 2003).

The Black-throated Thrush was first observed in Hungary on 1st March, 2013 in Debrecen. The bird was sighted every day during the next week until 7th March, and it was also seen on 12th March. The immature (2y) bird based itself around Lake Békás in the Nagyerdő at Debrecen, and was often observed at the fountain behind the spa and on the poplar and pine trees alongside the lake (Dezső 2013a). The occurrences of this species in Europe can be best explained by the northwestward and southwestward autumn dispersion of young birds (Slack 2009). Spring occurrences are rarer, when probably overwintering individuals are seen. Black-throated Thrushes can most frequently be observed in Fieldfare *(Turdus pilaris)* and Redwing *(Turdus iliacus)* flocks. The East-European and Siberian populations of these two common species migrate in an east–west direction, with overwintering sites situated in Europe, as evidenced by re-captures of ringed individuals (Milwright 1994). Black-throated Thrushes might arrive to Europe from Siberia mixed among such huge thrush flocks (Slack 2009).

Iduna caligata (Lichtenstein, 1823)
– Booted Warbler –

25th May, 2013, Hortobágy (Hajdú-Bihar County), Hortobágy Fishpond, 1 *ad.* exemplar (A. Szilágyi and others).

Breeding area of the Booted Warbler extends from the upper Yenisei river through the Ob and Irtysh area and the Ural Mountains to Lake Ladoga and Onega in the northwest and the Donetsk in the southwest (del Hoyo *et al.* 2006). In the East European part of the distribution range, it breeds mostly in riverbeds in knee-high shrublands dominated by *Spirea* spp., different legume species and low-growing willows (Morgan & Shirihai 1997).

A westward area expansion began in the second half of the 1970s from the northwestern part of its distribution range, during which it reached Saint Petersburg in the 1990's where it bred for the first time in 1997 (Slack 2009). In Finland, the first specimen was observed in 1981, followed by the observation of a revier-keeping male bird in 1986 and the first breeding pairs in 2000 (Kivivuori 2000). Since then, several revier-keeping males have been observed mostly in the eastern part of the country. Breeding is also probable, but it could not be proved for each year (Lindblom 2008). Between 1990 and 2000, the population size in the European part of Russia was estimated to be 30,000–80,000 pairs, for Finland, this was cca. 30 pairs between 2000 and 2002 with an increasing trend (BirdLife International 2004).

It is a rare vagrant in European countries west of its breeding areas. Most of its 115 occurrences in the British Isles are dated after 1975; it was deemed very rare before that year. However, since the late 1970's, there is an increase in occurrence data, indicating a westward area expansion of the species. British sightings are mostly from the late August to late October period (Slack 2009), which point to the reverse migration of young birds (Gilroy & Lees 2003, Lees & Gilroy 2009). Interestingly, the average arrival date of birds in the British Isles shifted ten days earlier in two decades (Slack 2009). Further autumn records are known from Estonia, Sweden, Norway, Denmark, The Netherlands, Belgium, France and Germany (Lewington *et al.* 1991). There is only one report from countries neighbouring Hungary: Austria, Rheindelta, September 1997 (Ranner 2002).

In Hungary, a Booted Warbler was caught and ringed on 25th May, 2013 on the southern part of the main dam of the Hortobágy Fishpond by Attila Szilágyi in the course of the CES bird ringing program (Szilágyi 2013, Dezső 2013b). This was not only the first record of the species in Hungary, but also in the Carpathian Basin as a whole.

Most occurrence data of the species in Europe are from the late August to early November period, dominated by young birds displaying reverse migration. Spring occurrences are very rare. The Hungarian datum from May can possibly be explained in two alternative ways. Either a young bird that overwintered in Western Europe migrated towards its breeding area, or, alternatively, a bird returning from East-Indian wintering areas performed overshooting.

Charadrius asiaticus Pallas, 1773
– Caspian Plover –

15–17th November, 2013, Kardoskút (Békés County), Lake Fehér, 1 *juv.* exemplar (Á. Kaczkó, Zs. Ampovics and others).

Breeding area of the Caspian Plover ranges from the steppes north and east of the Caspian Sea through the Central Asian deserts, semi-deserts and steppes to Lake Zaysan (del Hoyo *et al.* 1996). A small part of the distribution area runs into Europe west of the Ural river (Caspian Lowlands, Manych River valley) (Belik 1997).

In the middle of the 20th century, the northwestern border of its distribution area extended towards northwest, however, it has not changed since then (Belik 1998). The size of its European population was estimated to be 200–250 pairs between 1990 and 2000 by Belik (1997, 1998), and 130–500 pairs by BirdLife International (2004). The population size showed a considerable decline between 1970 and 1990, with no signs pointing to a halt in this trend, although there are no data to confirm it (BirdLife International 2004). The distribution range of the species is expected to expand westwards due to climate change (Huntley *et al.* 2007).

It is a rare spring and summer vagrant in Europe, i.e. in the British Isles, Norway, Finland, France, the Netherlands, Germany, Italy, Malta, Greece and Bulgaria (Lewington *et al.* 1991). Its only record from countries neighbouring Hungary was from Romania (Istria, May 1979) (Zimmerli 1980, Kiss 1980).

In Hungary, a young specimen of the Caspian Plover was observed for the first time by Ádám Kaczkó and Zsolt Ampovics on 15th November, 2013 in the afternoon at Lake Fehér near Kardoskút, in the company of Northern Lapwings *(Vanellus vanellus)* and European Golden Plovers *(Pluvialis apricaria)*. During the following two days, it was also seen by others observers at the same location, and several demonstrative photos were taken (Dező 2014). This was not only the first record of the species in Hungary, but also in the Carpathian Basin as a whole.

Most occurrence data of the species in Europe are from the spring and summer period, when adult birds, returning from the South and East African wintering sites, are drifted westwards from their breeding areas by weather events. The considerably fewer autumn sightings of young birds can possibly be explained by their pre-migratory multi-directional roaming.

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