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# Nesting success and productivity of the Common Barn-owl *Tyto alba*: results from a nest box installation and long-term breeding monitoring program in Southern Hungary[x]

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**Abstract** In this study, the results of a long-term nest box installation program of the Common Barn-owl *Tyto alba* (Scopoli, 1769) in Southern Hungary were evaluated, which program was conducted during a 24-year period (1995–2018). The percentages of occupied nest boxes ranged from 9.72 to 73.44% in the first breeding periods while this varied between 0 and 41.46% in the case of repeated clutches in the same nest boxes with second broods. A total of 1,265 breeding attempts were recorded including 1,020 (80.63%) in the first and 245 (19.36%) in the second breeding periods, from which a total of 210 (16.6%) clutches did not produce any fledglings. The modal clutch size was 7 eggs in both first and second annual clutches. However, the value of productivity was higher in the case of larger clutch sizes and we found significant linear relationship between initial clutch size and fledgling production per nesting attempt in both breeding periods. Significant variation of reproductive parameters was observed among the years. The proportion of egg loss showed significant decline, while the change of hatching success and the variation of annual productivity showed significant slight positive linear trend during the 24 years. Our results suggested that despite the outlier values of reproduction characteristics in the extreme years with negative effect, a relatively stable Common Barn-owl population can be maintained by the placement of nest boxes in the investigated region.

Keywords: nest box occupancy, clutch size, eggs and hatching losses, productivity

**Összefoglalás** Jelen tanulmányban a gyöngybagoly, *Tyto alba* (Scopoli, 1769) 24 év során (1995–2018) Dél-Magyarországon megvalósított hosszú távú költőláda telepítési programjának eredményeit értékeltük. A ládafoglalási arány az első költéseknél 9,72 – 73,44%, míg a másodköltések során ugyanabban a költőládában megismételt fészkelések aránya 0 – 41,46% között változott. Összesen 1265 megkezdett költést, 1020 (80,63%) első és 245 (19,36%) másodköltést regisztráltunk, melyekből összesen 210 (16,6%) költés nem produkált kirepülő fiókát. Mind az első, mind a másodköltéseknél a 7 tojásos fészekalj volt a leggyakoribb. A produktivitás értéke a nagyobb fészekalj méreteknél nagyobb volt, és mindkét költési periódusban szignifikáns lineáris összefüggést találtunk a kezdeti fészekalj méret és a megkezdett fészkelésekre vonatkozatott kirepülő fiókaprodukció között. A szaporodási paraméterek tekintetében évek közötti szignifikáns eltérést figyeltünk meg. A tojás veszteség aránya szignifikáns csökkenő, míg a kelési siker és az éves produktivitás változása enyhe, de szignifikáns pozitív trendet mutatott a 24 év során. Eredményeink azt sugallják, hogy a negatív hatású extrém években a szaporodási karakterisztikák kiugró értékei ellenére a vizsgált régióban a költőládák kihelyezésével viszonylag stabil gyöngybagoly populáció tartható fenn.

Kulcsszavak: költőláda foglalás, fészekalj méret, tojás és fióka veszteség, produktivitás

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## Introduction

The Common Barn-owl *(Tyto alba)*, as a cosmopolitan nocturnal raptor is characterized with worldwide distribution because it occurs in all the continents except Antarctica (Bunn *et al*. 1982, Taylor 1994, Gill & Donsker 2018). Within the areas of its range, Common Barn-owl was distributed across many biomes (continental steppes, savannas, pampas, rainforests), especially in preference to open fields and farmlands in the temperate region of South and North America as well as Europa (Taylor 1994, Roulin 2002a). As a secondary cavity-nesting bird, due to the limited availability of natural nesting and roosting sites, Common Barn-owl switched to using the open man-made structures, especially church towers and traditional farm buildings (Taylor 1994, Ramsden 1998, Golawski *et al*. 2003, Meyrom *et al*. 2008, Mainwaring 2015).

Despite the wide distribution and the successful adaptation to the anthropogenic environment, the decline of local populations of Common Barn-owl was reported already from the mid-80s (Colvin 1985, Shawyer 1987, Percival 1991, de Bruijn 1994, Taylor 1994, Heath *et al*. 2000, Toms *et al*. 2001) and was confirmed by a synthesis of its population size data in many regions (BirdLife International 2004). This population decline was caused by several factors such as the loss of suitable roosting and nesting sites (Taylor 1994, Ramsden 1998, Hindmarch *et al*. 2012), the loss of hunting areas especially the grassland due to land use conversions and the increase in agricultural activity which has influenced the available small mammal populations as main prey groups (Colvin 1985, Taylor 1994, Love *et al*. 2000, Askew *et al*. 2007), chemical poisoning by anticoagulant rodenticide (Newton *et al*. 1994, Gray *et al*. 1994, Albert *et al*. 2010, Geduhn *et al*. 2016) as well as the mortality effect of traffic and roads (Fajardo 2001, Boves & Belthoff 2012, Borda-de-Água *et al*. 2014, De Jong *et al.* 2018, Šálek *et al*. 2019).

However, numerous short and long-term studies have demonstrated that the application of nest boxes as artificial cavities is an appropriate practice to compensate for the effect of the factors causing the decrease of the populations and breeding successes (Marti *et al*. 1979, Johnson 1994, Leech *et al*. 2009, Mainwaring 2011), and to increase the pest control effect of Common Barn-owls (Meyrom *et al*. 2009, Kan *et al*. 2013, Paz *et al*. 2013, Kross *et al*. 2016, Wendt & Johnson 2017). The costs and benefits of man-made structures as nesting sites, especially in the case of artificial nest boxes were evaluated and contested (Johnson 1994, Møller 1994, McCafferty *et al*. 2001, Lambrechts *et al.* 2010, 2012, Mainwaring 2011, 2015). Although the earlier studies demonstrated that the application of nest boxes increased the clutch size and breeding success compared to natural nesting sites (Marti *et al*. 1979, Johnson 1994), the advantages of nest boxes were questioned by a Hungarian study, which showed that the survival of owls differed between the artificial nest box and the 'natural' environment of a church tower (Klein *et al*. 2007). Moreover, in the case of the artificial nest box application, more species could occupy the same nest boxes which realise competitive situation or predation (Charter *et al*. 2010a) such as the interspecific offspring killing which was reported in the interaction between Tawny Owl *(Strix aluco)* and Common Barn-owl (Mátics *et al*. 2008).

Nesting and breeding success of Common Barn-owls were investigated from more aspects covering the impact of habitat variability, land-use and landscape context of the hunting area (Martínez & Zuberogoitia 2004, Bond *et al*. 2005, Meek *et al*. 2009, Frey *et al*. 2011, Charter *et al*. 2012), the effect of urbanisation (Salvati *et al*. 2002, Hindmarch *et al*. 2014) and agricultural land use, such as intensive farming practise, restoration of the agricultural sector, ecological compensation areas (Leech *et al*. 2009, Arlettaz *et al*. 2010, Martin *et al*. 2010, Milchev & Gruychev 2014, Almasi *et al*. 2015), as well as the change of population size (Toms *et al*. 2001, Altwegg *et al*. 2006a, De Jong 2009). The studies of Common Barn-owl's breeding ecology demonstrated that the reproductive output and so the local size and survival of its populations were determined basically by habitat and nest-site qualities (Gubanyi *et al*. 1992, Bond *et al*. 2005, Frey *et al*. 2011), food supply, in particular the availability and density fluctuation of main prey species or groups (Taylor 1994, Klok & de Roos 2007, Charter *et al*. 2015, Pavluvčík *et al*. 2015), and weather conditions (Chausson *et al*. 2014a, Charter *et al*. 2017) especially extreme winters (Marti & Wagner 1985, 1997, Taylor 1992, Marti 1994, Altwegg *et al*. 2006b, Chausson *et al*. 2014b). The reproductive success of Common Barn-owls was investigated at the border of its distribution range where the lifetime productivity was determined significantly by winter weather, particularly the additive effect of cold temperature and the higher snow cover (Marti 1994, 1997, Tóth *et al*. 2004). Due to a severe winter, a large decline in the effective number of Common Barn-owls can lead to genetic bottlenecks, which has been investigated in a local population in Hungary (Mátics *et al*. 2017).

Clutch size, as one of the most important life history traits of birds (Lack 1947, Stearns 1976, Price & Liou 1989), has been assessed in detail in the breeding ecology of Common Barn-owls such as the comparison of first, replacement and second clutches (Marti 1994, Martínez & López 1999, Frey *et al*. 2011), seasonal (Baudvin 1986, Marti 1994, Roulin 2002b) and annual variation (Martínez & López 1999, Toms *et al*. 2001), and in relation to the abundance of main prey (Taylor 1994, Pavluvčík *et al*. 2015). Nevertheless, the variation of breeding characteristics related to initial clutch size and relationship between clutch size and productivity were evaluated only in a few studies on Common Barn-owls (Wilson *et al*. 1986, Johnson 1994, Martínez & López 1999). Lack (1947, 1954) proposed that clutch size corresponds to maximum number of young that parents can rear, and as the consequence of natural selection, the most productive clutch size is the most frequent. In contrast, numerous studies of birds demonstrated that the most frequent clutch size is smaller than the most productive which was determined by a trade-off between clutch size and future reproductive success (Stearns 1976, Partridge & Harvey 1988, Godfray *et al*. 1991). However, modal clutch size was the most productive clutch in case of Common Barn-owls in the Mediterranean region, and no significant variation was found between years in the average clutch size (Martínez & López 1999).

Birds of prey and owls, particularly Common Barn-owls were characterised by hatching asynchrony, which is an adaptive breeding strategy for producing marginal offspring (Clark & Wilson 1981, Stoleson & Beissinger 1995) and causes intra-brood size hierarchy and conflict (Viñuela 1999, 2000, Roulin *et al.* 1999, 2004). Numerous hypotheses have been proposed to explain asynchronous hatching (Clark & Wilson 1981, Stenning 1996). According to the 'brood reduction hypothesis' (Lack 1954), hatching asynchrony is an adaptive trait resulted in the mortality of the smallest offspring when food supply is low and not enough for parents to raise all hatchlings. In case of Common Barn-owl, the 'sibling negotiation hypothesis' was developed to understand the mechanism of competition between nestlings of different age, which highlighted the importance of nutritional need asymmetry between siblings (Roulin 2002b, 2004). Although the smaller nestlings can compensate their weaker competitive ability through the negotiation mechanism (Roulin 2004), the occurrence of brood reduction is frequent in the case of Common Barn-owls (Taylor 1994, Roulin 2002c), which can be realised in different behavioural mechanisms, such as lethal attacks on smaller siblings or siblicide (Mock 1985) and cannibalism (Baudvin 1978, Hamilton 1980, Roulin & Dreiss 2012). Furthermore, the results of video observation suggested that the risk of brood reduction increases as the female starts foraging after hatching, since access to food is reduced for the youngest nestling (Durant *et al.* 2004). It has also been proposed that the Common Barn-owl's female adjusts clutch size to the male's efficiency to feed the nestlings and herself in order to optimise fledging success (Durant *et al.* 2010). The level of brood reduction is an important and measurable feature of Common Barn-owls' breeding biology (Hindmarch *et al.* 2014) which can significantly influence reproductive success.

The objectives in this study are to evaluate the results of a long-term Common Barn-owl nest box installation and monitoring program in Southern Hungary, examining the variation of observed and calculated breeding characteristics, comparing first and second annual clutches (1), the relationship between clutch size and breeding success focusing on productivity (2) and the multi-annual change of reproductive output (3).

## Material and methods

### Study area, nest box installation and control protocol

Nest box installation and the breeding monitoring of Common Barn-owl was carried out in Baranya county (4429.6 km²) (46°04′N, 18°14′ E) which is situated in the south-eastern part of the Transdanubian region in Southern Hungary. The environmental conditions of this county are favourable for Common Barn-owls. The climate is determined by Mediterranean and sub-Mediterranean effect and is characterized by a high number of sunshine hours, relatively low fluctuations of temperatures and mild winters. Due to relatively high winter temperatures, the number of snow-covered days are low. The spatial structure of the county is characterized with a multitude of small villages, with 301 settlements altogether that actually represent 340 separate units of built and populated surface. The average administrative

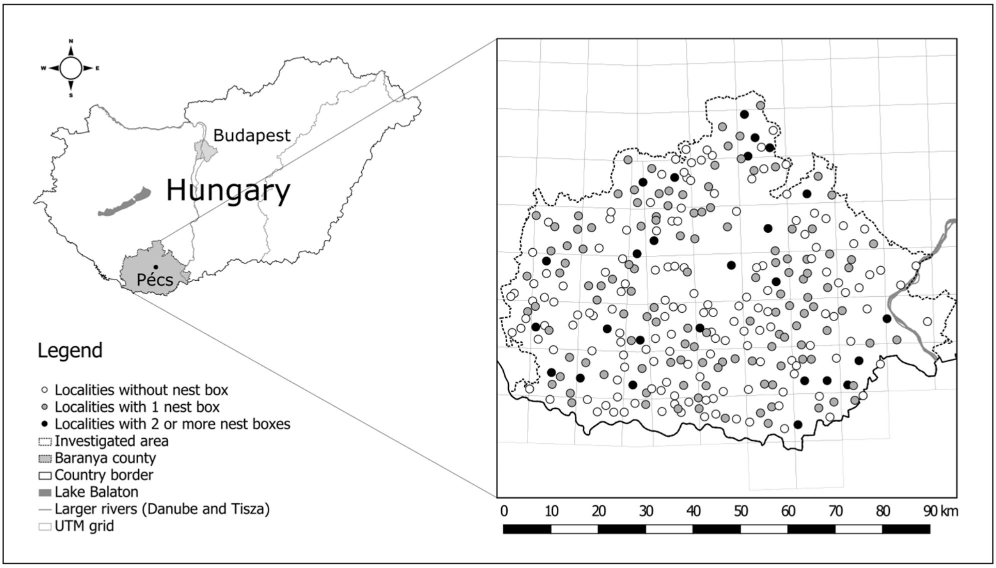

*Figure 1.* Spatial distribution of installed Common Barn-owl nest boxes in South-Hungary, Baranya County

*1. ábra* A kihelyezett gyöngybagoly költőládák térbeli eloszlása Dél-Magyarországon, Baranya megyében

area of the villages slightly exceeds 1,500 hectares. In 96% of the settlements, at least one church tower or chapel can be found and 21% have more such buildings.

A total of 163 nest boxes were placed in different buildings (95% in church towers, 5% in chapels and lofts of farm buildings) progressively from 1995 to 2018. The nest boxes were placed in a total of 150 settlements, 82% of which had one and 18% had more than one boxes *(Figure 1)*. The number of available nest boxes for Common Barn-owls in the consecutive years was determined by the number of installed new and removed nest boxes (due to dilapidation of boxes and church tower renovation). During the monitoring period, the number of settlements as nest site localities varied between 41 and 137 (108.16 ± 5.47 per year).

Nest boxes, measuring 100×50×50 cm were made from good quality pine boards, with a 15×15 cm entrance, a partition wall in the middle and a removable roof. The orientation of nest boxes within the towers was determined by the location of bell structures (racks, bins). Depending on these, the direction of east was preferred at the installation of net boxes. If this was not possible, the nest box was placed with western, southern or occasionally northern orientation. In the latter case, a dividing wall was built in the nest box for wind protection. In church towers, chapels and farm buildings nest boxes were placed 20–40 m and 4–10 m high, respectively.

During the 24 years, the nest boxes were regularly visited in the breeding season including first and second annual clutches to determine whether they were occupied or not by breeding pairs. Criterions of controls were determined by climate condition of Baranya county and life-history strategies and traits of Common Barn-owl. During the monitoring periods, the first visits were conducted between 1–15 April. However, the controls were started 8–10 days earlier after a mild winter. In the case of non-occupied nest boxes, controls were carried out until mid-September (4–5 times a year) and in the case of occupied nest boxes until the end of the second clutches, usually until mid-October. During the 24-year monitoring program, nest box checkings were implemented by volunteers (50–60 people) of the Baranya County Group of BirdLife Hungary based on a protocol developed for this purpose. The data were sent to the coordinator after each control. The date of the next visit was determined from the conditions observed at the first occasion (empty nest box, eggs, etc.). In addition, to evaluate the diet composition of Common Barn-owl pairs, pellet samples were collected from the nest boxes each time a control visit was executed.

### Observed and calculated breeding parameters

At each sampling locality, the presence/absence of Common Barn-owls and their breeding status were recorded. Nest boxes in which at least one egg was found, were considered 'occupied' (active nest) (Steenhof 1987, Charter *et al*. 2010b, Frey *et al*. 2011). The proportion of nest box occupancy was calculated from the number of occupied nest boxes in the first annual clutches, while in the second annual breeding seasons, this proportion was obtained relative to the occupied nest boxes by breeders of the first annual clutches. Furthermore, occupancy rate was calculated in the case of the breeding pairs which occupied a nest box and laid eggs only in the second annual breeding periods. Based on the total number of breeding attempts, nesting success was calculated as the proportion of pairs that raised at least one fledgling, and the percentage of unsuccessful pairs was also determined (Steenhof & Newton 2007). The following breeding parameters were recorded: clutch size, brood size at hatching and fledging. To determine reproduction loss, two more parameters were calculated: the number and proportion of unhatched eggs and brood reduction. Hatching success was calculated as the percentage of eggs that hatched within each clutch, and fledging success was obtained as the percentage of young that fledged from each brood. Reproductive success was calculated as the percentage of fledged young per eggs from each successful nest. In addition, productivity was defined as the rate of the number of fledglings per nesting attempts (Martínez & López 1999, Steenhof & Newton 2007) or per all observed breeding pairs (including unsuccessful breeders) which, as standardized fledging success value (Sasvári & Hegyi 2011, Hindmarch *et al*. 2014), is suitable for comparing productivity between different clutch sizes and years. In the first step, productivity was calculated from the number of young produced in all successful nests and from the cumulative number of fledglings considering initial clutch size. Secondly, annual productivity was determined from the pooled quantity of fledglings and nesting attempts of different years.

### Statistical methods

The results of nest box occupancy and proportion of occupied boxes were presented as range and mean ± SE from the first annual clutches, both in case of occupied nest boxes where the clutches were repeated by the nesting pairs and in case of nest boxes were the clutches were detected only in the second annual breeding periods. To assess the statistical difference of clutch failure and nesting success proportions between the first and second annual clutches, chi-square test was applied in the software R with the command prop.test. As regards all successful nests, the amount of all breeding parameters per nest and per year are presented as range and mean ± SE from the first and second annual clutches as well as from the whole annual breeding period, respectively. The distribution of clutch size, brood size, fledglings and annual productivity were represented with histograms and overlaid smoothed histograms with first and second order smoother in case of first and second annual clutches and total breeding seasons, respectively.

According to initial clutch sizes for which the exact reproductive history was detected, the cumulative number of breeding parameters, the percentage value of different successes and the calculated productivity rate as well as their mean and 95% confidence interval were presented in tables (clutch sizes only occurring once were excluded from the assessment) separately for the first and second annual breeding season. Considering different clutch sizes, the prop.test function was used to evaluate the difference in the proportion of unhatched eggs and brood reduction between the first and second annual breeding season, as well as in comparison of the proportion of egg and nestling losses within the given breeding periods. Boxplots (mean ± SE, lower and upper limits of 95% confidence interval) were used to present the annual variation of observed and calculated breeding parameters. The standard error and 95% confidence interval of mean were calculated in R using the 'Plotrix' (Lemon 2006) and 'Rmisc' (Hope 2016) package.

Mann-Whitney's U-test and the Kruskal-Wallis test (followed by Dunn's post hoc test for multiple comparisons) were used to compare the amount of breeding parameters between the first and second annual clutches and among the different years, respectively (Zar 2010).

Based on the data of all successful nests, linear regression method was used to assess the relationship between clutch size and productivity. Furthermore, linear regression was performed also to analyse the trend of variation of unhatched eggs, hatching success and annual productivity for the period 1995–2018. All statistical analyses were conducted in the R v3.4.0 environment (R Core Team 2017). Statistical tests were considered as significant at the level $P \leq 0.05$ as standard in all analyses (Sokal & Rohlf 1997).

## Results

### Nest box occupancy, number of breeding attempts and nesting success

During the 24 years, the total number of installed nest boxes varied between 43 and 163 (126.58 ± 6.91 per year) while nest box occupation ranged from 7 to 94 (42.5 ± 4.29 per year) in the first annual clutches. Considering Common Barn-owl pairs which occupied successfully a nest box in the first annual breeding season, the clutches were repeated in 2 to 26 nest boxes (8.37 ± 1.46 per year) in the second nesting periods. The number of boxes where the clutches were produced only in the second annual breeding seasons ranged from 1 to 11 (1.83 ± 0.54 per year). The percentage of occupied nest boxes ranged from 9.72 to 73.44% (34.22 ± 3.37%) in the first breeding periods, while the proportion of occupied nest boxes in the second annual clutches relative to the cumulative number of first nest box occupancy varied between 0% and 41.46% (18.58% ± 2.17%). In the case of breeding pairs for which nesting was detected only in the second annual periods, nest box occupancy rate varied between 0% and 9.02% (1.66% ± 0.47%).

Based on the results of nest box occupancy, 1,265 breeding attempts were recorded including 1,020 (80.63%) nesting attempts in the first and 245 (19.37%) in the second breeding

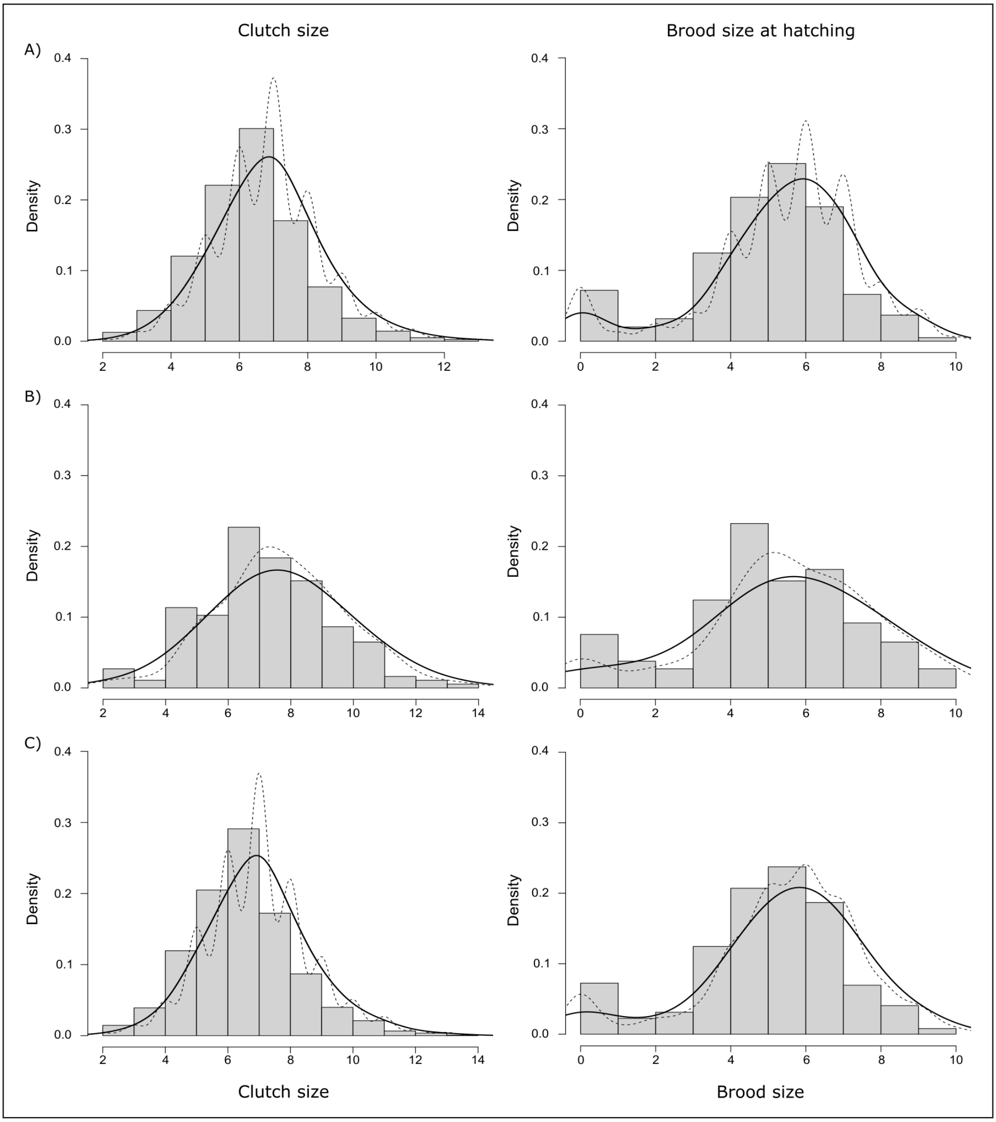

*Figure 2.* Histograms and smoothed histograms with first (dashed line) and second (solid line) order smoother of clutch size and brood size distribution in the first (A) and second (B) annual clutches as well as in whole breeding period (C)

*2. ábra* A fészekalj nagyság és a kikelt fiókaszám eloszlásának hisztogramja és simított hisztogramja első (szaggatott vonal) és másodrendű (folytonos vonal) simítással az első- (A) és másodköltés (B) esetén, valamint a teljes szaporodási időszakban (C) periods. From the total number of breeding attempts, 210 (16.6%) clutches did not produce any fledglings. Comparing the two annual nesting periods, the percentage of clutch failure was almost similar: 16.17% (165 out of 1,020 clutches) of the first and 18.37% (45 out of 245 clutches) of the second annual clutches did not produce fledglings. Thus, calculated nesting success was 83.39% (1055 productive clutches out of 1,265 nesting attempts) in the case of the total annual breeding season while 83.82% (855 out of 1,020 nesting attempts) of the first annual clutches and 81.63% (200 out of 245 nesting attempts) of the second annual clutches were successful where at least one young was produced by the breeding pairs. In the case of both successful and failed clutches, the number of nestlings did not differ from a homogeneous distribution in the comparison of the two annual breeding periods ($\chi^2 = 0.53$, $P = 0.464$).

## Clutch size, brood size and hatching success

From the total of 1,265 breeding attempts, 982 clutches ($N = 797$ for first and $N = 185$ for second annual clutches) were recorded where the complete reproductive history was known. Based on the sample size, the average size per nest of first clutches was 6.84 ± 0.05 eggs,

*Table 1.* Cumulative number and percentage value of Common Barn-owl breeding parameters in relation to initial clutch size for clutches where complete reproduction history was detected in the first annual breeding period

*1. táblázat* A gyöngybagoly költési paramétereinek összesített és százalékos értéke a kezdeti fészekalj méretek függvényében, melyeknél detektáltuk a teljes reprodukciós történetet az első költés időszakában

| **Clutch size** | **# of nesting attempts** | **# of clutches (complete history)** | **Total eggs** | **Unhatched eggs** | | **Eggs hatched** | | **Brood reduction** | | **Young fledged** | | **Productivity** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *n* | **%** | *n* | **%** | *n* | **%** | *n* | **%** | |
| 2 | 1 | 1 | 2 | 2 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 9 | 7 | 21 | 7 | 33.33 | 14 | 66.67 | 3 | 21.43 | 11 | 78.57 | 1.56 |
| 4 | 37 | 36 | 144 | 28 | 19.44 | 116 | 80.56 | 29 | 25.00 | 87 | 75.00 | 3.14 |
| 5 | 106 | 97 | 485 | 96 | 19.79 | 389 | 80.21 | 47 | 12.08 | 342 | 87.92 | 3.67 |
| 6 | 210 | 184 | 1104 | 170 | 15.40 | 934 | 84.60 | 158 | 16.92 | 776 | 83.08 | 4.45 |
| 7 | 272 | 240 | 1680 | 338 | 20.12 | 1342 | 79.88 | 235 | 17.51 | 1107 | 82.49 | 4.93 |
| 8 | 161 | 130 | 1040 | 221 | 21.25 | 819 | 78.75 | 156 | 19.05 | 663 | 80.95 | 5.09 |
| 9 | 77 | 61 | 549 | 110 | 20.04 | 439 | 79.96 | 82 | 18.68 | 357 | 81.32 | 5.70 |
| 10 | 32 | 28 | 280 | 88 | 31.43 | 192 | 68.57 | 23 | 11.98 | 169 | 88.02 | 6.00 |
| 11 | 8 | 8 | 88 | 37 | 42.05 | 51 | 57.95 | 5 | 9.80 | 46 | 90.20 | 6.38 |
| 12 | 4 | 4 | 48 | 29 | 60.42 | 19 | 39.58 | 3 | 15.79 | 16 | 84.21 | 4.75 |
| 13 | 1 | 1 | 13 | 4 | 30.77 | 9 | 69.23 | 0 | 0 | 9 | 100 | 9 |

*Table 2.* Cumulative number and percentage value of Common Barn-owl breeding parameters in relation to initial clutch size for clutches where complete reproduction history was detected in the second annual breeding period

*2. táblázat* A gyöngybagoly költési paramétereinek összesített és százalékos értéke a kezdeti fészekalj méretek függvényében, melyeknél detektáltuk a teljes reprodukciós történetet a másodköltés időszakában

| **Clutch size** | **# of nesting attempts** | **# of clutches (complete history)** | **Total eggs** | **Unhatched eggs** | | **Eggs hatched** | | **Brood reduction** | | **Young fledged** | | **Productivity** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *n* | % | *n* | % | *n* | % | *n* | % | |
| 2 | 2 | 2 | 4 | 0 | 0 | 4 | 100 | 0 | 0 | 4 | 100 | 2 |
| 3 | 3 | 3 | 9 | 2 | 22.22 | 7 | 77.78 | 3 | 42.86 | 4 | 57.14 | 1.33 |
| 4 | 3 | 2 | 8 | 4 | 50 | 4 | 50 | 1 | 25 | 3 | 75 | 1 |
| 5 | 22 | 21 | 105 | 31 | 29.52 | 74 | 70.48 | 18 | 24.32 | 56 | 75.68 | 2.55 |
| 6 | 23 | 19 | 114 | 21 | 18.42 | 93 | 81.58 | 20 | 21.51 | 73 | 78.49 | 3.17 |
| 7 | 51 | 42 | 294 | 99 | 33.67 | 195 | 66.33 | 65 | 33.33 | 130 | 66.67 | 2.55 |
| 8 | 40 | 34 | 272 | 59 | 21.69 | 213 | 78.31 | 44 | 20.67 | 169 | 79.34 | 4.23 |
| 9 | 30 | 28 | 252 | 77 | 30.56 | 175 | 69.44 | 36 | 20.57 | 139 | 79.43 | 4.63 |
| 10 | 18 | 16 | 160 | 45 | 28.13 | 115 | 71.88 | 23 | 20 | 92 | 80 | 5.11 |
| 11 | 14 | 12 | 132 | 39 | 29.55 | 93 | 70.45 | 16 | 17.2 | 77 | 82.8 | 5.5 |
| 12 | 3 | 3 | 36 | 10 | 27.78 | 26 | 72.22 | 1 | 3.85 | 25 | 96.15 | 8.33 |
| 13 | 2 | 2 | 26 | 16 | 61.54 | 10 | 38.46 | 2 | 20 | 8 | 80 | 4 |
| 14 | 1 | 1 | 14 | 7 | 50 | 7 | 50 | 1 | 14.29 | 6 | 85.71 | 6 |

7.71 ± 0.15 eggs for second clutches and 7.01 ± 0.05 eggs for the total annual breeding periods. The relative frequency distribution of clutch size and brood sizes at hatching observed during the monitoring period are given in *Figure 2*. Both in first and second clutches as well as in the case of all clutches, modal clutch size was 7 eggs which was detected with highest frequency (first annual clutches: 30.11%, second clutches: 22.7%, the entire annual periods: 28.72% of clutches) *(Figure 2)*. Although modal clutch size was equal in both nesting periods, clutches of 6 eggs were detected with the second highest frequency in the first annual clutches (23.09%), while the clutches of 8 eggs were also characterized with higher proportion in the second clutches (18.38%). The clutches of 6–7 eggs were typical for 53.2% of total clutches in the first and clutches of 7–8 eggs were typical for 41.08% of total clutches in the second nesting periods *(Figure 2)*. As a result we found significant difference in clutch size between first and second annual clutches (Mann-Whitney U-test: $Z = 5.66$, $P < 0.001$).

The numbers of unhatched eggs per nest ranged from 0 to 13 (1.57 ± 0.06) in the total annual breeding season while it changed between 0 and 12 (1.42 ± 0.07) in the first and 0 to 13 (2.22 ± 0.15) in the second annual clutches. The loss of eggs was significantly higher in the first than in the second annual nesting period (Mann-Whitney U-test: $Z = 5.65$, $P < 0.001$). In the case

*Table 3.* Variation of the main and 95% confidence interval of breeding parameters in relation to initial clutch size for clutches where complete reproduction history was known in the first annual breeding period

*3. táblázat* A költési paraméterek átlag és 95%-os konfidencia intervallum értékeinek eltérése a kezdeti fészekalj méretek függvényében, melyeknél ismert a teljes reprodukciós történet az első költés időszakában

| **Clutch size** | **Unhatched eggs** | | **Eggs hatched** | | **Brood reduction** | | **Young fledged** | | **Reproductive success** | | **Productivity** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* |
| 3 | 1.00 | -0.07-2.07 | 2.00 | 0.93-3.07 | 0.43 | -0.30-1.16 | 1.57 | 0.40-2.75 | 52.38 | 13.16-91.61 | 1.07 | 0.30-1.85 |
| 4 | 0.78 | 0.35-1.21 | 3.22 | 2.79-3.65 | 0.81 | 0.35-1.25 | 2.42 | 1.86-2.97 | 60.42 | 46.50-74.33 | 1.89 | 1.45-2.33 |
| 5 | 0.99 | 0.69-1.29 | 4.01 | 3.71-4.31 | 0.48 | 0.28-0.69 | 3.53 | 3.19-3.86 | 70.52 | 63.83-77.20 | 2.74 | 2.47-3.02 |
| 6 | 0.92 | 0.71-1.13 | 5.08 | 4.87-5.29 | 0.86 | 0.66-1.06 | 4.22 | 3.95-4.49 | 70.29 | 65.80-74.78 | 3.36 | 3.16-3.59 |
| 7 | 1.41 | 1.18-1.63 | 5.59 | 5.37-5.82 | 0.98 | 0.82-1.14 | 4.61 | 4.37-4.85 | 65.89 | 62.47-69.31 | 3.66 | 3.47-3.86 |
| 8 | 1.70 | 1.38-2.02 | 6.30 | 5.98-6.62 | 1.20 | 0.94-1.46 | 5.10 | 4.75-5.45 | 63.75 | 59.42-68.08 | 4.12 | 3.83-4.40 |
| 9 | 1.80 | 1.22-2.39 | 7.20 | 6.61-7.78 | 1.34 | 0.89-1.80 | 5.85 | 5.22-6.49 | 65.03 | 57.96-72.09 | 4.69 | 4.16-5.22 |
| 10 | 3.14 | 2.12-4.17 | 6.86 | 5.93-7.99 | 0.82 | 0.83-1.32 | 6.04 | 5.02-7.05 | 60.36 | 50.21-70.51 | 5.11 | 4.22-5.99 |
| 11 | 4.63 | 2.06-7.19 | 6.38 | 3.81-8.94 | 0.63 | -0.14-1.40 | 5.75 | 3.31-8.19 | 52.27 | 30.12-74.43 | 4.51 | 2.44-6.57 |
| 12 | 7.25 | -1.5-16.00 | 4.75 | -4.0-13.50 | 0.75 | -1.64-3.14 | 4.00 | -3.5-11.5 | 33.33 | -28.86-95.5 | 3.34 | -2.90-9.58 |

$\bar{x}$: mean value, *CI:* 95% Confidence Interval

of different clutch sizes for which the exact reproductive history was detected, the percentage of non-hatched eggs was higher in the case of smaller and larger clutch sizes while it was lower in the case of more frequent clutch sizes (clutches of 4–9 eggs) in the first annual clutches *(Table 1)*. Another type of percentage distribution of egg losses was obtained from the data of second annual clutches: the higher proportion of non-hatched eggs was detected in case of modal clutch size (7 eggs), in addition, the percentage value of egg losses was typically higher likewise in case of larger clutch sizes (13–14 eggs) *(Table 2)*. Considering the initial clutch sizes, the distribution of unhatched eggs' proportion was not homogeneous in the comparison of the first (20.72%, 1,130 non-hatched eggs out of 5,454 total eggs) and the second (28.75%, 410 non-hatched eggs out of 1,426 total eggs) nesting periods ($\chi^2 = 41.53$, $P < 0.001$). As regards the results of all successful nests, the mean of egg losses was higher in the case of larger clutches (9–12 eggs) in the first annual breeding period, however due to an overlap of 95% confidence interval, egg losses did not differ significantly between clutch sizes *(Table 3)*. Although the mean value of egg losses was higher in larger clutch sizes in the second annual

*Table 4.* Variation of the main and 95% confidence interval of breeding parameters in relation to initial clutch size for clutches where complete reproduction history was known in the second annual breeding period

*4. táblázat* A költési paraméterek átlag és 95%-os konfidencia intervallum értékeinek eltérése a kezdeti fészekalj méretek függvényében, melyeknél ismert a teljes reprodukciós történet a másodköltés időszakában

| **Clutch size** | **Unhatched eggs** | | **Eggs hatched** | | **Brood reduction** | | **Young fledged** | | **Reproductive success** | | **Productivity** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* | $\bar{x}$ | *CI* |
| 2 | 0 | – | 2 | – | 0 | – | 2 | – | 100 | – | 1.61 | 1.20-2.02 |
| 3 | 0.67 | -0.77-2.10 | 2.33 | 0.90-3.77 | 1 | -1.48-3.48 | 1.33 | -0.1-2.77 | 44.44 | -3.36-92.25 | 0.84 | -0.29-1.97 |
| 4 | 2 | - | 2 | - | 0.5 | - | 1.5 | - | 37.5 | - | 1.03 | - |
| 5 | 1.48 | 0.58-2.37 | 3.52 | 2.63-4.42 | 0.86 | 0.40-1.32 | 2.67 | 1.82-3.51 | 53.33 | 36.46-70.2 | 1.97 | 1.33-2.61 |
| 6 | 1.11 | 0.45-1.77 | 4.89 | 4.23-5.56 | 1.05 | 0.53-1.57 | 3.84 | 3.19-4.49 | 64.04 | 53.24-74.83 | 2.89 | 2.41-3.37 |
| 7 | 2.36 | 1.70-3.02 | 4.64 | 3.98-5.30 | 1.55 | 1.02-2.08 | 3.10 | 2.43-3.76 | 44.22 | 34.69-53.74 | 2.41 | 1.87-2.95 |
| 8 | 1.74 | 1.09-2.69 | 6.26 | 5.61-6.92 | 1.29 | 0.79-1.79 | 4.97 | 4.33-5.62 | 62.13 | 54.06-70.20 | 3.81 | 3.17-4.49 |
| 9 | 2.75 | 2.11-3.39 | 6.25 | 5.61-6.89 | 1.29 | 0.74-1.83 | 4.96 | 4.28-5.95 | 55.16 | 47.52-62.80 | 4.14 | 3.46-4.83 |
| 10 | 2.81 | 1.69-3.93 | 7.19 | 6.07-8.31 | 1.44 | 0.74-2.14 | 5.75 | 4.53-6.97 | 57.5 | 45.27-69.73 | 4.84 | 3.56-6.12 |
| 11 | 3.25 | 2.01-4.50 | 7.75 | 6.51-8.99 | 1.33 | 0.55-2.12 | 6.42 | 5.08-7.76 | 57.33 | 43.15-70.51 | 5.17 | 4.08-6.26 |
| 12 | 3.33 | 1.90-4.77 | 8.67 | 7.23-10.10 | 0.33 | -1.1-1.77 | 8.33 | 6.90-9.77 | 69.44 | 57.49-81.40 | 7.44 | 2.74-12.15 |
| 13 | 8.00 | – | 5.00 | – | 1.00 | – | 4.00 | – | 30.77 | – | 3.28 | – |

$\bar{x}$: mean value, *CI:* 95% Confidence Interval

clutches, the average number of unhatched eggs was more balanced than in the first breeding periods. Due to the overlap between 95% confidence intervals of means we did not find significant difference in the comparison of different clutch sizes *(Table 4)*.

The mean brood size per nest of the first annual clutches was 5.42 ± 0.07, 5.44 ± 0.07 for second clutches, and 5.43 ± 0.07 for the total annual breeding periods. The number of nestlings did not differ between the first and second annual clutches (Mann-Whitney U-test: $Z = 0.9$, $P = 0.771$). In contrast, the mean of hatching success per nest was higher in the first (79.81 ± 0.93%) than in the second clutches (71.86 ± 1.98%) (Mann-Whitney U-test: $Z = 4.9$, $P < 0.001$). The average value of hatching success was 78.31 ± 0.85% for the whole annual breeding periods.

Brood sizes at hatching of 6 (25.72%), 5 (19.95%) and 7 (18.57%) nestlings were observed most frequently in the first annual clutches, the cumulative proportion of these three brood sizes being 64.24% of all clutches. In the case of the second annual clutches, the modal brood size was 5 nestlings which was detected with the highest frequency (23.24%) and the relative frequency of brood size of 7 (16.76%) and 6 (15.14%) nestlings was even higher. Therefore, the cumulative percentage of these three brood sizes was 55.14% of all clutches. In addition, in the case of total annual breeding seasons the brood size of 6 (23.73%), 5 (20.57%) and 7 (18.23%) nestlings were detected with higher frequency, the cumulative percentage of these three brood sizes adding up to 62.53% of the total clutches *(Figure 2)*.

Regarding brood size and hatching success in relation to initial clutch size, the cumulative number of hatchlings was the highest in the case of modal clutch size (7 eggs) in the first annual clutches and the clutch size of 8 eggs in the second clutches *(Table 1–2)*. In contrast, the percentage distribution of hatching success in the first annual clutches was similarly high in the case of more clutch sizes (4–9 eggs), while higher proportion of hatching success was observed not only for the most frequent clutch sizes but also for smaller and larger ones in the second nesting period *(Table 1–2)*. Considering different clutch sizes, the mean of brood size was higher in the case of larger clutch sizes (7–10 eggs) in the first annual breeding period, which average values were significantly higher than the mean of smaller clutch sizes (2–6 eggs), due to the lack of overlapping confidence intervals *(Table 3)*. The mean of nestlings was similarly higher in larger clutch sizes in the second annual breeding season, due to the separation of confidence intervals; the average values of clutch size of 8–12 eggs were significantly higher than in the case of smaller clutch sizes (5–7 eggs) *(Table 4)*.

## Brood reduction, young fledged and fledging success

In the case of first annual clutches, the average number of brood reduction per nest was 0.93 ± 0.05, 1.24 ± 0.101 for the second clutches and 0.98 ± 0.04 for the whole annual breeding periods. Brood reduction was higher in the second than the first annual clutches (Mann-Whitney U-test: $Z = 3.41$, $P < 0.001$). Considering the initial clutch sizes, the loss of nestlings was the highest in the case of modal clutch size (7 eggs), but the proportion of brood reduction was also higher in the case of larger (8–9 eggs) and smaller (3–4 eggs) clutch sizes in the first breeding season *(Table 1)*. Similarly, brood reduction was the highest in the case of modal clutch size (7 eggs) in the second annual clutches, but the largest percentage value of brood reduction was typical only for this clutch size *(Table 2)*. The distribution of brood reduction was not homogeneous in the comparison of first (17.14%, 741 out of 4,324 total hatchlings) and second annual breeding periods (22.64%, 230 out of 1,016 total hatchlings) ($\chi^2 = 16.37$, $P < 0.001$), the degree of hatchling losses being higher in the second than the first annual clutches. Comparing egg and hatchling losses, the loss of eggs was larger in both the first ($\chi^2 = 19.77$, $P < 0.001$) and the second ($\chi^2 = 11.15$, $P < 0.001$) annual clutches. Based on data of all successful nests, the mean of brood reduction per different clutch sizes ranged from 0.43 to 1.34 in the first annual clutches, the degree of brood reduction did not differ significantly in the comparison of clutch sizes *(Table 3)*. The average number of hatchling losses per different clutch sizes varied between 0.5 and 1.55 in the second annual breeding period, however due to overlap of the 95% confidence intervals considering the loss of hatchlings we did not find significant difference between clutch sizes *(Table 4)*.

The mean of young fledged per nest varied between 0 and 9 (4.45 ± 0.07) in the total annual breeding season while it varied in the same range in the first (4.49 ± 0.07) and in the second (4.25 ± 0.17) annual clutches. There was no significant difference in the amount of fledglings between the first and second annual breeding season (Mann-Whitney U-test: $Z = 1.71$, $P = 0.088$), while fledging success was greater in the first (77.91 ± 1.09%) than in the second (71.47 ± 2.3%) annual clutches (Mann-Whitney U-test: $Z = 3.41$, $P < 0.001$).

The distribution of fledglings showed that 4–6 fledged young birds were observed most frequently in the first annual clutches, so the cumulative proportion of these three brood sizes at fledgling was 60.1% of all clutches. In the case of the second annual breeding seasons, 3–6 fledglings were produced by Common Barn-owls most frequently, the cumulative proportion of these four brood sizes at fledging being 61.63% of all breeding pairs. As regards the whole breeding periods, 4–6 fledged young birds were observed most frequently, the cumulative percentage of these three brood sizes at fledging adding up to 57.43% of total clutches *(Figure 3)*.

Regarding brood size at fledging in relation to initial clutch size, the cumulative number of fledglings was the highest in the case of modal clutch size (7 eggs) in the first annual clutches and the clutch size of 8 eggs in the second clutches *(Table 1–2)*. However, the percentage value of fledging success was higher in the clutch size of 5 eggs and other larger clutch sizes (10–13 eggs) in the first breeding period while in the case of the second breeding season, higher degrees of fledging success were detected in larger clutch sizes (8–14 eggs), except for the clutch size of 2 eggs *(Table 1–2)*.

## Reproductive success and clutch size productivity

The mean of percentage value of reproductive success per nest of first annual clutches was 66.12 ± 1.05%, 55.09 ± 1.99% for second clutches and 64.04 ± 0.94% for the whole annual breeding periods. There was significant difference in reproductive success between the first and second annual clutches (Mann-Whitney U-test: $Z = 5.63$, $P < 0.001$). Considering initial clutch size, the average value of reproductive success was higher in the case of clutch sizes of 5–9 eggs, however, due to the 95% overlapping confidence intervals, it did not significantly differ in the comparison of clutch sizes in the first annual breeding season *(Table 3)*. The mean of reproductive success was the highest in case of clutch size of 12 eggs in the second annual breeding period, but the lack of non-overlapping confidence intervals we did not find significant difference between clutches *(Table 4)*. As regards initial clutch size, calculated productivity rate was not the highest from the pooled data in the case of modal clutch size; productivity showed an increasing trend relative to clutch sizes which was typical in both breeding periods *(Table 1–2)*. According to the results of all successful clutches, the mean of productivity was higher in case of larger clutch sizes (6–11 eggs) thus, the rate of young produced was significantly lower in the clutch size of 3–5 eggs than in case of other larger clutch sizes (6–11 eggs) in the first annual breeding season *(Table 3)*. The calculated productivity value from the second annual clutches similarly increased depending on clutch size, the rate of productivity being significantly lower in clutch sizes of 3–5 eggs than in larger clutch sizes (6–10 eggs), except for the clutch sizes 11 and 12 eggs due to the overlapping of confidence intervals *(Table 4)*.

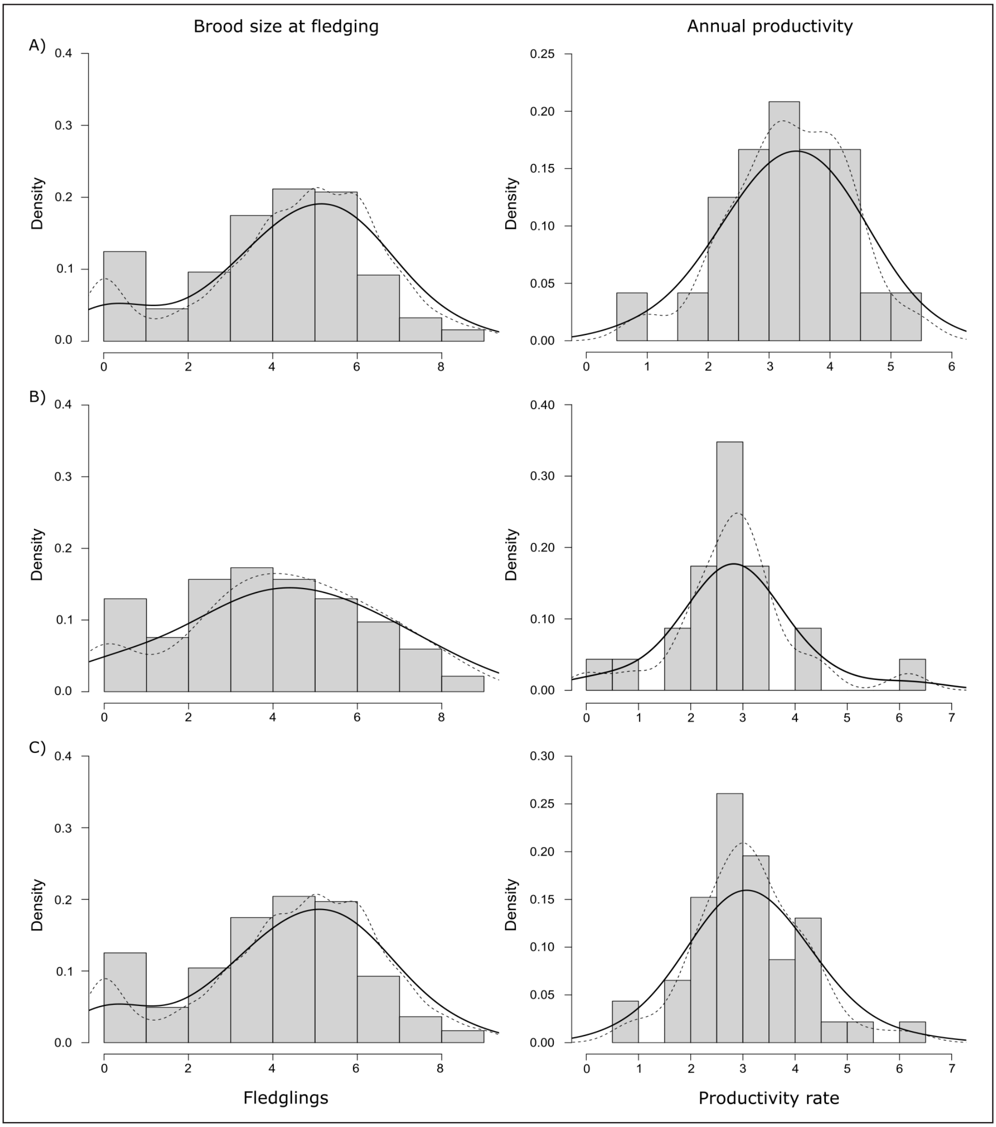

*Figure 3.* Histograms and smoothed histograms with first (dashed line) and second (solid line) order smoother of fledgling numbers and annual productivity distribution in the first (A) and second (B) annual clutches as well as in whole breeding season (C)

*3. ábra* A kirepült fiókaszám és az éves produktivitás eloszlásának hisztogramja és simított hisztogramja első- (szaggatott vonal) és másodrendű (folytonos vonal) simítással az első (A) és másodköltés (B), valamint a teljes szaporodási időszakban (C)

Considering all successful clutches we found significant positive linear regression between clutch size and productivity rate in both the first ($R^2 = 0.15$, $F = 142.1$, $P < 0.001$; $B_{slope} = 0.45$, $t = 11.92$, $P < 0.001$) and the second ($R^2 = 0.27$, $F = 66.39$, $P < 0.001$; $B_{slope} = 0.52$, $t = 8.15$, $P < 0.001$) breeding season *(Figure 4)*.

## Annual patterns of breeding parameters and productivity

The average number of eggs laid per year of first annual clutches was 227.25 ± 26.31 (range 29 – 518), 64.82 ± 12.36 (range 6 – 206) for second clutches and 149.56 ± 19.11 (range 6 – 518) for the whole annual breeding seasons. The number of eggs per year was significantly different between the two annual breeding periods (Mann-Whitney U-test: $Z = 4.76$, $P < 0.001$). Based on data of complete annual breeding cycles, the variation of clutch size showed fluctuation during the years (Kruskal-Wallis test: $H(23, N = 982) = 144.52$, $P < 0.001$) which was detected at its largest average clutch size value in 2014. It was significantly higher than the clutch size obtained in the other years, except for 1995 (post hoc Dunn test: $z = 4.02 – 9.01$, $P < 0.05$) *(Figure 5A)*.

The average proportion of egg loss per year for first clutches was 21.65 ± 1.74% (range 10.17 – 48.74%), 25.45 ± 2.88% (range 0 – 50%) for second clutches and 23.47 ± 1.66% (range 0 – 50%) for the whole annual breeding periods. Although the higher proportion of non-hatched eggs was observed in the second annual clutches, egg losses did not differ significantly between the two annual breeding seasons (Mann-Whitney U-test: $Z = 0.78$, $P = 0.431$). Considering the whole annual breeding periods, the percentage value of egg loss varied among the years (Kruskal-Wallis test: $H(23, N = 982) = 47.59$, $P < 0.01$), the highest proportion of non-hatched eggs being detected in 2010 *(Figure 5B)*. During the 24 years, the rate of egg loss showed decline with significant negative linear trend ($R^2 = 0.099$, $F = 4.85$, $P < 0.05$; $B_{slope} = – 0.51$, $t = 2.25$, $P < 0.05$) *(Figure 6A)*.

As regards the brood size at hatching, the average number of hatchlings per year of first annual clutches was 180.17 ± 21.91 (range 26 – 419), 46.18 ± 8.88 (range 6 – 146) for the second clutches and 116.08 ± 15.66 (range 6 – 419) for the whole annual breeding periods.

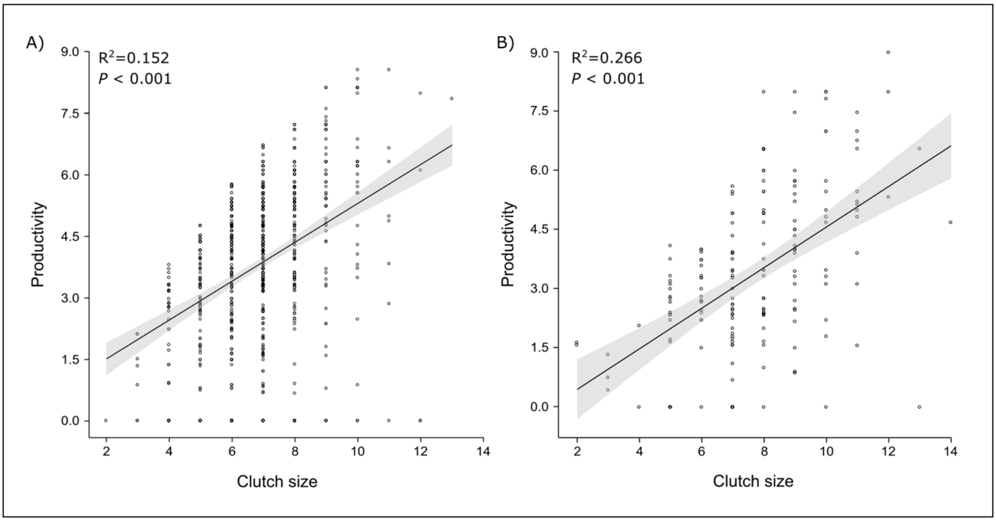

*Figure 4.* Relationship between clutch size and productivity (fledglings per nesting attempt) in the first (A) and second (B) annual clutches

*4. ábra* A fészekalj méret és produktivitás (kirepült fiókák/megkezdett fészkelések száma) összefüggése az első (A) és a másodköltés (B) időszakában

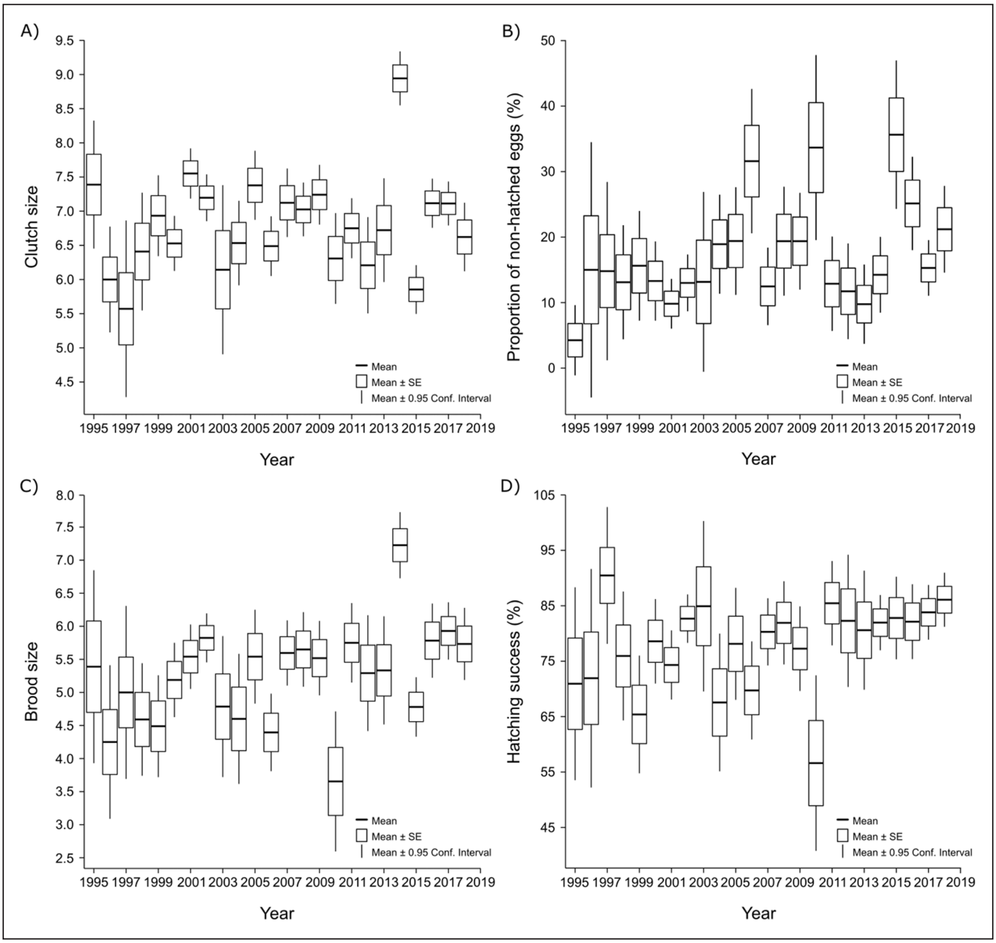

*Figure 5.* Fluctuation of the annual values (mean ± SE, 95% CI) of clutch size (A), proportion of egg loss (B), brood size (C) and hatching success (D) during the 24 years

*5. ábra* A fészekalj méret (A), a tojás veszteség arányának (B), a kikelt fiókák számának (C) és a kelési siker (D) éves értékének (átlag ± standard hiba, 95%-as konfidencia intervallum) fluktuációja a 24 év során

A significant difference in hatchling numbers was observed in the comparison of first and second clutches (Mann-Whitney U-test: $Z = 4.76$, $P < 0.001$). Considering the total breeding periods, brood size varied similarly to the amount of eggs laid during the monitoring period and it was significantly different among years (Kruskal-Wallis test: $H(23, N = 982) = 114.11$, $P < 0.001$). The maximum average value of nestlings was detected in 2014 similarly to egg productivity but a significantly lower average value of brood size was observed in 2010 compared to several years (2002, 2014, 2016, 2017) (post hoc test: $z = 3.79 – 6.53$, $P < 0.05$) *(Figure 5C)*.

Taking into account the above, the mean of hatching success per year of the first annual clutches was 78.35 ± 1.74% (range 51.26 – 89.83), 74.08% ± 2.81% (range 50 – 100) for second clutches and 76.31% ± 1.63% (range 50 – 100) for the whole annual breeding seasons.

Significant difference was not observed between two annual breeding periods (Mann-Whitney U-test: Z = 1.53, $P = 0.125$). Considering the whole breeding seasons, despite that the degree of hatching success was less fluctuating during the monitoring period, it differed significantly among years (Kruskal-Wallis test: H(23, $N = 982$) = 47.59, $P < 0.01$). The lowest average rate of hatching success was detected in 2010 *(Figure 5D)*. Despite this minimum value, hatching success increased with significant positive linear trend ($R^2 = 0.091$, F = 4.42, $P < 0.05$; $B_{slope} = 0.48$, t = 2.10, $P < 0.05$) during the 24 years *(Figure 6B)*.

The average proportion of brood reduction per year of the first annual clutches was 18.35 ± 2.08% (range 3.61 – 50.82%), 24.29% ± 2.89% (range 0 – 51.72%) for second clutches and 21.19% ± 1.79% ($N = 46$, range 0 – 51.72%) for the whole annual breeding period. Although the loss of hatchlings was higher in the second annual clutches, significant difference was not found between the two annual breeding seasons (Mann-Whitney U-test: Z =1.35, $P = 0.176$). The percentage value of this parameter from the total annual clutches varied significantly among the years (Kruskal-Wallis test: H(23, $N = 982$) = 69.32, $P < 0.001$). Higher average proportions of brood reduction were observed in three years (2007, 2010, 2015) while the degree of nestling loss was the lowest in 1995 (post hoc test: z = 3.76 – 4.19, $P < 0.05$) *(Figure 7A)*.

Considering brood sizes at fledging, the average number of fledglings per year was 149.29 ± 19.38 (range 21 – 364), 35.5 ± 7.54 (range 6 – 125) for the second clutches and 94.87 ± 13.59 (range 6 – 364) for the whole annual breeding periods. The quantity of fledglings was significantly higher in the first than in the second annual clutches (Mann-Whitney U-test: Z = 4.78, $P < 0.001$). As regards the total breeding seasons, the amount of fledglings significantly differed among the years (Kruskal-Wallis test: H(23, $N = 982$) = 145.46, $P < 0.001$). The greatest number of fledglings was observed in 2014 which was significantly higher compared to other years (post hoc test: z = 3.83 – 7.61, $P < 0.05$). Due to the higher degree of brood reduction, the significantly smaller number of fledglings was also typical in 2010 (post hoc test: z = 3.75 – 7.61, $P < 0.05$) *(Figure 7B)*.

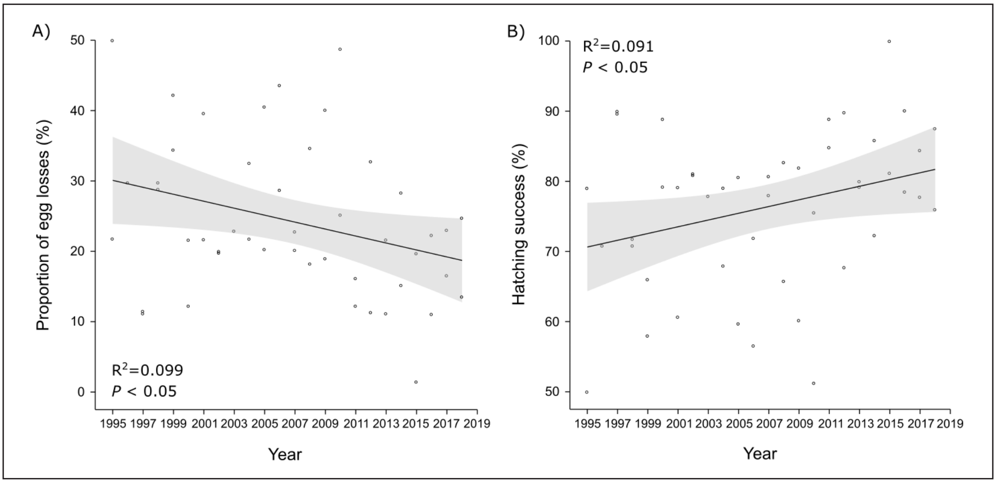

*Figure 6.* Temporal change of the proportion of egg loss (A) and hatching success (B) during the monitoring period

*6. ábra* A tojás veszteség (A) és a kelési siker (B) időbeli változása a monitorozási periódus alatt

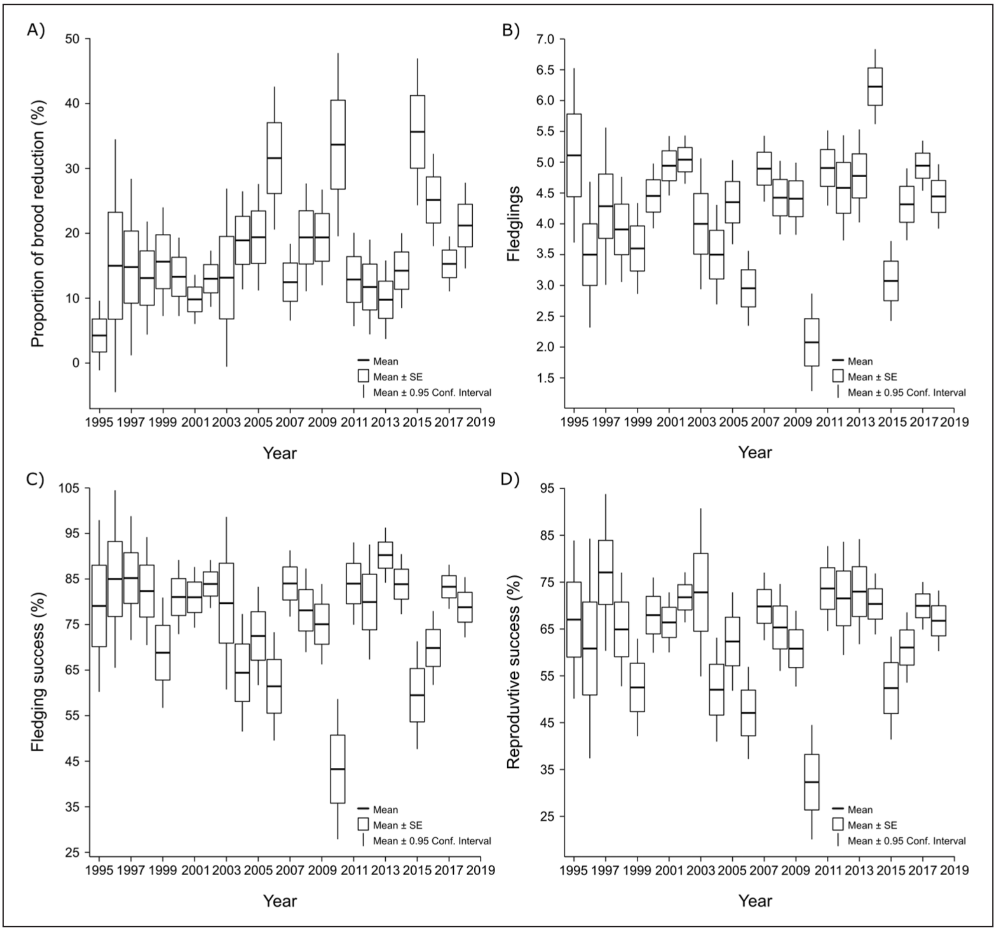

*Figure 7.* Fluctuation of the annual values (mean ± SE, 95% CI) of brood reduction (A), fledglings (B), fledging success (C) and reproductive success (D) during the 24 years

*7. ábra* A kikelt fiókák vesztesége (A), a kirepült fiókák számának (B), a kirepülési (C) és a szaporodási siker (D) éves értékének (átlag ± standard hiba, 95%-as konfidencia intervallum) fluktuációja a 24 év során

The mean of fledging success per year varied within the same range (48.27 – 100%) in the first (81.65% ± 2.08%), second (75.70% ± 2.89%) clutches and in the whole annual breeding seasons (78.81% ± 1.79%). As regards the whole annual breeding seasons, the fledging success significantly differed between years (Kruskal-Wallis test: H(23, $N$ = 982) = 79.97, $P < 0.001$). Due to the high degree of brood reduction, these results of median test were determined essentially by the lowest rate of fledging success in 2010, which differed significantly in the comparison of several years (post hoc: z = 3.75 – 7.61, $P < 0.05$) *(Figure 7C)*.

The rate of reproductive success per year ranged from 25.21 to 79.66% (64.39 ± 2.38%) in the first, from 28 to 100% (56.40% ± 3.46%) in the second clutches and from 25.21 to 100% (60.57 ± 2.13%) in the total annual breeding seasons. Considering the whole breeding periods, reproductive success showed similar annual fluctuation to fledging success, which

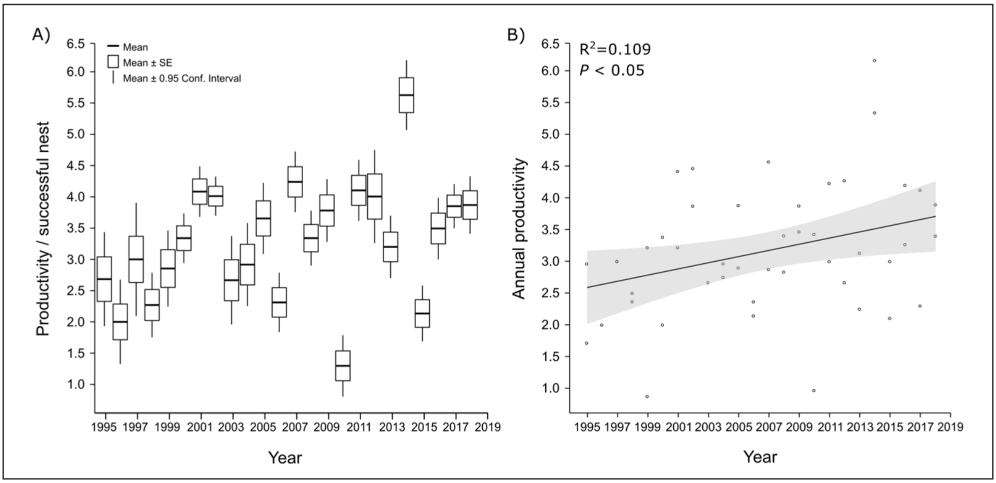

*Figure 8.* Fluctuation of the annual values (mean ± SE, 95% CI) of productivity per successful nest (A) and the changes of annual productivity of Common Barn-owls (B) during the 24-year monitoring period

*8. ábra* A sikeres fészkek produktivitás értékének (átlag ± standard hiba, 95%-as konfidencia intervallum) fluktuációja (A) és a gyöngybaglyok éves produktivitásának változása (B) a 24 éves monitoring során

differed among the years (Kruskal-Wallis test: H( 23, $N = 982$) = 81.53, $P < 0.001$) because a significant yearly decline in reproductive success was observed in 2010 in comparison to several years (post hoc test: $z = 3.75 – 4.99$, $P < 0.05$) *(Figure 7D).*

Based on the number of fledglings of successful nests, the mean of annual productivity fluctuated between 0.97 and 5.34 (3.44 ± 0.19) in the first, 0.87 and 6.17 (2.96 ± 0.23) in the second annual clutches, and between 0.87 and 6.17 (3.16 ± 0.15) in the total annual breeding seasons. We did not find significant difference of productivity between the first and second annual clutches (Mann-Whitney U-test: $Z = 1.85$, $P = 0.064$). Based on the distribution of annual productivity rate, 2.8 – 4.5 fledglings per nesting attempt were observed most frequently in the first breeding seasons, so this range of productivity was typical in 17 cases out of total sample (72%) *(Figure 3)*.

In case of second clutches, 8 fledglings per nesting attempt were observed most frequently (36%, 8 out of 22 case numbers) while productivity of 2.5 – 3.5 fledglings per nesting attempt was calculated most frequently (46%, 21 out of 46 samples) in the whole annual breeding periods *(Figure 3)*. The annual productivity of Common Barn-owls differed significantly among the years (Kruskal-Wallis test: H(23, $N = 982$) =223.94, $P < 0.001$). The greatest productivity rate was observed in 2014 which was significantly higher compared to other years (post hoc test: $z = 4.20 – 9.23$, $P < 0.01$). Due to lower fledgling production, the significant low productivity was typical in 2010 (post hoc test: $z = 4.42 – 9.23$, $P < 0.01$) *(Figure 8A)*. Considering the complete annual breeding cycles, the annual variation of productivity showed significant slightly positive linear trend ($R^2 = 0.109$, $F = 5.38$, $P < 0.05$; $B_{slope} = 0.048$, $t = 2.32$, $P < 0.05$) during the 24 years *(Figure 8B)*.

## Discussion

In this study, we evaluated the results of a long-term Common Barn-owl nest box installation programme in Southern Hungary. The number of placed nest boxes varied from 43 to 163 during the 24-year-long monitoring period, and the average percentage of nest box occupancy per year was 34.22 ± 3.37% (yearly range 9.72 – 73.44%) at the start of first annual clutches which was lower than that reported in other studies. In the USA (northern Utah) 50% of installed nest boxes were occupied in the first and 80% of boxes were used in the second year, which was observed when a low number of boxes were placed ($N = 30$) (Marti *et al.* 1979) and the average percentage of occupied nest boxes was 81.35 ± 6.32% (yearly range 53.3 – 96.7%) during the 6 years (Marti & Wagner 1985). Also during the 6 years, 41 nest boxes were installed in a similar program in the USA, however, the rate of nest box occupancy per year was 65.29 ± 6.41% (Looman *et al.* 1996). In a long-term study (13 breeding seasons), 51.7 ± 3.7% (yearly range = 25.7 – 73.5%) of all placed nest boxes ($N = 309$) per year were occupied by Common Barn-owl pairs in the Middle-East (Beit She'an Valley, Israel) (Charter *et al.* 2017). The first five-year evaluation of this monitoring program is also worth highlighting, when the mean percentage of nest boxes ($N = 248$) occupied was 53.5 ± 2.1% (Meyrom *et al.* 2009). Although the yearly range of nest box occupancy rate was greater according to our results than the occupancy range defined in the Middle East (Charter *et al.* 2017), but the maximum percentage value of occupied nest boxes was very similar in the comparison of the two long-term studies. The lower average proportion of nest box occupancy showed by our results presumably can be traced back to two basic reasons. First, some natural nesting and roosting sites (open church towers, farm buildings and lofts) are still available for the Common Barn-owl in the monitored county which is characterized with a multitude of small villages (Bank 1990). Second, the size of the potential regional population of Common Barn-owl showed several collapses due to the impact of extreme periods during the 24 years, which was indicated by the lowest percentage values of nest box occupancy in 1997 (9.72%), 2003 (16.28%), 2012 (14.57%) and 2013 (14.47%), so these low proportion values influenced the calculated average. Based on the reported nest box occupancy data of Common Barn-owl from Cyprus, the yearly average proportion of occupied nest box was lower (18.58 ± 2.98%) compared to our results (Kassinis & Roulin 2017). Furthermore, a low nest box occupancy rate was also found in the semiarid pampas of Argentina where the Common Barn-owl occupied the nest boxes only occasionally, which was a consequence of the fact that the applied nest boxes were smaller than in other studies focusing specifically on the Common Barn-owl (Liébana *et al.* 2013).

The mean proportion of double brood pairs ranged from 0 to 41.46% in the second annual clutches. This average percentage was higher than that reported by Martínez and Lopez (1999) in the Mediterranean region, where the number of pairs laying a second clutch was 33.3%. The second clutches are frequent in the case of the Common Barn-owl (Roulin *et al.* 1999), which is an adaptive strategy because regarding the whole breeding season the reproductive success of double brooding pairs is higher than of single-brooded owls (Béziers & Roulin 2016).

Although the proportion of occupied nest boxes was lower in the investigated region, nesting success showed higher percentage value in the whole annual breeding season (83.39%), indicating the role of the artificial nest boxes in promoting the Common Barn-owl's nesting efficiency (Marti *et al.* 1979, de Bruijn 1994, Marti 1994, Petty *et a*l. 1994, Taylor 1994, Frey *et al.* 2011, Charter *et al.* 2017), similarly to nest box installation programs implemented in other countries. For example, 71% (Marti 1994) and 85.85% (Looman *et al.* 1996) of nesting attempts was successful in the USA, the yearly range of 73.2 – 93.5% nesting success was detected in the Middle-East (Charter *et al.* 2017), and 87.24% of nesting attempts was successful in western Switzerland based on a 23-year dataset of nest boxes (Frey *et al.* 2011).

According to our results, the average clutch size of first clutch per nest (6.84 ± 0.05, $N$ = 797) was higher than that reported in other countries of Europe such as Netherlands ($\bar{x}$ = 4.0) (Braaksma & de Bruijn 1976), England ($\bar{x}$ = 4.68) (Bunn *et al.* 1982), Scotland ($\bar{x}$ = 4.6, $N$ = 425) (Taylor 1994), France (Burgundy) ($\bar{x}$ = 5.89, $N$ = 765), Czech Republic ($\bar{x}$ = 5.85, $N$ = 193) (Poprach 1996), Spain (Valencia) ($\bar{x}$ = 4.63, $N$ = 30) (Martínez & Lopez 1999) and Switzerland ($\bar{x}$ = 5.85, $N$ = 193) (Frey *et al.* 2011). Furthermore, smaller average clutch size was found in other parts of the world such as Mali ($\bar{x}$ = 6.05, $N$ = 140) (Wilson *et al.* 1986), Pakistan ($\bar{x}$ = 5.83, $N$ = 28) (Mahmood-Ul-Hassan *et al.* 2007), Utah ($\bar{x}$ = 5.8, $N$ = 28) (Looman *et al.* 1996), and even smaller clutch size ($\bar{x}$ = 3.8, $N$ = 17) was reported from Arkansas (Radley & Bednarz 2005). Nevertheless, in the first annual breeding period similarly high average clutch size has already been observed in peninsular Malaysia ($\bar{x}$ = 6.6, $N$ = 36) (Lenton 1984), northern Utah ($\bar{x}$ = 7.17, $N$ = 275) (Marti 1994) and British Columbia ($\bar{x}$ = 6.5, $N$ = 23) (Andrusiak & Cheng 1997). Considering the geographical variation of clutch size, our results confirmed that the first clutch size was larger in Hungary than in Spain, contributing to the earlier observation that the clutch size of Common Barn-owl increase from Spain to Hungary in mainland Europe (Roulin 2002a). We found that size of the second annual clutches of Common Barn-owl was significantly larger than the size of first clutches which is in accordance with the results of other studies (Schönfeld & Gibrig 1975, Kaus 1977, Poprach 1996, Frey *et al.* 2011). Conversely, the mean of clutch size was significantly larger in the first than the second annual clutches in northern Utah (Marti 1994), Scotland (Taylor 1994) and in Spain, but in the latter case the difference of clutch size was not significant between the two breeding seasons (Martínez & Lopez 1999). As regards the variation of Common Barn-owl clutch size, the studies showed that the size of second clutches are larger than the first in case of *Tyto alba guttata* subspecies while that difference is reversed in *Tyto alba alba* population (Roulin 2002a). Modal clutch size was larger (7 eggs) in our study area than that reported by some other studies since it was 5 eggs in Spain (Martínez & Lopez 1999), 6 eggs in Mali (Wilson *et al.* 1986) and in western Switzerland (Chausson *et al.* 2014a). However, clutches of 7 eggs were detected with the highest frequency in USA (Looman *et al.* 1996) and Cyprus (Kassinis & Roulin 2017) which is consistent with our results.

During the 24 years of our study, the average values of unhatched eggs per nest was 1.42 ± 0.07 in the first annual breeding period, and egg losses were significantly higher in the second than in the first clutches. Mean of disappeared eggs was higher ($\bar{x}$ = 1.7) in northern

Utah (USA) (Marti 1994) and smaller in Switzerland ($\bar{x}$ = 0.42) (Chausson *et al.* 2014a). Considering the initial clutch sizes, we found that the percentage of unhatched eggs was higher in the case of smaller and larger clutch sizes, while it was lower in the case of clutch sizes with high frequency in the first annual breeding period. In contrast, a larger proportion of egg losses was typical in the case of modal and larger clutch size in the second clutches. In addition, the higher degree of egg losses in the second clutches was also confirmed by the inhomogeneous distribution of the pooled quantity of unhatched eggs between the two breeding periods. Contrarily to the present study, unhatched eggs were found only in clutches with 4 or more eggs in Spain (Martínez & Lopez 1999). However, our results are consistent with this earlier study in that egg losses were higher in the case of larger clutch size which was mainly typical of the second breeding season in our study area.

Mean brood size per nest was higher ($\bar{x}$ = 5.42 ± 0.07) in the first clutches than that detected in other European countries such as Scotland ($\bar{x}$ = 3.4) (Taylor 1994), Czech Republic ($\bar{x}$ = 3.82) (Poprach 1996), Spain ($\bar{x}$ = 3.32) (Martínez & Lopez 1999) and Slovakia ($\bar{x}$ = 4.5) (Sárossy 2000). This difference also exists in comparison with previous studies since average brood size ranged from 2.4 to 4.3 in Germany (Schönfeld & Gibrig 1975) and from 3.0 to 5.1 in eastern France (Müller 1990). Compared to our results, the mean number of nestlings was also smaller in other continents, such as in Mali ($\bar{x}$ = 4.79) (Wilson *et al.* 1986), in Pakistan ($\bar{x}$ = 4.15) (Mahmood-Ul-Hassan *et al.* 2007), in Malaysia ($\bar{x}$ = 4.6) (Lenton 1984) and in different parts of North America such as north central Utah: $\bar{x}$ = 3.97 (Looman *et al.* 1996), British Columbia: $\bar{x}$ = 3.3 (Andrusiak & Cheng 1997) and Florida: $\bar{x}$ = 2.87 (David 1996). However, a higher average number of nestlings was detected in northern Utah (Marti 1994), thus as regards the brood size at hatching of the Common Barn-owl, our result is consistent with this study. We found that brood size was not significantly different between the first and second annual clutches and it is in accordance with the result which was reported by Marti *et al.* (1994). In contrast, the average number of nestlings was significantly larger in the first than in the second breeding period in Switzerland (Frey *et al.* 2011). According to our results, the mean of hatching success per nest was significantly higher in the first (79.81%) than in the second clutches (71.86%), but these values were lower than it had been reported from the Mediterranean area (Spain) (83%) (Martínez & Lopez 1999).

Several studies pointed out that brood reduction takes place in the first 3 weeks after hatching for various reasons. Nestling losses frequently occur by starvation due to the reduction of food availability, but siblicide and more frequent cannibalism also reduce brood size (Roulin, 2002b). We found that the average number of brood reduction per nest was significantly higher in the second ($\bar{x}$ = 1.24) than in first ($\bar{x}$ = 0.93) clutches. Based on the cumulative number of disappeared nestlings, the proportion of brood reduction was not homogeneous in comparison of the first (17.14%) and the second (22.64%) breeding periods, confirming the higher level of brood reduction in the case of second annual clutches.

Additionally, our results showed that the degree of egg losses before hatching was larger than the loss of nestlings after hatching in both the first and second annual clutches, and this result is in agreement with those reported by Marti (1994) in northern Utah. Considering initial clutch sizes, the proportion of brood reduction was also higher in case of larger and smaller clutch sizes than the modal one, but the degree of brood reduction did not differ significantly in the comparison of initial clutch sizes. Nevertheless, higher level of brood reduction was reported in the case of large than in small brood size (Taylor 1994). Similar to the distribution of egg losses, Martínez and Lopez (1999) found that the partial loss of nestlings was typical in clutches with 4 or more eggs.

We found that, the average number of fledglings per nest varied in the same range in the first ($\bar{x}$ = 4.49) and in the second ($\bar{x}$ = 4.25) annual clutches as well as in the total annual breeding season ($\bar{x}$ = 4.45). The range of average value of fledglings was similar in France (first: $\bar{x}$ = 4.29 and second clutches: $\bar{x}$ = 4.8) (Baudvin & Jouaire 2001), in the Middle-East ($\bar{x}$ = 4.91) (Meyrom *et al.* 2008), in northern Utah (USA) (first: $\bar{x}$ = 5.09 and second clutches: $\bar{x}$ = 4.94), and in north central Utah (USA) ($\bar{x}$ = 4.0) (Looman *et al.* 1996), while it was higher in the Czech Republic (first: $\bar{x}$ = 4.62 and second clutches: $\bar{x}$ = 6.75) (Poprach 1996) and lower in British Columbia ($\bar{x}$ = 3.4) (Andrusiak & Cheng 1997), in Africa ($\bar{x}$ = 3.19) (Wilson *et al.* 1986) and in Malaysia ($\bar{x}$ = 3.7) (Lenton 1984). There was no significant difference in the amount of fledglings between the two annual breeding periods in our investigated area. However, we found that calculated fledging success was greater in the first than in the second annual clutches. The lack of significant difference in the numbers of young fledged between two annual breeding periods was reported from the USA (Marti 1994), however, no significant difference was found in the case of fledging success in the Spanish Mediterranean area (Martínez & Lopez 1999).

Regarding brood size at fledging in relation to initial clutch size, the percentage value of fledging success was lower in modal clutch size while higher values of this breeding parameter were typical in the case of larger clutch sizes in our study area. Our results showed that, larger clutch sizes were more productive than the modal clutch size which in the first approach support the general hypothesis that the most productive clutch size is larger than the most frequent (Klomp 1970, Perrins & Moss 1975, Stearns 1976). In contrast, modal clutch size (5 eggs) was the most productive in the Mediterranean region in Spain (Martínez & Lopez 1999) and in north central Utah (USA) where the modal and most productive clutch size was higher (7 eggs) (Looman *et al.* 1996), the same clutch size having been identified in the present study as the modal, but not the most productive for Southern Hungary. In addition, we found significant linear regression between clutch size and young fledged production per nest attempt. Similarly, the number of fledglings increased with clutch size in Switzerland (Frey *et al.* 2011). The results of these two long-term studies (24- and a 23-year datasets) seemed to support the general hypothesis.

In the case of the Spanish population, the authors suggested that the coincidence of modal and the most productive clutch size may be explained by the alternative hypothesis by Boyce and Perrins (1987) because in terms of adult survival, the reproductive costs were low or were not measurable with owls. According to this alternative hypothesis, the cost of reproduction is not a necessary and sufficient factor for the optimization of clutch size because it is beneficial for the birds in the long term to lay clutches smaller than the most productive clutch size (Boyce & Perrins 1987). The low reproduction costs observed in Spain can be traced back to the lack of fluctuation of environmental variables, such as climate and food resources (availability of rodents) because variation in the reproductive parameters of the Common Barn-owl was not detected during the 7 years, the average laying date and clutch size did not differ between years (Martínez & Lopez 1999). The coincidence of modal and the most productive clutch size was observed in a shorter study (6-year dataset) also in north central Utah (USA). However, this study detected significant variation in clutch size among the years (Looman *et al*. 1996). In contrast, Marti (1994) reported the lack of significant difference of clutch size among years and among nest sites during a 16-year sampling period. Conversely, our results showed that all observed and calculated breeding parameters for the whole annual breeding season varied significantly among the years. As already highlighted above in case of percentage values of nest box occupancy, the impact of extreme years ('good-year' or 'bad-year effect') influenced the reproductive output of the Common Barn-owl during the 24 years. The largest average value of clutch size, brood size, fledglings and productivity rate were detected in 2014, caused by the extreme population outbreak of the Common Vole *(Microtus arvalis)* (Pallas, 1778). The multiannual population cycles of the Common Vole were widely investigated (Jacob *et al*. 2014) and three-year-long population cycles were documented in Europe (Tkadlec & Stenseth 2001, Lambin *et al*. 2006). Predominance of Common Vole was typical in diet of Barn Owls from the pellet analysis which was conducted in Baranya County (Horváth 1999, Horváth *et al*. 2018). The direct monitoring of Common Vole activity in the intensively used alfalfa fields in our investigated area was started in the collapse phase after the 2014 outbreak, based on counting reopened burrow entrances, and detected the next increasing phase of this rodent in 2017 (Somogyi & Horváth 2019). Earlier studies of Common Barn-owl's breeding biology had already reported that the number of nesting and the proportion of double brood pairs as well as the values of reproductive output of owls were larger in the outbreak than in the non-outbreak periods of Common Vole (Schönfeld & Girbig 1975, Kaus 1977, Baudvin 1979, de Brujin 1994). In contrast to this 'good-year effect', due to extreme large participation in the first clutches period, the highest proportion of egg loss, the lowest average value of brood size and hatching success, the higher degree of brood reduction, as well as the lowest rate of fledging success and annual productivity were detected in 2010, as a prominent negative impact ('bad-year effect'). Boyce and Perrins (1987) already emphasized the importance of long-term studies, since the impact of extreme years on clutch size optimization and the variation of reproductive outputs could not be detected without multi-annual dataset, also pointing out the Spanish study in the case of Common Barn-owl clutches. Although we have no data on the reproductive cost of the owls or the lack of it but our data seem to support the hypothesis of Boyce and Perrins (1987), because Common Barn-owls laid more often smaller clutches than most productive ones in our investigated area in South-Hungary where the fluctuating environment was typical. While in the case of Spanish population, due to the more stable environment, the variance of reproductive success was not typical and thus modal clutch size was the same as the most productive clutch size (Martínez & Lopez 1999). In this study, we had no purpose to examine the effect of environmental variables, however, based on our long term dataset, it is necessary to test the impact of weather parameters and small mammals, particularly the Common Vole as the main prey, on the reproductive output of the Common Barn-owl.

Among the breeding parameters, we emphasize the results of three variables such as egg loss, hatching success and annual productivity. During the 24 years, the rate of egg loss showed decline with significant negative linear trend while hatching success increased with significant positive linear trend. Based on the distribution of annual productivity rate 2.5 – 3.5 fledglings per nesting attempt were calculated most frequently for the whole annual breeding periods and we did not find significant difference of productivity between the first and second annual clutches which result is consistent with the study by Martínez and Lopez (1999). Similar productivity rate ($\bar{x}$ = 3.5) was calculated in north central Utah (Looman *et al.* 1996) which average value is equal to the upper limit of the most common annual productivity range of investigated Hungarian Common Barn-owl population. Nevertheless, lower average productivity ($\bar{x}$ = 2.7) was detected in the agricultural landscape of British Columbia (Hindmarch *et al.* 2014), however this value was similar to the lower limit of the most frequent annual productivity range which we calculated in our investigated area. The Canadian study suggested that food availability was reduced in more urbanized landscapes which lead to a higher degree of brood reduction and thus low productivity in Common Barn-owls (Hindmarch *et al.* 2014). Additionally, considering complete annual breeding seasons, the annual variation of productivity showed significant, slightly positive linear trend during the 24 years.

Although the monitoring of the Common Barn-owl's breeding biology was conducted in the continental region of European temperate zone in Southern Hungary, our results were compared to studies of different geographical and climatic zones where the environmental variability and the availability of food resources differs from those found in our study area. Considering all of the above, the comparative evaluation suggested that the optimization of clutch size for the stable or variable environment is an evolutionarily stable strategy of Common Barn-owls to maximize its lifetime reproductive success. In the light of our findings, despite the outlier values of reproduction characteristics in the extreme years with negative effect, a relatively stable regional Common Barn-owl population can be maintained by the placement of nest boxes in the investigated Southern Hungarian region.

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# Investigating the relationship between the prey composition of Barn Owls *(Tyto alba)* and the habitat structure of their hunting range in the Marcal Basin (Hungary), based on pellet analysis

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**Abstract** Little was known about the small mammal fauna of the Marcal Basin to date, therefore we collected 1,144 Barn Owl pellets from 15 locations in 2017. After the analysis of the pellets, remnants of 3,063 prey items were identified, of which 97.5% were small mammals, belonging to 21 species, while the remaining 2.5% were birds, frogs and insects. Mammal prey items consisted of Cricetidae 41%, Muridae 31% and Soricidae 28%, and in some samples, we found the remnants of European Mole *(Talpa europaea)*, Kuhl's Pipistrelle *(Pipistrellus kuhlii)*, Hazel Dormouse *(Muscardinus avellanarius)* and Least Weasel *(Mustela nivalis)*. Small mammal species were classified into four functional groups based on their preferences for urban, open, forest or wetland habitats. We investigated whether their relative abundances match with the proportions of the four habitat types in the assumed Barn Owl hunting ranges (cca. 2 km radius circle) in five sample sites. The relative abundance of small mammal species preferring urban habitats showed concordance with the proportion of the appropriate habitat types in the hunting area in two samples, while such concordance was proved for species favouring open, forest and wetland habitats just in one out of five samples. Small mammal functional groups represented in the prey composition do not directly correspond to the proportion of their typical habitats. We conclude that the abundance of various prey types is not suitable for characterising the landscape within the Barn Owl's hunting range.

Keywords: pellets, small mammals, habitat preference, landscape structure

**Összefoglalás** A Marcal-medence kisemlős faunájáról ezidáig keveset tudtunk, ezért 2017-ben 15 településről 1144 gyöngybagolyköpetet gyűjtöttünk. Szétbontásuk és elemzésük során 3063 zsákmány maradványa került elő, melynek 97,5%-át 21 kisemlős faj egyedei tették ki, míg a fennmaradó 2,5% madár, béka, illetve rovar volt. Az emlőszsákmány 41%-a hörcsögfélékből (Cricetidae), 31%-a egérfélékből (Muridae) és 28%-a cickányfélékből (Soricidae) állt, de előkerültek közönséges vakond *(Talpa europaea)*, fehérszélű törpedenevér *(Pipistrellus kuhlii)*, mogyorós pele *(Muscardinus avellanarius)* és eurázsiai menyét *(Mustela nivalis)* maradványok is. A baglyok zsákmányából kimutatott kisemlősöket funkcionális csoportokba soroltuk, az alapján, hogy urbán, nyílt, erdős vagy vizes élőhelyeket preferálnak. Azt vizsgáltuk, hogy részesedésük mutat-e egyezést a felsorolt négy élőhelytípus részesedésével a baglyok feltételezett 2 km sugarú körön belüli vadászterületein, öt mintaterületen. Az urbán élőhelyeket preferáló fajok részesedése két mintában, míg a nyílt, erdei és vizes élőhelyeket preferáló fajok részesedése csak egy-egy mintában mutatott hasonlóságot a megfelelő élőhelytípus részesedésével a feltételezett vadászterületen belül. A zsákmányból kimutatott kisemlősök funkcionális csoportjainak részesedése nem egyezett meg a megfelelő élőhelyeik arányával. Megállapíthatjuk, hogy ezzel a módszerrel a kisemlős zsákmány alapján nem tudunk következtetni a vadászterület élőhelyeinek mintázatára.

Kulcsszavak: köpetek, kisemlősök, élőhely preferencia, táj struktúra

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## Introduction

Small mammals are the main preys of the Barn Owl *(Tyto alba)* (Mikkola 1983). Many rare or elusive species occur among the prey, just as well ones that can be hardly caught by trapping (Torre *et al.* 2004, 2015). On the basis of the prey composition found in the pellets, valuable data can be obtained about the species in the owl's hunting area, therefore this indirect method is often used for surveying the fauna (e.g. Schmidt 1976, Taylor 1994, Yom-Tov & Wool 1997). The composition of small mammal communities can be better estimated based on these data in comparison with standard direct sampling methods, e.g. trapping (Heisler *et al.* 2016). However, such studies should not ignore the seasonal dynamics of small mammals, the population outbreaks, and the fact that Barn Owls can show prey preference during hunting (Tores *et al.* 2005, Askew *et al.* 2007, Meek *et al.* 2012). The structure of small mammal communities is also influenced by the landscape (Torre *et al.* 2015), therefore, the results of pellet analysis can be used for the description of the landscape (Heisler *et al.* 2016), moreover the changes in land use can be detected by using data of long-term owl pellet analysis (Cooke *et al.* 1996, de la Peña *et al.* 2003, Rodríguez & Peris 2007).

Little was known about the small mammal fauna of the Marcal Basin to date (Bihari *et al.* 2007). A few previous studies of Barn Owl pellet analysis were performed (e.g. Schmidt 1976, 1979, Lázár 1983, Varga 1986, 1991, Purger & Reider 1998, Szép & Purger 2013). In the southern part of the Marcal Basin two surveys were conducted at the same place, but in different times (Lázár 1983, Szép & Purger 2013), and upon comparison of the results of the studies it was suggested that differences in the relative abundance of species found in Barn Owl pellets may indicate changes in land use (Szép & Purger 2013). This example pointed out that results from previous sporadic surveys can provide a good basis for comparisons if more pellets can be collected in the same sites. However, if pellet samples are collected at the same time, from several areas with similar landscape features, we assume that the differences in the small mammal composition refer to the habitat conditions of the owls' hunting areas.

The aims of this study were: 1) to widen our knowledge on the small mammal fauna of the Marcal Basin based on Barn Owl pellet analysis, 2) to find connection between the proportions of the functional groups of small mammals in the diet and the proportion of their favoured habitats in the owls' hunting areas.

## Materials and methods

The Marcal Basin is mostly flat, lowland area (1,583 km$^2$) situated in the north-western part of Hungary (Dövényi *et al.* 2010). Its greater part is agricultural landscape, while the small patches of natural vegetation consist of oak-hornbeam forests, gallery forests as well as tall-sedge beds along the Marcal and other watercourses (Mesterházy 2008). Approximately 18% of the area is covered by forests, and out of this 70% comprise plantations of black pine *(Pinus nigra)* and black locust *(Robinia pseudoacacia)* (Mesterházy 2008). The catchment area of River Marcal is in the basin, with a lot of watercourses (Dövényi *et al.* 2010). The climate is temperate continental, with an average annual temperature of 10.0 °C, and annual precipitation varying between 580 and 700 mm (Dövényi *et al.* 2010).

Barn Owl pellets were collected in the Marcal Basin in 2017 *(Figure 1)*. The dates indicate only the time of collection *(Table 1a, b)*. Small mammals detected in the pellets were identified on the basis of skeletal parameters (Schmidt 1967, Tvrtković 1979, Tvrtković *et al.* 1980, Ujhelyi 1989, Kryštufek & Janžekovič 1999, März 2011). Their quantity was calculated by counting the number of skulls and their corresponding jaws. The identification of amphibians was performed based on Paunović's identification key (1990), and that of the birds on Kessler's identification key (2015).

Small mammals detected in the owl pellets were classified into four functional groups according to their preferences for urban, open, forest or wetland habitats *(Table 1a, b)*. In order to study the connection between the proportions (in Barn Owl diet) of the functional groups of small mammals of habitats in the hunting range, we used the 5 largest samples *(Table 1a, b)*. To our knowledge, Barn Owls hunt at a distance of about 1-3 km from its nesting or roosting place, but in most studies the assumed hunting range is considered to be a circle with cca. 2 km radius (Lovari *et al.* 1976, Martinez & Zuberogoitia 2004, Torre *et al.* 2015). On the map of the national scale CORINE Land Cover Project of 2012, 1:50 000 (Feranec *et al.* 2015), circles with 2 km radius were marked around the five Barn Owl nesting and roosting places in QGIS program to estimate the distribution of the various landscape types (QGIS 2013). These landscape structures (e.g. Broad-leaved forest, Non-irrigated arable land, Pastures) were classified into 4 habitat types (urban, open, forest and wetland). The comparison of the relative abundances of small mammal functional groups detected in the five samples and the proportion of the habitats within the corresponding hunting ranges were carried out by a homogeneity test G. Canonical correspondence analysis was performed for the relative abundance of small mammal functional groups detected in the five samples, and the proportions of the four habitats in the hunting ranges, which were considered to be environmental variables (Hammer *et al.* 2001).

## Results

We collected 1,144 Barn Owl pellets in the Marcal Basin from 15 settlements in 2017, in which 3,063 prey items were found. 97.5% of the prey belonged to 21 small mammal species, while the remaining 2.5% were birds, frogs and insects *(Table 1a, b)*. Mammal preys consisted of Cricetidae 40.58%, Muridae 31.15% and Soricidae 28.09%, and the remnants of European Mole *(Talpa europaea)* (0.03%), Kuhl's Pipistrelle *(Pipistrellus kuhlii)* (0.03%), Hazel Dormouse *(Muscardinus avellanarius)* (0.09%) and Least Weasel *(Mustela nivalis)* (0.03%) were also found in a few samples *(Table 1a, b)*.

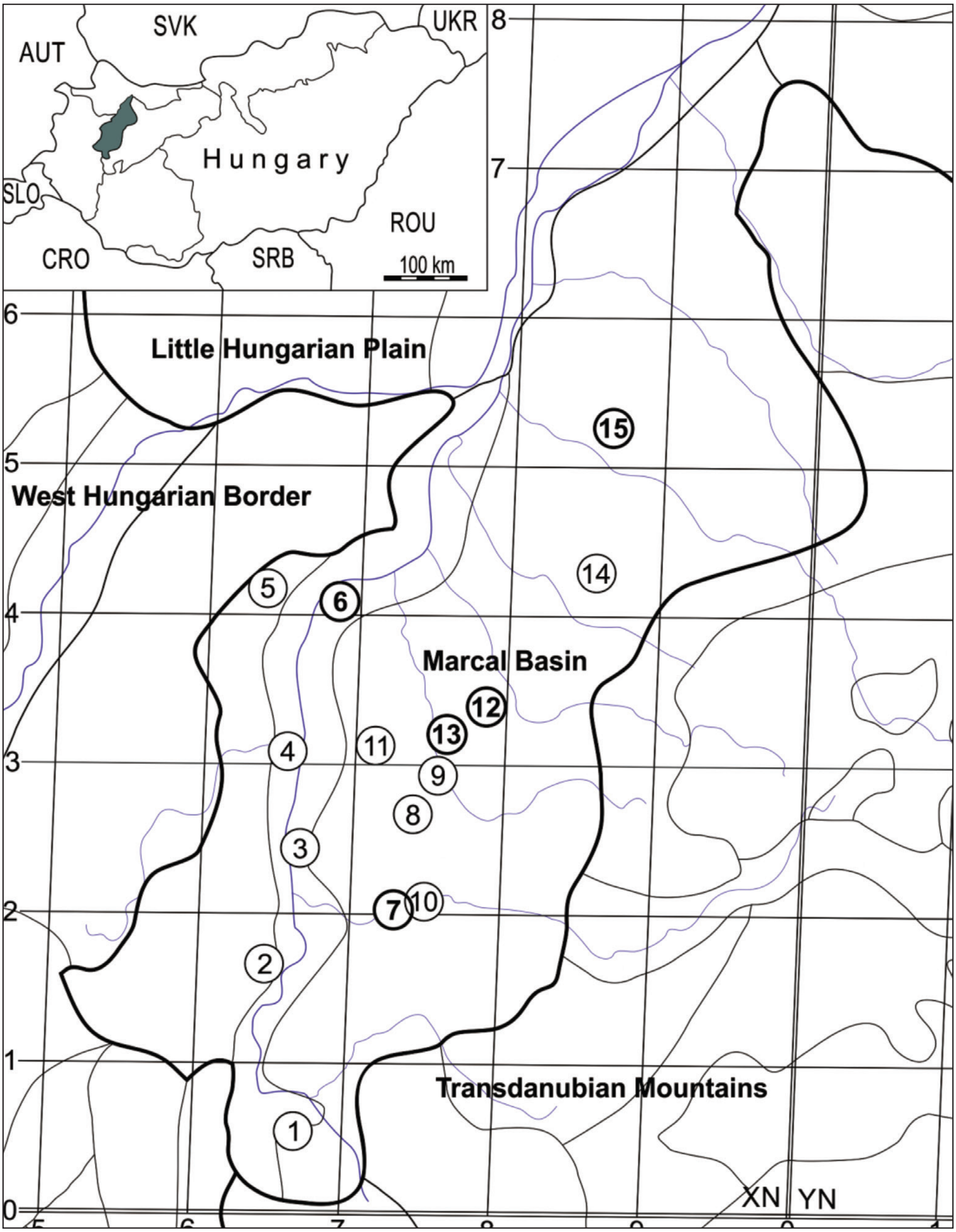

*Figure 1.* The situation of Marcal Basin in Hungary and sampling locations in the UTM: 1 – Mihályfa, 2 – Nemeskeresztúr, 3 – Nagykamond, 4 – Nemeskocs, 5 – Kemenesszentmárton, 6 – Külsővat, 7 – Apácatorna, 8 – Iszkáz, 9 – Kisszőlős, 10 – Tüskevár, 11 – Csögle, 12 – Vid, 13 – Nagyalásony, 14 – Kéttornyúlak, 15 – Takácsi (bold circles and numbers – the five sample sites used in the analysis)

*1. ábra* A 15 mintavételi hely elhelyezkedése a Marcal-medence UTM térképén ábrázolva (félkövér körök számokkal – az öt mintavételi hely, melyek szerepeltek az elemzésekben)

*Table 1a* Number of prey specimens in Barn Owl pellets in sampling sites (1–8). Abbreviations: Hp – habitat preference, u – urban habitat, o – open habitat, f – forest, w – wetland, cat – catholic church, ref – reformed church, farm – stables, granaries, UTM – Universal Transverse Mercator coordinate system, the site names of the five largest samples are markt by asterix

*1a táblázat* A köpet lelőhelyekről (1–8) előkerült zsákmányállatok egyedszáma. Rövidítések: Hp – habitat (élőhely) preferencia: u – urbán élőhely, o – nyílt élőhely, f – erdő, w – vizes élőhely, cat – katolikus templom, ref – református templom, farm – istállók, magtárak, UTM – Universal Transverse Mercator koordináta rendszer, az öt legnagyobb minta gyűjtési helye csillaggal van jelölve

| **Sampling site number** | **Hp** | **1.** | **2.** | **3.** | **4.** | **5.** | **6.** | **7.** | **8.** |
|---|---|---|---|---|---|---|---|---|---|
| **Place (locality), date** | | **Mihályfa (cat) 18.07.2017.** | **Nemeskeresztúr (cat) 18.07.2017.** | **Nagykamond (cat) 18.07.2017.** | **Nemeskocs (cat) 15.02.2017.** | **Kemenesszentmárton (cat) 04.02.2017.** | **Külsővat* (farm) 26.05.2017.** | **Apácatorna* (farm) 18.07.2017.** | **Iszkáz (cat) 02.06.2017.** |
| **UTM (10 × 10 km)** | | **XN60** | **XN61** | **XN62** | **XN63** | **XN64** | **XN64** | **XN72** | **XN72** |
| *Crocidura leucodon* | o | 0 | 0 | 1 | 2 | 5 | 9 | 6 | 4 |
| *Crocidura suaveolens* | o | 1 | 3 | 1 | 3 | 35 | 12 | 35 | 11 |
| *Sorex araneus* | f | 23 | 3 | 5 | 5 | 21 | 35 | 27 | 13 |
| *Sorex minutus* | f | 5 | 0 | 0 | 0 | 1 | 20 | 9 | 2 |
| *Neomys anomalus* | w | 0 | 0 | 0 | 2 | 3 | 5 | 9 | 1 |
| *Neomys fodiens* | w | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 0 |
| *Talpa europaea* | o | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pipistrellus kuhlii* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Muscardinus avellanarius* | f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Microtus agrestis* | w | 2 | 2 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Microtus arvalis* | o | 3 | 35 | 27 | 30 | 47 | 103 | 155 | 106 |
| *Microtus subterraneus* | o | 0 | 0 | 0 | 3 | 6 | 6 | 4 | 1 |
| *Arvicola amphibius* | w | 1 | 0 | 2 | 3 | 0 | 13 | 1 | 0 |
| *Myodes glareolus* | f | 0 | 1 | 1 | 1 | 3 | 5 | 1 | 0 |
| *Apodemus agrarius* | f | 1 | 4 | 0 | 16 | 38 | 17 | 11 | 11 |
| *Apodemus flavicollis* | f | 0 | 5 | 2 | 14 | 11 | 5 | 0 | 6 |
| *Apodemus sylvaticus* | f | 0 | 12 | 2 | 9 | 11 | 28 | 10 | 14 |
| *Apodemus* sp. | | 0 | 6 | 1 | 4 | 1 | 10 | 5 | 4 |
| *Micromys minutus* | w | 0 | 0 | 0 | 4 | 15 | 7 | 6 | 1 |
| *Mus musculus* | u | 0 | 6 | 0 | 1 | 4 | 1 | 1 | 3 |
| *Rattus norvegicus* | u | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 |
| *Rattus* sp. | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Mustela nivalis* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Passer* sp. | | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Hirundo* sp. | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Turdus* sp. | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Phoenicurus* sp. | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Aves (indet.) | | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 |
| *Pelobates fuscus* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Anura (*Rana* sp.) | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Anura (indet.) | | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 |
| Insecta (Heteroptera) | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Insecta (Coleoptera) | | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |
| Prey | | 37 | 77 | 45 | 99 | 204 | 289 | 285 | 181 |
| Pellet | | 8 | 48 | 22 | 45 | 62 | 113 | 127 | 68 |

*Table 1b* Number of prey specimens in Barn Owl pellets in sampling sites (9–15)
*1b táblázat* A köpetlelőhelyekről (9–15) előkerült zsákmányállatok egyedszáma

| **Sampling site number** | **9.** | **10.** | **11.** | **12.** | **13.** | **14.** | **15.** | **Σ** |
|---|---|---|---|---|---|---|---|---|
| **Place (locality), date** | **Kisszőlős (farm) 18.07.2017.** | **Tüskevár (farm) 06.02.2017.** | **Csögle (cat) 26.05.2017.** | **Vid* (cat) 02.06.2017.** | **Nagyalásony* (cat) 02.06.2017.** | **Kéttornyúlak (ref) 02.06.2017.** | **Takácsi* (ref) 31.05.2017.** | **Total** |
| **UTM (10 × 10 km)** | **XN72** | **XN72** | **XN73** | **XN73** | **XN73** | **XN84** | **XN85** | |
| *Crocidura leucodon* | 1 | 3 | 0 | 12 | 16 | 0 | 9 | 68 |
| *Crocidura suaveolens* | 8 | 15 | 1 | 78 | 30 | 4 | 12 | 249 |
| *Sorex araneus* | 15 | 5 | 78 | 29 | 70 | 12 | 106 | 447 |
| *Sorex minutus* | 0 | 1 | 21 | 23 | 22 | 1 | 21 | 126 |
| *Neomys anomalus* | 2 | 4 | 9 | 9 | 1 | 0 | 17 | 62 |
| *Neomys fodiens* | 0 | 0 | 0 | 1 | 3 | 0 | 4 | 13 |
| *Talpa europaea* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Pipistrellus kuhlii* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Muscardinus avellanarius* | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 3 |
| *Microtus agrestis* | 0 | 0 | 5 | 0 | 3 | 0 | 0 | 15 |
| *Microtus arvalis* | 46 | 46 | 37 | 216 | 171 | 55 | 149 | 1226 |
| *Microtus subterraneus* | 0 | 0 | 1 | 14 | 12 | 4 | 24 | 75 |
| *Arvicola amphibius* | 1 | 0 | 0 | 3 | 1 | 0 | 1 | 26 |
| *Myodes glareolus* | 1 | 1 | 4 | 9 | 10 | 0 | 15 | 52 |
| *Apodemus agrarius* | 2 | 2 | 10 | 60 | 31 | 5 | 54 | 262 |
| *Apodemus flavicollis* | 4 | 0 | 3 | 17 | 25 | 5 | 11 | 108 |
| *Apodemus sylvaticus* | 14 | 6 | 9 | 65 | 40 | 52 | 34 | 306 |
| *Apodemus* sp. | 0 | 0 | 1 | 22 | 8 | 20 | 11 | 93 |
| *Micromys minutus* | 0 | 1 | 3 | 35 | 19 | 2 | 12 | 105 |
| *Mus musculus* | 0 | 2 | 2 | 51 | 27 | 6 | 10 | 114 |
| *Rattus norvegicus* | 0 | 1 | 0 | 47 | 22 | 1 | 5 | 82 |
| *Rattus* sp. | 0 | 0 | 0 | 4 | 2 | 0 | 0 | 6 |
| *Mustela nivalis* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Passer* sp. | 0 | 0 | 0 | 0 | 2 | 0 | 5 | 9 |
| *Hirundo* sp. | 0 | 0 | 0 | 1 | 15 | 0 | 0 | 16 |
| *Turdus* sp. | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Phoenicurus* sp. | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 4 |
| Aves (indet.) | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 9 |
| *Pelobates fuscus* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Anura (*Rana* sp.) | 0 | 0 | 0 | 3 | 4 | 1 | 5 | 15 |
| Anura (indet.) | 0 | 0 | 0 | 0 | 2 | 3 | 2 | 10 |
| Insecta (Heteroptera) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Insecta (Coleoptera) | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 8 |
| Prey | 94 | 87 | 185 | 705 | 544 | 174 | 57 | 3063 |
| Pellet | 28 | 37 | 37 | 240 | 204 | 72 | 33 | 1144 |

The proportions of the four functional groups of small mammals detected in the five Barn Owl pellet sampling sites and the proportions of urban, open, forest and wetland habitats within the hunting areas were significantly different in 15 comparisons (75%) and overlapped only in 5 comparisons (25%) *(Table 2)*. In the samples from Nagyalásony and Takácsi the proportion of species preferring urban habitats showed correlation with the proportion of urban habitats within the assumed hunting areas *(Table 2)*. The proportion of small mammal species preferring open and forest habitats overlapped with the proportion of open and forest habitats within the assumed hunting range in the Apácatorna sample site only *(Table 2)*. The proportion

*Table 2.* Proportion of small mammals with different habitat preferences (h. pref.) detected from the owl pellet samples collected at the five sampling sites (%), and the comparison of these values with the share (%) of habitats (hab.) in the assumed Barn Owl hunting ranges (2 km radius circle)

*2. táblázat* Az öt mintvételi helyen gyűjtött gyöngybagoly köpetmintából kimutatott kisemlősök részesedése (%) élőhely-preferenciájuk (h. pref.) alapján, és ezeknek az értékeknek az összevetése a baglyok feltételezett vadászterületén (2 km-es sugarú kör) belül kimutatott élőhelyek (hab.) %-os részesedésével

| **Külsővat** | **h. pref.** | **hab.** | **G** | **p** |
|---|---|---|---|---|
| urban | 1.47 | 8.95 | 5.97 | <0.05 |
| open | 47.80 | 91.05 | 13.70 | <0.001 |
| forest | 40.44 | 0.00 | 56.06 | <0.001 |
| wetland | 10.29 | 0.00 | 14.27 | <0.001 |
| **Apácatorna** | **h. pref.** | **hab.** | **G** | **p** |
| urban | 0.73 | 5.27 | 3.91 | <0.05 |
| open | 71.94 | 75.89 | 0.11 | NS. |
| forest | 20.86 | 18.84 | 0.10 | NS. |
| wetland | 6.47 | 0.00 | 8.98 | <0.01 |
| **Vid** | **h. pref.** | **hab.** | **G** | **p** |
| urban | 14.61 | 3.08 | 8.16 | <0.01 |
| open | 47.69 | 94.27 | 15.24 | <0.001 |
| forest | 30.55 | 2.65 | 27.20 | <0.001 |
| wetland | 7.15 | 0.00 | 9.73 | <0.01 |
| **Nagyalásony** | **h. pref.** | **hab.** | **G** | **p** |
| urban | 9.72 | 5.88 | 0.96 | NS. |
| open | 45.63 | 82.88 | 10.96 | <0.01 |
| forest | 39.29 | 11.24 | 16.18 | <0.01 |
| wetland | 5.36 | 0.00 | 7.43 | <0.01 |
| **Takácsi** | **h. pref.** | **hab.** | **G** | **p** |
| urban | 3.09 | 9.44 | 3.37 | NS. |
| open | 40.00 | 80.62 | 13.95 | <0.01 |
| forest | 49.90 | 7.84 | 34.15 | <0.001 |
| wetland | 7.01 | 2.10 | 2.80 | NS. |

of species preferring wetland habitats was 5–10% in every hunting area, and did not overlap with the proportion of wetland habitats within the hunting areas, except for the sample of Takácsi *(Table 2)*.

According to the results of the canonical correspondence analysis, the relative abundance of small mammals preferring urban habitats and the proportion of urban habitats were different, and showed opposite values. We obtained similar results in the cases of open and forest habitats and small mammals preferring those habitats. The proportion of small mammal species preferring wetland habitats was similar to the proportion of the wetland area in the assumed circle of the hunting range. In the corresponding analysis the sample site Apácatorna was very distinguished, since there was a higher proportion of forest in the Barn Owls' hunting range *(Figure 2)*.

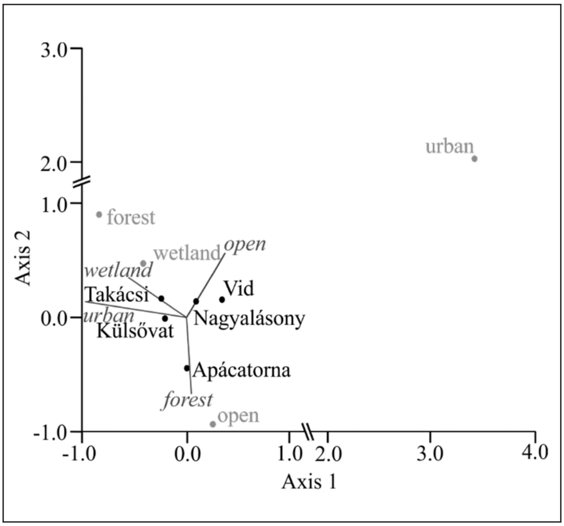

*Figure 2.* Distribution of sampling sites (names of settlements), habitats (letters in italics) and the habitat preference of small mammal species (normal gray letters) by canonical correspondence analysis

*2. ábra* A mintavételi helyek (a települések neve), az élőhelyek (dőlt betűk) és az azokat preferáló fajok (normál szürke betűk) eloszlása kanonikus korrespondancia vizsgálat alapján

## Discussion

The presence of most of the small mammal species detected in the Marcal Basin was expected, as they are common in the surrounding area (Bihari *et al.* 2007). Our results contributed to the knowledge of distribution patterns of small mammal species in the study area, since out of our 15 sampling sites similar surveys had been previously carried out only in 3 locations: Mihályfa, Nemeskeresztúr and Nemeskocs (Lázár 1983, Varga 1991, Purger & Reider 1998). The detection of Kuhl's Pipistrelle from Vid village suggested that individuals of this species occurred farther to the north-east from the already known distribution area (Fehér 2007).

Our results suggested that the representation of small mammal functional groups in the Barn Owl's diet and the proportion of various habitats in the assumed hunting ranges correlated only in 25% of the comparisons. The presumed hunting range was a circle with a 2 km radius and since pellet collecting sites were located in the central part of the mostly small rural settlements, thus urban habitats covered only 3–9%. It was expected that the proportion of urban species in the Barn Owls' diet will be similar, as the owls frequently fly over to urban habitats. Contrary to this expectation, such concordance was shown only in two of the five sample sites, while in other two cases the proportion of small mammal species preferring urban habitats was significantly lower, and in one case it was significantly higher than the proportion of urban habitats in the respective hunting range. Brown Rat *(Rattus norvegicus)* and House Mouse *(Mus musculus)* were detected in higher numbers in two samples collected from two settlements (Vid, Nagyalásony), which can be explained by the fact that several livestock farms are located there. It is widely known that the role of Brown Rat, House Mouse and House Sparrow in the food source of Barn Owls largely depends on the intensity of livestock farming (Latková 2008). The proportion of these small mammal species was similar in the two samples also because these two settlements are close to each other, thus the hunting ranges of the Barn Owls overlapped substantially.

The proportion of small mammal species preferring open habitats was in concordance with the distribution of open habitats in the Barn Owl hunting range only in one sample, while it was significantly smaller in the other four samples. A possible reason for such discrepancy can be the rough categorisation of habitats in CORINE map, where "Land principally occupied by agriculture, with significant areas of natural vegetation" (e.g. tree lines, reed beds, shrubs) was also classified as open habitat, despite the fact that it can favour other small mammal species with different habitat preferences, too. Barn Owls hunt mainly in open fields (Taylor 1994), and the proportion of species preferring forest or wetland habitats in their prey is higher due to the presence of treelines, shrubs and reed beds, while these small mammal species in the surrounding open areas are more likely to be predated. The proportion of small mammals preferring open habitats was the highest in Apácatorna, although the proportion of open habitats within the assumed hunting range was the smallest there. Apacatorna is one of the settlements affected by red mud disaster in 2010, where the highly alkaline, heavy metal contaminated flood ran through the stream Torna (Uzinger *et al.* 2015, Mayes *et al.* 2016). The effects of the disaster cannot be evaluated because of the absence of previous small mammal surveys. We cannot provide satisfactory explanation for our current results, since it is not clear why the highest concordance was revealed between small mammals' preference and the pattern of habitats in owl hunting range only in this site. The highest concordance between species preferring forests and the pattern of forest habitats was revealed in the same sampling site (Apácatorna). In all the other sampling sites, the proportion of species preferring forest habitats in the pellets was much higher than the proportion of forests within the Barn Owl hunting range.

The proportion of species preferring wetland habitats in the pellets showed some concordance with the extent of their habitats within the hunting area in one sample (Takácsi), while in the other sampling sites significantly higher proportions were revealed for such species than the extent of wetland habitats in the corresponding hunting ranges. We assumed that such result is not quite realistic, as there are hidden wetland habitats in the hunting ranges that could not be shown due to the resolution of the used map. Moreover, as mentioned above, the CORINE map shows that many of the wetland habitats are found in the open area habitat category.

Barn Owl pellets had been previously collected in 3 out of our 15 sample sites in the study area. Our current samples were small, therefore the comparison with the results of previous surveys have only informative values. In the sample collected in Mihályfa in 2017, species preferring forest habitat dominated (78%), similarly to the previous survey in 1977, when their proportion reached 60% (Lázár 1983). In the sample collected in 2017 from Nemeskeresztúr, the proportion of small mammals preferring open and forest habitats was 49%, and 40%, respectively, while in the sample from 1984 this difference was even higher: 69% of species preferring open habitat versus only 19% of species preferring forest habitats (Varga 1991). About 50% of the prey items from Nemeskocs in 2017 were made up of species preferring forest habitats, 39% were species preferring open habitats, and 10% were small mammal species typical for wetlands. In the survey conducted in 1996, the species preferring open habitats were highly dominant (82%) in the diet of the owls, while the proportion of species preferring forest habitats (17%) was much lower (Purger & Reider 1998).

From the comparisons it can be seen that the proportion of functional groups of small mammals preferring different habitats in the diet of Barn Owl may change significantly over time. The causes of these changes are difficult to detect and explain, though it is expected that changes in the landscape structure influence small mammal communities in the owls' hunting ranges. The limitations of the method applied in this study were highlighted by the fact that owl hunting ranges can differ in size and quality (Arlettaz *et al.* 2010) and their diet composition is influenced by the availability of small mammal species and the finer structure of the landscape (e.g. Bond *et al.* 2004, Lyman 2012, Horváth *et al.* 2018). For this reason, we should try to collect samples from the study area for as many years as possible, with seasonal frequency (Fehér & Fehér 2004). The limitations of the usability of this method are also influenced by the fact that owls hunt not only within the assumed hunting range, and are likely to prefer more accessible species (Moysi *et al.* 2018). We suggest improving the efficiency of the method by using finer structure of the landscape and more precise definition of habitats. For finding evidence that small mammal prey composition reflects landscape habitat structure the best fitting hunting range size should be established.

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# Little Owl's *(Athene noctua)* vertebrate food composition during breeding season with high frog dominance in grasslands

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**Abstract** The aim of our study was to investigate the feeding of the Little Owl *(Athene noctua)* during the breeding period in three protected sites (Upper Kiskunság Puszta, Upper Kiskunság Lakes, Peszéradacs Meadows) in an extensively managed lowland plain area (Upper Kiskunság) of the Carpathian Basin. A further objective was to provide a detailed assessment of the vertebrate prey spectrum and dominance structure based on the analyses of pellets. Little Owl pellets were collected in September 2015 and 2016 from 20 artificial nest boxes in which successful breeding occurred in both years. Mean pellet number was calculated per individuals. Distribution of individual number and biomass of vertebrate prey taxa were also examined. The number of collected and dissected owl pellets was 2,094 in 2015 and 2,024 in 2016, respectively. The average rate of pellet regurgitation was 25.57 pellets/ind. in 2015, and 27.74 pellets/ind. in 2016. From the 40 samples (4,118 owl pellets) a total of 2,017 vertebrate preys were determined. Cumulative species richness was 21, including 12 mammalian, 1 amphibian, 4 reptile and 4 bird species. Mammals were dominant in the food (average 50.83%), and the consumption of amphibians was similar (48.06%). The consumption of birds and reptiles was not significant. Amphibians were represented by a single species, the Common Spadefoot *(Pelobates fuscus)* in remarkably high proportions among the prey items, followed by the Common Vole *(Microtus arvalis)* by approx. 37% proportion. The high proportion of the latter two species was also clearly reflected in the biomass amounts. Among the birds, the Starling *(Sturnus vulgaris)* proved to be the most commonly predated species apart from other species closely related to farmland habitats *(Motacilla alba, M. flava, Passer montanus)*.

Keywords: nutrition, owl pellet analysis, Kiskunság, grassland, Strigidae, Amphibia

**Összefoglalás** A kutatás célja a kuvik *(Athene noctua)* költési időszakra vonatkozó táplálkozásának vizsgálata volt a Felső-Kiskunság három védett területegységén (Felső-Kiskunsági Puszta, Felső-Kiskunsági Tavak, Peszéradacsi Rétek). Célunk volt a kuvik gerinces zsákmányállataira kiterjedő részletes, nagyobb mintaszámú vizsgálata, e közösség tekintetében a faj táplálkozási szokásainak és alkalmazkodási képességének feltárása. 2015-ben és 2016-ban célzottan került sor köpetgyűjtésre, a kirepülést követően (szeptember) azon odúkból, amelyekben sikeres költés zajlott mindkét évben. Megállapítottuk az egy egyedre eső átlagos köpetszámot, valamint területi és gyűjtési év elkülönítésben vizsgáltuk a gerinces zsákmányfajok egyedszám és biomassza-tömeg szerinti megoszlását. A meghatározott/gyűjtött köpetszám 2015-ben 2094, 2016-ban 2024 volt. Az odúkban lezajlott köpetelések egy egyedre vonatkoztatott száma átlagosan 25,57 köpet/egyed volt 2015-ben, 27,74 köpet/egyed 2016-ban. A gyűjtött 40 mintában (4118 köpet) összesen 2017 gerinces zsákmányegyedet határoztunk meg. A mintákban azonosított fajok száma a két évre összességében 21 volt, amelyből 12 emlős-, 1 kétéltű-, 4 hüllő- és 4 madárfaj. A kuvikok az emlősöket zsákmányolták elsődlegesen (átlag 50,83%), és ehhez hasonló mértékű volt a kétéltűek fogyasztása is (átlag 48,06%). A madarak és a hüllők fogyasztása nem volt jelentős. A kétéltűeket egyetlen faj, a barna ásóbéka *(Pelobates fuscus)* képviselte, amely mennyisége és aránya igen figyelemre méltó volt (átlagosan 41,68%). A második meghatározó táplálékforrás a területen a mezei pocok *(Microtus arvalis)* volt ~37% részaránnyal. Előbbi két domináns faj magas egyedszám szerinti részaránya a biomassza-tömeg szerinti értékekben is egyértelműen tükröződött. A madarak közül a seregély *(Sturnus vulgaris)* bizonyult a leggyakrabban zsákmányolt fajnak más mezőgazdasági élőhelyekhez szorosan kötődő énekesmadarak *(Motacilla alba, M. flava, Passer montanus)* mellett.

Kulcsszavak: táplálkozás, bagolyköpet-elemzés, Kiskunság, gyepterületek, Strigidae, Amphibia

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## Introduction

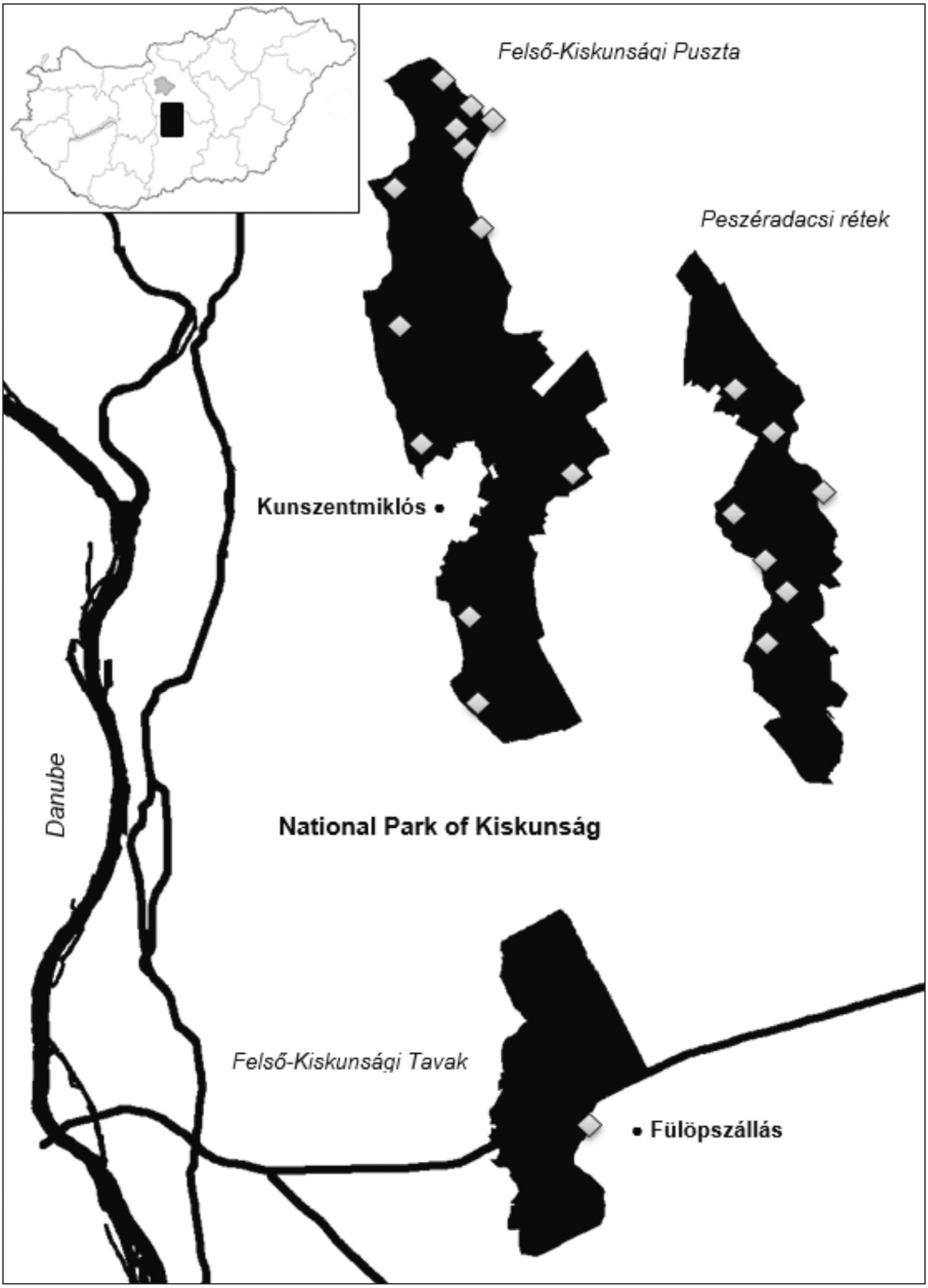
The population of the Little Owl *(Athene noctua)* has declined in many European countries, especially in the western areas (Cramp 1985, Mánez 1994, Heath *et al.* 2000, Génot & Van Nieuwenhuyse 2002, Zmihorski *et al.* 2006, Šálek & Schröpfer 2008, Van Nieuwenhuyse *et al.* 2008, Sunde *et al.* 2009, BirdLife International 2016). The number of breeding pairs in Hungary is estimated to be between 1,500 and 4,000 pairs, the population trend is unknown (Gorman 1995, Hadarics & Zalai 2008, Šálek *et al.* 2013, BirdLife International 2016, Hámori 2017b). In certain regions of the Great Plain (e.g. Békés and Bács-Kiskun counties), the species has a significant population with increasing population trend observed in the past decade (Bozó & Csathó 2017, Hámori *et al.* 2017b). As a consequence of their population decline, the conservation and research of the Little Owl have become important priorities in most European countries (e.g. Zerunian *et al.* 1982, Génot 1994, Angelici *et al.* 1997, Tomialojc & Stawarczyk 2003, Zmihorski *et al.* 2006, Van Nieuwenhuyse *et al.* 2008). The ecological mechanisms responsible for these negative tendencies are less known. To date, many hypotheses have been raised as explanations, which include habitat-structural changes, habitat fragmentation, decline in feeding sites, and other ecological factors (Zerunian *et al.* 1982, Génot 1994, Angelici *et al.*1997, Schaub *et al.* 2006, Sunde *et al.* 2009, Zmihorski *et al.* 2009, Le Gouar *et al.* 2011). Most of the research related to Little Owls was carried out in Western Europe (e.g. Denmark, The Netherlands, Germany, Portugal, Spain); therefore the mechanisms described in these studies are not necessarily relevant to the Central and Eastern European populations (Van Nieuwenhuyse *et al.* 2008, Tryjanowski *et al.* 2011). The decreasing population trend of the Little Owl and related issues, such as detailed feeding biology, require further studies in Central and Eastern Europe. Agricultural intensification also contributed to the decline in food availability for many wild species (Newton 2004, Morris *et al.* 2005). This negative tendency can be observed also in the case of farmland bird species in Hungary (Szép & Nagy 2006, Báldi & Batáry 2011, Szép *et al.* 2012). Nevertheless, in addition to nesting-site availability, the trend of a given Little Owl population is closely related to the feeding possibilities and food availability (Génot & Van Nieuwenhuyse 2002, Zmihorski *et al.* 2006, Thorup *et al.* 2010, Apolloni *et al.* 2018). In general, the effects of agricultural intensification may result in a decrease in the abundance of arthropods and small mammals (Morris 2000), which are the primary food sources for the Little Owl (Van Nieuwenhuyse *et al.* 2008). Furthermore, habitat transformations in agricultural areas may further reduce the availability of food to the owls (Apolloni *et al.* 2018). The Little Owl has various haunting techniques. As a polytypical species, and as the result of its large distribution area, the Little Owl catches a large number of different prey species (e.g. Mikkola 1983, Cramp 1985, Schönn *et al.* 1991, Angelici *et al.* 1997, Milchev & Nikolay 2017). Primarily, small mammals and invertebrates dominate the Little Owl diet, but feed also on songbirds, amphibians, reptiles, and rarely fishes (Glutz von Blotzheim & Bauer 1980, Cramp 1985, Schmidt 1998). The Little Owl is fundamentally generalist, so there is no clear correlation between the number of species and the number of pellets (Lanszki 2006, Van Nieuwenhuyse *et al.* 2008). According to the pellet analyses carried out in European and Middle Eastern countries, the Little Owl's diet consists mostly of insects, but its feeding habits may differ according to the habitat and geographical region (Herrera & Hiraldo 1976, Cramp 1985, Gorzel & Grzywaczewski 2003, Obuch & Kristin 2004). Several studies on food composition and feeding habits have been carried out in the Mediterranean region, Western Europe and the Middle East (e.g. Obuch & Kristin 2004, Alivizatos *et al.* 2005, Van Nieuwenhuyse *et al.* 2008, Kayahan & Tabur 2016). Detailed studies on feeding biology are also essential in Central Europe to support nature conservation strategies. In Hungary, Little Owl feeding data are mostly pre-millenial or based on small number samples (Greschik 1911, 1924, Marián & Schmidt 1968, Molnár 1984, Andrési & Sódor 1986, Endes 1990), and only in some cases seasonal or fully processed (Lanszki 2006, Hámori *et al.* 2017a). In this respect, the Little Owl is one of the least studied owls in Hungary.

The main goal of our study was to investigate the vertebrate prey items of the Little Owl by analyzing a large number of pellets collected during the breeding period in an extensively managed lowland plain area of the Carpathian Basin; and thereby to explore the feeding habits and adaptation ability of this species. A further aim was to provide a detailed assessment of the vertebrate prey spectrum and dominance structure based on the analyses of pellets collected in the study sites.

## Material and methods

### Study area

The research was carried out in protected areas managed by the Kiskunság National Park in the north-western part of the Great Plain, in Pest and Bács-Kiskun counties *(Map 1)*. The continental climate is dominant in the area. Average annual rainfall is moderate (540–670 mm), warm summer and relatively cold winter (average annual temperature 13.3 °C) are the characteristics of this region. The average altitude is 84 meters. The landscape of the Kiskunság is uniform, established by the ancient Danube river. Large-scale agricultural intensification has begun since the turn of the 19th century. Nowadays, more than 60% of the cultivated land is utilized by modern agricultural practices (Rakonczay 2001). A large part of the grasslands were maintained by grazing (sheep, cattle) and traditional grassland management. The elements of today's landscape are the canal systems, large plains, pastures, sand dunes, smaller salty lakes, bogs, reeds, sandy forests, as well as man-made arable land, orchards, vineyards, and the typical boonies of huge ecological importance for Little Owls. Traditional farming is still in existence and the typical farm life plays a significant role in preserving natural values (Voloscuk 1999). The Little Owl pellets were collected from the study sites Upper Kiskunság Puszta, Upper Kiskunság Lakes and Peszéradacs Meadows, a brief description of which is given below (Kollárik 1999, Voloscuk 1999, Rakonczay 2001).



*Map 1.* Map of the study sites and sampling locations (artificial nest boxes)
*1. térkép* A gyűjtések alapjául szolgáló mesterséges kuvikodúk elhelyezkedése a kutatási területen

### *Upper Kiskunság Puszta (11,061 ha)*

The surrounding settlements of the Little Owl nesting places sampled are Apaj, Bugyi, Kiskunlacháza, Kunbábony and Kunszentmiklós. The hydrological conditions of the area have changed dramatically over the last century due to drainage works. The former wild waters were diverted and a channel system was constructed. As a consequence, salinization processes accelerated. Salty meadows and pastures are characterized by shallow lakes and other water bodies. The Solonchak-Solonetzic soils that characterize the area have resulted in the formation of salt-tolerant and halophilic vegetation. The vegetation of alkaline steppes has a mosaic-structure, which is due to the richness of the microrelief. The extensive area of permanent and temporary bodies provides favorable conditions for breeding and migratory birds as well as for amphibians. Traditional farming in this area is in decline. The few family sheep-farming are more and more replaced by dairy cattle farms. In the northern part of the area, organic farming is dominant, characterized primarily by the Hungarian gray cattle and water buffaloes. The sampling places of pellets are located in the close neighborhood of different farm buildings.

### *Upper Kiskunság Lakes (3,905 ha)*

The adjacent settlement of Little Owl pellet sampling location is Fülöpszállás. The lakes in this area provide food supply (e.g. insect larvae, crustaceans) to the bird communities typical for halophytic habitats. A significant part of the area is covered by alder–narrow-leaved ash swamp forests. The pellet sampling was carried out next to an abandoned farming unit on the edge of the area.

### *Peszéradacs Meadows (5,757 ha)*

Settlements neighbouring the Little Owl nesting places are Kunpeszér and Tatárszentgyörgy. In this sparsely populated countryside, grazing and traditional farming are characteristic. Water management has removed or transformed landscapes in most places. Among its varied habitats, wetlands, marshes, wet meadows and sandy grasslands and sandy forests are worth mentioning. The proportion of hay fields and wet meadows is high. The sampling places are mainly located in the immediate vicinity of the various farm buildings where usually sheep is housed.

## Pellet sampling and analysis

Little Owl pellets were collected in September 2015 and 2016, in three different sites. The sampled material included all pellets found in the next boxes affected. Within the tree sites, mean distance between the sampling plots (nest boxes) was 2,660 m. Prior to sampling, we removed the old pellet remains from each nest box before the nesting period of the given year (15–31 March). The collected samples, therefore, contained food remains accumulated during the 6 months of the breeding season (spring and summer) by adults and their nestlings. The collected material therefore included part of the food remnants of the adult pair as well as total food remnants by the nestlings until their fledging from the nest. A significant part of the pellet material collected from the nest boxes were trampled by the young Little Owls. For the purpose of determining the approximate pellet number, any other extraneous material (e.g. chips) was first removed and the volume of the sample was measured. Based on the measurements of undamaged pellets (N = 218; mean: 5.62 cm$^3$) and on the basis of literature data (Sageder 1990, Gorzel & Grzywaczewski 2003), the estimated pellet number of each sample was determined as the average of three measurements. The pellets were dried and processed by standard methods (Schmidt 1967, Raczyński & Ruprecht 1974). The remains were analysed by using a stereo microscope under 15.75× or 25.2× magnification. Vertebrate and arthropod remains were selected separately from the pellet material for possible future determination. Small mammals were identified from skulls, mandibles and teeth based on the works of Schmidt (1967), Topál (1969), Móczár (1984), März (1987), Ujhelyi (1989), Diesener and Reicholf (1997). Birds were determined on the basis of skulls, bills, femurs and feathers (Brown *et al.* 1993, Kessler 2015), while amphibians and reptiles were identified by the lower arm bones, femoral bones and skulls (Dely 1967, 1978), taking into account the fronto-parietale in case of amphibians. The number of vertebrate prey was evaluated based on the highest number of a certain type of body remains. Whenever it was possible, specimens were identified to species level. For determining biomass, weight of the prey species was derived from various literature (Dely 1967, 1978, Topál 1969, Goddard 1984, Ujhelyi 1989, Petrescu 1994, Fattorini *et al.* 1999, Grzywaczewski *et al.* 2006, Kitowski & Pawlega 2010, Romanowski *et al.* 2013).

### Data analysis

Mean pellet number was determined for each site for each study year. Mean pellet number was also calculated per individuals, taking into account the successfully fledged juveniles and the female adult bird, which predominantly drops the pellets inside the nest box during the breeding season. Distribution of individual number and biomass of vertebrate prey taxa were examined for each site and year.

## Results

The number of collected and dissected owl pellets was 2,094 in 2015 and 2,024 in 2016, respectively (4,118 altogether); these were collected from the same 20 nest-boxes located in the three study sites: 12 in Upper Kiskunság Puszta, 7 in Peszéradacs Meadows, and a single in Upper Kiskunság Lakes. In all of the nest boxes the hatching was successful in both years. Further data on the sampling were summarized in *Table 1*. The number of owlets that have successfully left their nest boxes was 62 in 2015 (3.1 in average), and 69 in 2016 (3.45 in average); the average number of owl pellets per nest-box was 105 in 2015 and 101 in 2016. Based on these datasets and considering the habits and methods of regurgitation of pellets in adult and pullus individuals during the nesting period (March–September), the average rate of pellet regurgitation was 25.57 pellets/ind. in 2015, and 27.74 pellets/ind. in 2016.

*Table 1.* Summary of Little Owl pellet sampling parameters and the total number of pellets per area

*1. táblázat* A kuvik köpetminták gyűjtésének fontosabb adatai és a teljes köpetszám területegységenként

| **Name of area** | **Site** | **Number of sampling points** | **ID of artificial nest boxes** | **Calculated number of collected pellets (2015)** | **Total number of pellets per area (2015)** | **Calculated number of collected pellets (2016)** | **Total number of pellets per area (2016)** |
|---|---|---|---|---|---|---|---|
| Upper Kiskunság Puszta | Apaj | **12** | 269 | 46 | **1374** | 110 | **1227** |
| | Bugyi | | 245 | 156 | | 110 | |
| | Bugyi | | 296 | 82 | | 110 | |
| | Bugyi | | 343 | 266 | | 64 | |
| | Bugyi | | 237 | 137 | | 73 | |
| | Bugyi | | 240 | 156 | | 73 | |
| | Bugyi | | 292 | 128 | | 119 | |
| | Kiskunlacháza | | 181 | 92 | | 137 | |
| | Kunbábony | | 227 | 82 | | 201 | |
| | Kunszentmiklós | | 211 | 82 | | 82 | |
| | Kunszentmiklós | | 213 | 55 | | 110 | |
| | Kunszentmiklós | | 253 | 92 | | 37 | |
| Peszéradacs Meadows | Kunpeszér | **7** | 221 | 92 | **677** | 92 | **696** |
| | Kunpeszér | | 256 | 46 | | 192 | |
| | Kunpeszér | | 284 | 92 | | 137 | |
| | Kunpeszér | | 285 | 165 | | 64 | |
| | Kunpeszér | | 286 | 92 | | 82 | |
| | Kunpeszér | | 187 | 137 | | 46 | |
| | Tatárszentgyörgy | | 260 | 55 | | 82 | |
| Upper Kiskunság Lakes | Fülöpszállás | **1** | 201 | 46 | **46** | 101 | 101 |
| | | | | *Total* | ***2097*** | *Total* | ***2024*** |

A total of 2,017 vertebrate preys were determined from the 40 samples (4,118 owl pellets), (935 from the year 2015 and 1,082 from 2016). The total number of species identified in the samples was 21, including 12 mammalian, 1 amphibian, 4 reptile and 4 bird species. Relative proportion of each prey categories as mammals, amphibians, reptiles and birds is presented in *Figure 1*.

According to the prey communities, it is clear that in the examined area there is no material difference in the proportions based on the results of the two collection years. Mammals were dominant in the food (average 50.83%), and the consumption of amphibians was similar (average 48.06%). According to our data, the consumption of birds and reptiles was not significant, predation of these groups rarely occurred (birds and reptiles totalled 2.22%).

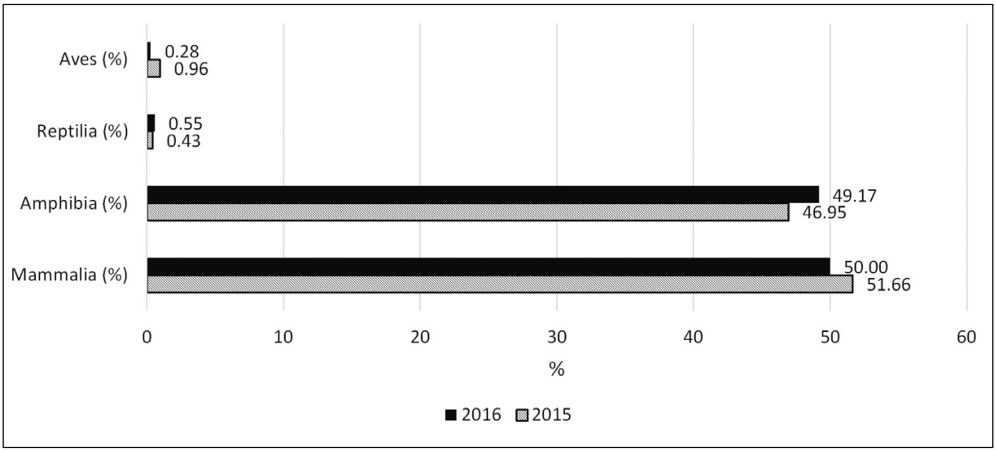


*Figure 1.* Proportion of vertebrate diet of Little Owls (period March–September in 2015 and 2016; $N_{2015}$=935 and $N_{2016}$=1018 prey individuals)

*1. ábra* A kuvik gerinces zsákmányállatainak összesített megoszlása (2015 és 2016 március-október; 935 és 1018 meghatározott egyed alapján)

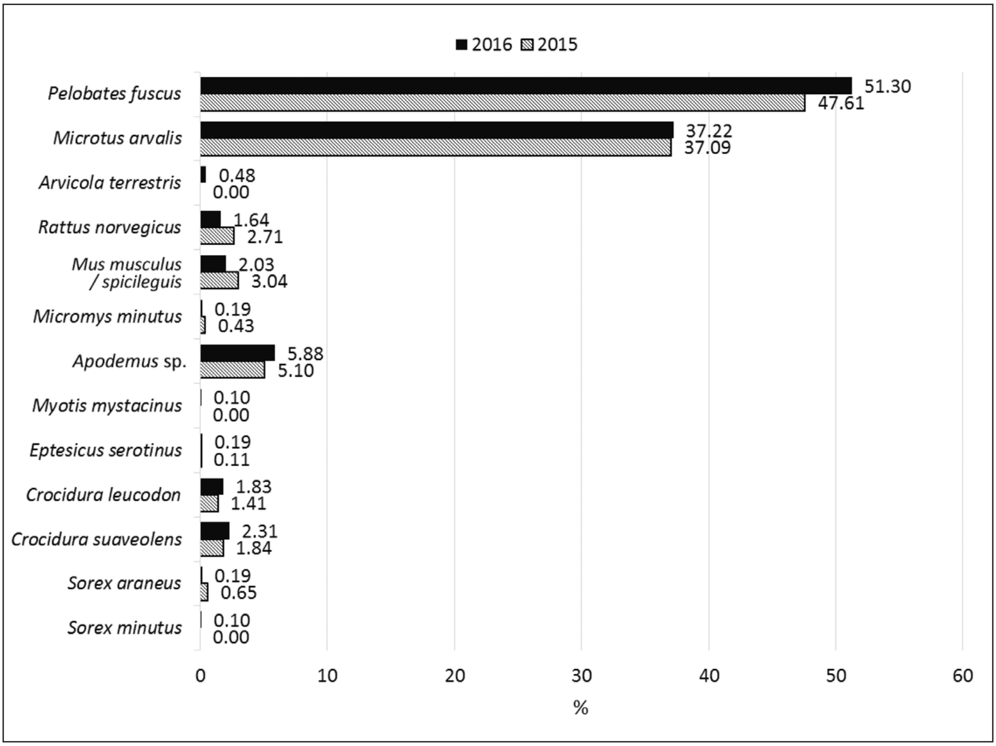


*Figure 2.* Proportion of mammal and amphibian preys by taxon in 2015 and 2016

*2. ábra* Emlősök és kétéltűek taxononkénti megoszlása 2015-ben és 2016-ban

*Table 2.* Vertebrate food composition of the Little Owl in the study sites; *g* – grams, *N* – number of prey, *m* – pray biomass

*2. táblázat* A kuvik gerincestáplálék-összetétele a vizsgált élőhelyeken; *g* – gramm, *N* – zsákmányállatok száma, *m* – zsákmányállatok biomassza tömege

| **Taxa** | **Weight** | **Felső-Kiskunsági Puszta** | | | | **Felső-Kiskunsági Tavak** | | | | **Peszéradacsi rétek** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **2015** | | **2016** | | **2015** | | **2016** | | **2015** | | **2016** | |
| | **(g)** | **% *N*** | **% m** | **% *N*** | **% m** | **% *N*** | **% m** | **% *N*** | **% m** | **% *N*** | **% m** | **% *N*** | **% m** |
| **Class AMPHIBIA** | | ***51.16*** | ***31.96*** | ***46.26*** | ***35.85*** | ***0.00*** | ***0.00*** | ***56.82*** | ***46.62*** | ***41.46*** | ***21.30*** | ***54.41*** | ***27.05*** |
| *Pelobates fuscus* | 20.0 | 51.16 | 31.96 | 46.26 | 35.85 | | | 56.82 | 46.62 | 41.46 | 21.30 | 54.41 | 27.05 |
| **REPTILIA** | | ***0.33*** | ***1.88*** | ***0.85*** | ***0.57*** | ***0.00*** | 0.00 | 0.00 | 0.00 | 0.63 | 0.63 | 0.00 | 0.00 |
| *Podarcis taurica* | 18.5 | | | 0.71 | 0.51 | | | | | | | | |
| *Lacerta agilis* | 12.5 | 0.17 | 0.06 | 0.14 | 0.07 | | | | | 0.32 | 0.10 | | |
| *Coronella austriaca* | 65.0 | | | | | | | | | 0.32 | 0.53 | | |
| *Emys orbicularis* | 350.0 | 0.17 | 1.82 | | | | | | | | | | |
| **Class AVES** | | ***1.16*** | ***1.73*** | ***0.14*** | ***0.13*** | ***0.00*** | ***0.00*** | ***0.00*** | ***0.00*** | ***0.63*** | ***0.81*** | ***0.61*** | ***0.80*** |
| *Motacilla flava* | 18.0 | 0.17 | 0.09 | | | | | | | 0.32 | 0.15 | | |
| *Motacilla alba* | 23.0 | 0.33 | 0.24 | | | | | | | | | | |
| *Passer montanus* | 24.0 | 0.17 | 0.12 | 0.14 | 0.13 | | | | | | | 0.30 | 0.18 |
| *Sturnus vulgaris* | 82.0 | 0.50 | 1.28 | | | | | | | 0.32 | 0.67 | 0.30 | 0.62 |
| **Class MAMMALIA** | | ***47.34*** | ***64.43*** | ***52.61*** | ***63.39*** | ***100.0*** | ***100.0*** | ***43.18*** | ***53.38*** | ***56.96*** | ***77.21*** | 44.98 | 72.14 |
| *Sorex minutus* | 5.0 | | | 0.14 | 0.03 | | | | | | | | |
| *Sorex araneus* | 10.0 | 0.50 | 0.16 | | | | | | | 0.95 | 0.24 | 0.30 | 0.08 |
| *Crocidura suaveolens* | 5.0 | 1.50 | 0.23 | 2.82 | 0.55 | 11.76 | 2.04 | | | 1.90 | 0.24 | 1.22 | 0.15 |
| *Crocidura leucodon* | 10.5 | 1.00 | 0.33 | 1.27 | 0.52 | | | 2.27 | 0.98 | 2.22 | 0.60 | 2.74 | 0.71 |
| *Apodemus* sp. | 25.0 | 4.32 | 3.37 | 5.36 | 5.19 | | | 4.55 | 4.66 | 6.65 | 4.27 | 6.38 | 3.97 |
| *Micromys minutus* | 5.0 | 0.50 | 0.08 | 0.28 | 0.05 | | | | | | | | |
| *Mus musculus et spicilegus* | 21.0 | 1.66 | 1.09 | 2.40 | 1.95 | | | | | 5.70 | 3.07 | 1.22 | 0.63 |
| *Rattus norvegicus* | 375.0 | 1.99 | 23.35 | 0.28 | 4.10 | | | | | 4.11 | 39.64 | 4.56 | 42.51 |
| *Arvicola terrestris* | 125.0 | | | 0.42 | 2.05 | | | | | | | 0.61 | 1.89 |
| *Microtus arvalis* | 32.0 | 35.71 | 35.69 | 39.35 | 48.79 | 88.24 | 97.96 | 36.36 | 47.74 | 35.44 | 29.14 | 27.66 | 22.01 |
| *Eptesicus serotinus* | 26.0 | 0.17 | 0.13 | 0.14 | 0.14 | | | | | | | 0.30 | 0.20 |
| *Myotis mystacinus* | 5.0 | | | 0.14 | 0.03 | | | | | | | | |
| **Species richness** | | **16** | | **15** | | **2** | | **4** | | **12** | | **12** | |
| **Cumulative species richness** | | **20** | | | | **5** | | | | **15** | | | |

Based on the results of *Figure 1*, only the mammals and amphibians, by taxonomic distribution, are evaluated as percentages *(Figure 2)*.

Dominance of the Common Spadefoot *(Pelobates fuscus)* was the highest among the prey items; its relative proportion was similar in both years (47.61 and 51.3%), and it was followed by the Common Vole *(Microtus arvalis)* by approx. 37% proportion. The next items were far behind of these two species, and they did not reach even 6%. Field mice (*Apodemus* sp.) reached 5.1 and 5.88%, while the occurrence of other items was insignificant (see *Table 2*). By the number of species identified in a given site, the most species (20 vertebrate species) were found in the Upper Kiskunság Puszta. In all three sites and in both study years, except for Upper Kiskunság Lakes in 2015, mammals and amphibians were present in roughly the same number. Amphibians were represented by a single species, the Common Spadefoot in remarkably high proportions. Based on the identified prey items, mammals were dominated in almost all of the years and sites. Their proportion was the lowest in Peréradacs Meadows in 2016 (44.98%), and it was exceeded even by the Common Spadefoot (54.41%). Predation on Common Vole was detected in all three areas in 27.66 and 88.24%; the Common Spadefoot was absent only in the samples of the Upper Kiskunság Lakes collected in 2015. However, its proportion was the highest in all of the years if we analysed the dataset by species and not by higher taxonomical units, except at the Upper Kiskunság Lakes in 2015. The second most common mammal prey was the Field Mice (*Apodemus* sp.) by 4.32 – 665%, while the proportion of the House Mouse/Mound-building Mouse *(Mus musculus, M. spicilegus)* was lower (1.2 – 5.7%), and they were completely missing from the samples of Upper Kiskunság Lakes. Brown Rat *(Rattus norvegicus)* was also found in quite high numbers in the samples of the Peszéradacs Meadows in 2016 (4.56%). Besides the rodent species, several shrew species (Soricomorpha) were also identified such as the Lesser White-toothed Shrew *(Crocidura suaveolens)*, the Bicolored Shrew *(C. leucodon)*, the Eurasian Pygmy Shrew *(Sorex minutus)* and the Common Shrew *(S. araneus)*. Bats were represented by 3 individuals of the Serotine Bat *(Eptesicus serotinus)* and a single specimen of the Whiskered Bat *(Myotis mystacinus) (Table 2)*. Proportion of the birds was generally low and varied depending on the specificity of the territory. Their proportion exceeded 1% (1.16%) only in a single case, in the Upper Kiskunság Puszta area in 2015. Their highest proportion was recorded in the samples of the Upper Kiskunság Puszta, while they were completely missing from the samples of Upper Kiskunság Lakes.

Regarding birds, the Starling *(Sturnus vulgaris)* proved to be the most commonly predated species, but other species closely related to farmland habitats; White Wagtail *(Motacilla alba)*, Western Yellow Wagtail *(Motacilla flava)*, Eurasian Tree Sparrow *(Passer montanus)* were also hunted by the owls. Though predation on reptiles was insignificant (a total of 1.81% in this study), emergence of the Smooth Snake *(Coronella austriaca)* among prey items was remarkable. Besides this, reptiles were represented by few individuals of the Sand Lizard *(Lacerta agilis)* and the Balkan Wall Lizard *(Podarcis taurica)*, and a juvenile European Pond Turtle *(Emys orbicularis)*, which was found in a nest box located close to a fishpond.

The high proportion of the two dominant species (Common Spadefoot and Common Vole) was also clearly reflected in the biomass amounts. The rate by weight of Common Vole in all sites and years, except for the 2016 collections of Peszéradacs Meadows, slightly exceeded the weight ratio of the Common Spadefoot. Although the majority of species were dominated by the Common Spadefoot, predominance of the Common Vole was dominant in the weight and nutritional aspects of the breeding season (March–September). Furthermore, the total biomass of amphibians, reptiles and birds did not approach mammalian in neither of the cases. Based on these results, generally it can be stated that at the level of animal communities, the surveyed Little Owl population primarily preferred mammals and secondly amphibians in their diet.

## Discussion

The Little Owl is basically a generalist predator, its hunting behaviour is adapted to the availability of potential prey species (Cramp 1985, Schönn *et al.* 1991, Laiu & Murariu 1997, Van Nieuwenhuyse *et al.* 2008, Šálek *et al.* 2010). As it was already previously known, it hunts for a wide variety of prey due to its large distribution area and various hunting techniques (Mikkola 1983, Cramp 1985, Angelici *et al.* 1997, Van Nieuwenhuyse *et al.* 2008). This is well reflected in the prey composition of Little Owls of different geographical regions (Shehab *et al.* 2004, Charter *et al.* 2006, Kayahan & Tabur 2016), and in different habitats within the same geographical region (Van Nieuwenhuyse *et al.* 2008, Apolloni *et al.* 2018). The role of small mammals in the Southern European region is generally less important; however, vertebrates can be dominant in some Mediterranean regions (Goutner & Alivizatos 2003); in Central Europe the proportion of small mammals is usually high (Zerunian *et al.* 1982, Mánez 1983, Schönn *et al.* 1991, Ille 1992, Genot & Van Nieuwenhuyse 2002, Gorzel & Grzywaczewski 2003, Tomé *et al.* 2008, and the present study).

Within vertebrates, the proportion of mammals (43.18 – 100%) was less than it was reported by previous Hungarian (Greschik 1911, 1924, Schmidt 1967, Marián & Schmidt 1968, Lanszki 2006) and Central European studies (Romanowski 1988, Ille 1992, Génot & Bersuder 1995, Laiu & Murariu 2000, Schmid 2003, Georgiev 2005, Grzywaczewski *et al.* 2006, Romanowski & Zmihorski 2006, Kitowski & Pawlega 2010, Romanowski *et al.* 2013) due to the predominance of amphibians. Contrary to other Hungarian studies (Greschik 1911, 1924, Marián & Schmidt 1968, Molnár 1984, Andrési & Sódor 1986, Endes 1990, Kovács & Cserkész 2005, Lanszki 2006), amphibians gave the most to the prey of Little Owls in this study.

The Common Spadefoot was the most frequent prey, which was followed by the Common Vole, a common species of grasslands and agricultural fields. Since only very few records exist on higher rates of amphibians in owl pellets (Uttendörfer 1939, Festetics 1955), the observed high proportion of the Common Spadefoot in the Little Owl pellets merits a special mention. Although, some authors emphasized the importance of seasonal availability of frog species (Mikkola 1983), none of the Hungarian and Central European studies have found so far such a high proportion of amphibians (including the Common Spadefoot); generally, the proportion of amphibians remains under 5%.

The Common Spadefoot was totally missing from the samples of Upper Kiskunság Lakes in 2015; this was when the owls switched their prey preference and started to hunt for

Common Voles, which consisted 88.24% of their prey items. However, in 2016 the results were already similar to the other sites with a proportion of 56.82% the Common Spadefoot. This could be explained by the dry weather of February-April 2015 when the water-covered areas were reduced, and the salt lakes on the periphery area dried out. These effects could have had a significant impact on the abundance of the Common Spadefoot. Although the Little Owl is considered to be a generalist raptor, it seems by the large number of frogs in its diet, that it is apt to hunt opportunistically if the prey is abundant enough and easy to catch. For an owl it is easy to hunt for frogs at sunset, especially if they are concentrated in a relatively small area (Nyström *et al.* 2002). The weight of the Common Spadefoot is similar to that of the Common Vole (Dely 1967) and compared to other prey species, it can be hunted with a lower energy investment.

Remnants of *Mus* species, often representing a significant source of food (Chenchouni 2014), were found in all of the sampling sites, where livestock farms located within the territory of the owl. However, unlike in other studies carried out in Hungary (e.g. Marián & Schmidt 1968), the number of mice was low, despite the numerous buildings and objects present within most of the territories. Similar to other studies, larger body sized species (e.g. European Pond Turtle, Smooth Snake, Brown Rat, bats) appeared rarely (Schmidt 1998, Van Nieuwenhuyse *et al.* 2008, Kayahan & Tabur 2016); however, in the Middle East region several bat species were consumed in large numbers (Shehab *et al.* 2004).

Reptilians play an important role in the food composition of the Little Owl, especially in the Mediterranean region (Mastrorilli *et al.* 2001, Arcidiacono *et al.* 2007). However, in Central Europe, reptiles are less preferred, which is also reflected in our results. According to our analyses, reptiles were marginal and the fishes were completely absent from the diet; although, some authors noted regular presence of these items in Little Owl pellets (Mikkola 1983, Angelici *et al.* 1997, Schmidt 1998). In general, birds do not play a key role in the diet of the Little Owl (Laursen 1981, Cramp 1985, Lanszki 2006, Romanowski *et al.* 2013). Similar to other Central European studies (Simeonov 1983), the importance of passerines were small because for the Little Owl, these small birds are difficult to hunt. Among bird species, the Starling proved to be the most commonly caught prey, but bird species like the White Wagtail *(Motacilla alba)*, the Western Yellow Wagtail *(M. flava)* and the Eurasian Tree Sparrow *(Passer montanus)*, closely related to other farmland habitats, were also preyed by Little Owls. These songbirds are definitely connected also to grassland habitats (Marián & Schmidt 1968, Grzywaczewski *et al.* 2006, Shao & Liu 2008, Kitowski & Pawlega 2010, Pocora *et al.* 2012). The lack of birds in the owl pellets collected in the Upper Kiskunság Lakes can be explained by the habitat characteristics, being a large open area, free from any trees and bushes.

Previous studies on demographic and dispersion subjects in the research area found that the Little Owl population of the Upper Kiskunság was strongly delimited by the availability of nesting sites, which was also supported by the fact that in 2016: 34.2% of the artificial nest boxes were occupied by Little Owls (Hámori *et al.* 2017b). Thus, successful occupation of the nest boxes for breeding purposes contributes significantly to the increasing number of breeding pairs in the study area. Moreover, this also demonstrates that besides the successful conservation of the species (Leigh 2001, Gottschalk *et al.* 2011) the nest box provides novel opportunities for feeding ecological studies. The new owl pellet collecting method (samples derived from artificial nesting boxes) used also in this study might have also contributed to the differences compared to previous observations made by earlier feeding biological studies of the Central European region. These types of collections are important because they contain pellets of both the parents and owlets, produced during the periods of pairing, egg laying and incubation up until the fledging of owlets and the beginning of dispersal. Another great advantage of these materials is that we could determine not only the material usually present in the owl pellets but also the lacerated but not ingested remains of prey items (e.g. Common Spadefoot, Passeridae). In the area of the Upper Kiskunság Puszta we could record the almost entire spectrum (20 vertebrate species). In the Peszéradacs Meadows 15, while in the Upper Kiskunság Lakes only 5 species were identified, which can be explained by the lower available sample sizes. The high diversity of the Upper Kiskunság Puszta is mainly due to the mosaic habitat structure, the dense network of livestock farms and the high proportion of grasslands managed by traditional extensive methods. Here, half of the nest boxes (N = 6) were located in Juhászföld and Ürbőpuszta belonging to the outer region of Bugyi city, which had high breeding outputs compared to other nets boxes between 2012 and 2016 with 4.63 successfully fledged owlets per nest box (Hámori 2017a). This also demonstrates that the area provides excellent habitat conditions for the Little Owls.

Based on these results, it can be stated that regarding hunting strategy and prey preference the Little Owls are able to adapt easily to characteristics of their habitat and prey resource. The 21 vertebrate prey species identified represent a relatively broad range of available prey source and provide important information not only for feeding biology, but also for the conservation of the Little Owl. In the future, we need to encourage further feeding biology analyses in other lowland regions of Hungary by collecting owl pellets from the operating nest box network. In addition, similarly to recent Western European studies (e.g. Alivizatos *et al.* 2006, Lanszki 2006, Romanowski *et al.* 2013), seasonal analyses are also needed, not only for vertebrate prey species, but also for predated arthropods, earthworms, potentially consumed plant substances and their derivatives.

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# Spectrum of plant and animal diet of European Great Bustard *(Otis tarda tarda)* – an overview

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**Abstract** We have pointed out 272 plant and 217 animal, altogether 489 taxa in the diet of Great Bustard on the basis of data received from 9 (10) countries for *Otis tarda tarda* (Portugal, Spain, United Kingdom, Germany, Austria, Slovakia, Hungary, Ukraine, Kazakhstan, former Soviet Union). Out of 272 plant taxa, 40 were classified as cultivated plants, 232 wild plants and weeds. From the latter, 43 taxa were monocotyledons and 189 were dicotyledons. Animal food is shared among Annelida (n = 3), Arthropoda (189) Mollusca (2) and Vertebrata (23) phyla. Arthropods are mostly represented with Insecta (181), Arachnoidea (3), Chilopoda (2), Diplopoda (2) and Crustacea (mostly Isopoda) (1) classes. The component of the diet is possibly not related to selection but to the change of the abundance and availability of food and the ever present demand for animal food needed for the organism. Owing to the high number of taxa known as food, Great Bustard is definitely a generalist species. Due to the wide spectrum of animal taxa and because of the ability to subsidize the inefficient quality of food with quantity, Great Bustards can be regarded as a species with positive adaptation ability. It can be explained with a wide plant and animal food spectrum that Great Bustards even in intensive agricultural habitats can find food with indispensable quantity and quality.

Keywords: European Great Bustard, *Otis tarda tarda*, plant diet, animal diet, spectrum of diet

**Összefoglalás** Az *Otis tarda tarda* areájának 9 (10) országából (Portugália, Spanyolország, Egyesült Királyság, Németország, Ausztria, Szlovákia, Magyarország, Ukrajna, Kazahsztán, egykori Szovjetunió) származott közlések alapján a túzok táplálékaként 272 növényi és 217 állati, összesen 489 taxont mutattunk ki.

A 272 növényi taxon közül 40 termesztett növény, 232 vadon élő, illetve gyomnövény volt. Ez utóbbi közül 43 taxon egyszikű és 189 taxon kétszikű volt. Az állati táplálék az Annelida (3 taxon), Arthropoda (189) a Mollusca (2) és Vertebrata (23) törzsek között oszlott meg. Az Arthropodákat leginkább az Insecta (181), Arachnoidea (3), Chilopoda (2), Diplopoda (2), Crustacea (elsősorban Isopoda) (1) osztályok képviselik. A táplálék összetétele feltehetően nem a válogatással, hanem a táplálék bőségének, hozzáférhetőségének változásával, illetve a szervezet állati táplálék iránti mindenkori igényével függ össze. A táplálékként ismert taxonok magas száma okán a túzokot egyértelműen generalista fajnak kell tekinteni. A fogyasztott növény és állati taxonok széles spektruma miatt, továbbá azon képessége alapján, hogy a táplálék elégtelen minőségét mennyiséggel tudja pótolni a túzok, a faj pozitív adaptációs képességének tekinthető.

A széles növényi és állati táplálékspektrummal magyarázható, hogy a túzok még az intenzív mezőgazdasági területeken is megtalálja a számára elengedhetetlen mennyiségű és minőségű táplálékot.

Kulcsszavak: európai túzok, *Otis tarda tarda*, növényi táplálék, állati táplálék, táplálékspektrum

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## Introduction

During the conservation of the declining population (Alonso 2014) of the globally threatened Great Bustard *(Otis tarda),* it is inevitable to possess information on one of the most important segments of its feeding ecology, the trophic relations.

The former, general ornithological monographs (Glutz *et al.* 1973, Cramp & Simmons 1980, Morales & Martín 2002 etc.) address the diet of Great Bustard. In a previous work, Faragó (1986) detected 114 plant and 155 animal taxa as Great Bustard food on the distribution area of *Otis tarda tarda*, mostly based on bromathologic investigations collected by hunting. In many cases, the authors have provided only the family names of plants or animals, and the more precise classification was not possible as a result of the digestibility. Since our knowledge on this topic has increased, mostly because of the examination of faeces and many other new data found in specific literature resources, we have found it adequate to provide an overview on the bustard's diet spectrum.

## Material and methods

The basis of the classification of the food list was given by the following publications, in which well-defined plant and animal taxa were shown for the Great Bustard. The publication years of these papers range 1781 and 2018. The study locations of these articles are as follows, listed by countries.

**Portugal:** Rocha *et al*. (2005)
**Spain:** Gil-Lletget (1945), Palaus Soler (1960), Palacios *et al.* (1975), Lucio (1985), Redondo & Tortosa (1994), Hellmich (1995), Lane *et al.* (1999), Suárez (2002), Alonso & Palacín (2009), Bravo *et al.* (2012), Bravo *et al.* (2014), Bravo *et al.* (2016)
**United Kingdom:** Jourdain (1948), Gooch *et al.* (2015)
**Germany:** Rörig (1900), Hennicke (1905), Niethammer (1942), Gewalt (1954), Gewalt (1959), Mansfeld (1958), Glutz *et al.* (1973), Heneberg (2016)
**Austria:** Dangel & Winkler (1971), Rab *et al.* (2015)
**Slovakia:** Nečas & Hanzl (1956)
**Hungary:** Huszthy (1781), Chernel (1899), Bodnár (1924), Greschik (1939), Vasvári (1949), Horváth (1958), Fodor *et al.* (1971), Sterbetz (1977), Faragó (1981), Faragó (1986), Faragó & Csatári (1993), Faragó (2018)
**Former Soviet Union:** Dementiev & Gladkov (1951), Spangenberg (1951), Stegman (1955), Isakov & Flint (1989)
**Ukraine:** Spangenberg (1951), Kistjakinskij (1957)
**Kazakhstan:** Dolgushin (1962), Rjabov & Ivanova (1971)

Since the Great Bustard is an omnivorous species, we separately discuss the plant and animal diet. Owing to the fact that in the taxonomy of plants and animals respectively, certain countries use different terminologies, and at the same time, we can find scientific synonyms in previous investigations, we also give both the scientific and the well-known synonyms as a compromise solution. However, we also give the source-publication as well in the case of each taxon.

In the case of the food list for plants, we declare the spectrum of the species in terms of cultivated plant, wild plants and weeds and then we give the family names – within that – in alphabetical order. In relation with plants, we use the Király (2009) nomenclature.

In the animal food list – due to its different particularity of taxonomy – we also share the ranging of phylum, classis, ordo, family, genus and species. Within orders (ordo) we give taxa in alphabetical order (including family, subfamily, genus and species). In relation with Coleoptera we have used the names of Merkl and Vig (2009).

## Result

### Plant diet of Great Bustard

#### *Cultivated plants consumed by Great Bustard*

*Allium sativum* – Spangenberg (1951), Cramp & Simmons (1980)
*Avena sativa* – Gil-Lletget (1945), Mansfeld (1958), Fodor *et al.* (1971), Suárez (2002)
*Beta vulgaris – Chernel* (1899), Dangel & Winkler (1971), Glutz *et al*. (1973), Cramp & Simmons (1980)
*Brassica napus* – Chernel (1899), Rörig (1900), Nečas & Hanzl (1956), Mansfeld (1958), Gewalt (1959), Fodor *et al*. (1971), Glutz *et al*. (1973), Sterbetz (1977), Cramp & Simmons (1980), Isakov & Flint (1989), Gooch *et al.* (2015), Raab *et al*. (2015)
*Brassica juncea* – Gooch *et al.* (2015)
*Brassica nigra* – Glutz *et al*. (1973), Lucio (1985), Bravo *et al*. (2016)
*Brassica oleracea* – Jourdain (1948), Mansfeld (1958), Glutz *et al*. (1973), Cramp & Simmons (1980), Suárez (2002)
*Brassica rapa* – Jourdain (1948), Mansfeld (1958), Glutz *et al*. (1973), Cramp & Simmons (1980)
*Cicer arietinum* – Palacios *et al*. (1975), Lucio (1985), Bravo *et al.* (2012), Bravo *et al.* (2016)
*Citrullus lanatus* – Hellmich (1995)
*Cucurbita pepo* – Gooch *et al.* (2015)
*Eruca vesicaria* – Cramp & Simmons (1980), Lucio (1985), Morales & Martín (2002), Bravo *et al*. (2016)
*Fragaria ananassa* – Gewalt (1954)
*Helianthus annuus* – Fodor *et al*. (1971), Sterbetz (1977)
*Hordeum sativum* – Stegman (1906), Mansfeld (1958), Fodor *et al.* (1971), Gooch *et al.* (2015)
*Hordeum vulgare* – Lucio (1985), Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al*. (2016)
*Lens culinaris* – Palacios *et al*. (1975), Lucio (1985)

*Lupinus angustifolia* – Lane *et al.* (1999)
*Medicago sativa* – Mansfeld (1958), Fodor *et al.* (1971), Glutz *et al.* (1973), Palacios *et al.* (1975), Cramp & Simmons (1980), Lucio (1985), Isakov & Flint (1989), Lane *et al.* (1999), Bravo *et al.* (2012), Gooch *et al.* (2015)
*Olea europaea* – Palacios *et al.* (1975), Redondo & Tortosa (1994), Suárez (2002), Bravo *et al.* (2012), Delibes *et al.* (2012), Bravo *et al.* (2016)
*Onobrychis viciifolia* – Mansfeld (1958), Fodor *et al.* (1971), Glutz *et al.* (1973), Cramp & Simmons (1980)
*Oryza sativa* – Fodor *et al.* (1971)
*Panicum miliaceum* – Stegman (1906), Fodor *et al.* (1971)
*Papaver somniferum* – Mansfeld (1958), Fodor *et al.* (1971)
*Phaseolus vulgaris* – Stegman (1906)
*Pisum sativum* – Jourdain (1948), Nečas & Hanzl (1956), Mansfeld (1958), Fodor *et al.* (1971), Glutz *et al.* (1973), Cramp & Simmons (1980), Bravo *et al.* (2016)
*Prunus domestica* – Glutz *et al.* (1973)
*Raphanus sativus* – Mansfeld (1958), Glutz *et al.* (1973), Cramp & Simmons (1980)
*Ribes rubrum* – Glutz *et al.* (1973)
*Secale cereale* – Mansfeld (1958), Fodor *et al.* (1971)
*Sorgum* sp. – Fodor *et al.* (1971)
*Trifolium* sp. – Jourdain (1948)
*Trifolium pratense* – Mansfeld (1958), Fodor *et al.* (1971), Glutz *et al.* (1973), Cramp & Simmons (1980)
*Trifolium repens* – Mansfeld (1958), Fodor *et al.* (1971), Glutz *et al.* (1973), Cramp & Simmons (1980)
*Triticum* sp. – Palacios *et al.* (1975)
*Triticum aestivum* – Chernel (1899), Bodnár (1924), Gil-Lletget (1945), Nečas & Hanzl (1956), Mansfeld (1958), Fodor *et al.* (1971), Palacios *et al.* (1975), Sterbetz (1977), Lucio (1985), Lane *et al.* (1999), Gooch *et al.* (2015), Bravo *et al.* (2016)
*Triticum turgidum* – Suárez (2002)
*Vicia sativa* – Bodnár (1924), Fodor *et al.* (1971), Lucio (1985), Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al.* (2016)
*Vitis vinifera* – Gil-Lletget (1945), Palacios *et al.* (1975), Lucio (1985), Lane *et al.* (1999), Suárez (2002), Bravo *et al.* (2012), Bravo *et al.* (2016)
*Zea mays* – Stegman (1906), Mansfeld (1958), Fodor *et al.* (1971)

### ***Wild plants and weeds consumed by Great Bustrad***

**Dicotyledonopsida**
**Fagaceae**
  *Quercus* sp. – Glutz *et al.* (1973)
  *Quercus coccifera* – Spangenberg (1951)
**Polygonaceae**
  *Polygonum* sp. – Thaisz (1899)

*Polygonum aviculare* – Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al.* (2016)
*Polygonum convolvulus* – Kistjakinskij (1957)
*Polygonum lapathifolium* – Mansfeld (1958), Fodor *et al.* (1971)
*Rumex pulcher* – Bravo *et al.* (2012)

**Chenopodiaceae**
*Atriplex hastata (prostrata)* – Lucio (1985)
*Chenopodium* sp. – Bravo *et al.* (2012)
*Chenopodium album* – Lane *et al.* (1999), Gooch *et al.* (2015), Bravo *et al.* (2016)
*Salsola kali* – Palacios *et al.* (1975)

**Amaranthaceae**
*Amaranthus* sp. – Lucio (1985), Bravo *et al.* (2012)

**Caryophyllaceae**
**Silenoideae** – Palacios *et al.* (1975)
*Cerastium holosteoides* – Lane *et al.* (1999), Bravo *et al.* (2016)
*Holosteum umbellatum* – Lane *et al.* (1999), Bravo *et al.* (2016)
*Sagina apetala* – Lucio (1985)
*Silene* sp. – Lane *et al.* (1999)
cf. *Spergula* sp. – Palacios *et al.* (1975)
*Spergula arvensis* – Palacios *et al.* (1975)
*Spergularia* sp. – Lane *et al.* (1999)
*Spergularia rubra* – Lucio (1985), Suárez (2002)
*Stellaria media* – Mansfeld (1958), Fodor *et al.* (1971)
*Vicia* sp. – Suárez (2002)

**Ranunculaceae**
*Ranunculus arvensis* – Lucio (1985), Lane *et al.* (1999), Bravo *et al.* (2016)
*Ranunculus repens* – Lucio (1985)

**Papaveraceae**
*Papaver roeas* – Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al.* (2016)
*Roemeria hybrida* – Bravo *et al.* (2016)

**Brassicaceae (Cruciferae)**
**Brassiceae** – Palacios *et al.* (1975)
*Alyssum minus* – Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al.* (2016)
*Biscutella auriculata* – Bravo *et al.* (2012), Bravo *et al.* (2016)
*Brassica* sp. – Palacios *et al.* (1975), Lucio (1985), Suárez (2002)
*Brassica barrelieri* – Palacios *et al.* (1975)
*Camelina* sp. – Lane *et al.* (1999), Bravo *et al.* (2012)
*Camelina microcarpa* – Lane *et al.* (1999), Bravo *et al.* (2016)
*Camelina sativa* – Glutz *et al.* (1973), Lane *et al.* (1999)
*Capsella bursa-pastoris* – Mansfeld (1958), Fodor *et al.* (1971), Lucio (1985), Lane *et al.* (1999), Suárez (2002), Bravo *et al.* (2012), Gooch *et al.* (2015), Bravo *et al.* (2016)
*Descurainia sophia* – Bravo *et al.* (2012), Bravo *et al.* (2016)
*Diplotaxis* sp. – Cramp & Simmons (1980)
*Diplotaxis catolica* – Palacios *et al.* (1975)

*Diplotaxis erucoides* – Lane *et al.* (1999), Bravo *et al*. (2016)
*Erophila verna* – Lane *et al.* (1999), Suárez (2002)
*Lepidium* sp. – Lucio (1985)
*Lepidium heterophyllum* – Lucio (1985)
*Malcolmia africana* – Bravo *et al*. (2016)
*Neslia paniculata* – Bravo *et al*. (2016)
*Rapistrum* sp. – Bravo *et al.* (2016)
*Raphanus raphanistrum* – Rörig (1900), Mansfeld (1958), Glutz *et al.* (1973), Palacios *et al.* (1975), Cramp & Simmons (1980), Bravo *et al.* (2012), Bravo *et al*. (2016)
*Sinapis arvensis* – Chernel (1899), Bodnár (1924), Fodor *et al.* (1971)
*Sisymbrium* sp. – Bravo *et al.* (2012)

**Resedaceae**

*Reseda lutea* – Gooch *et al.* (2015)

**Rosaceae**

*Potentilla anserina* – Fodor *et al.* (1971)
*Sanguisorba minor* – Palacios *et al.* (1975), Lane *et al.* (1999)

**Fabaceae (Papilionaceae)**

*Anthyllis vulneraria* – Gooch *et al.* (2015)
*Astragalus* sp. – Lucio (1985), Bravo *et al.* (2012)
*Astragalus incanus* – Bravo *et al*. (2016)
*Cicer* sp. – Palacios *et al.* (1975)
*Cicer arietinum* – Suárez (2002)
*Coronilla scorpioides* – Lane *et al.* (1999), Bravo *et al*. (2016)
*Lathyrus* sp. – Lucio (1985), Bravo *et al*. (2016)
*Lathyrus sativus* – Gil-Lletget (1945)
*Lens squlenta* – Bravo *et al.* (2016)
*Lotus* sp. – Lucio (1985)
*Medicago* sp. – Palacios *et al.* (1975), Cramp & Simmons (1980), Suárez (2002), Bravo *et al.* (2012), Bravo *et al*. (2016)
*Medicago turbinata* – Palacios *et al.* (1975)
*Medicago minima* – Palacios *et al.* (1975)
*Medicago cf. polycarpa* – Palacios *et al.* (1975)
*Medicago polymorpha* – Lucio (1985)
*Melilotus* sp. – Palacios *et al.* (1975)
*Ononis* sp. – Suárez (2002)
*Ononis spinosa* – Lucio (1985), Bravo *et al.* (2012), Bravo *et al*. (2016)
cf. *Ornithopus* sp. – Palacios *et al.* (1975)
*Ornithopus compressus* – Lane *et al.* (1999), Suárez (2002), Bravo *et al*. (2016)
*Ornithopus sativus* – Mansfeld (1958)
*Scorpiurus* sp. – Palacios *et al.* (1975)
*Trifolium* sp. – Palacios *et al.* (1975), Lane *et al.* (1999), Suárez (2002), Bravo *et al.* (2012), Gooch *et al.* (2015), Bravo *et al*. (2016)
*Trifolium angustifolium* – Lane *et al.* (1999), Bravo *et al*. (2016)

*Trigonella monspeliaca* – Bravo *et al*. (2016)
*Vicia* sp. – Palacios *et al.* (1975), Bravo *et al.* (2012), Bravo *et al*. (2016)
**Geraniaceae**
*Erodium* sp. – Bravo *et al*. (2016)
*Erodium cicutarium* – Lane *et al.* (1999)
*Geranium* sp. – Bravo *et al.* (2012)
*Geranium molle* – Lane *et al.* (1999)
**Linaceae**
*Linum* sp. – Fodor *et al*. (1971)
**Euphorbiaceae**
*Euphorbia serrata* † – Lucio (1985)
**Malvaceae**
*Malva sylvestris* – Bravo *et al.* (2012), Bravo *et al*. (2016)
**Onagraceae**
*Epilobium* sp. – Bravo *et al.* (2012)
**Apiaceae (Umbelliferae)**
**Daucoideae** – Palacios *et al.* (1975)
*Caucalis* sp. – Bodnár (1924)
*Conium maculatum* † – Glutz *et al.* (1973), Cramp & Simmons (1980)
*Daucus* sp. – Palacios *et al.* (1975), Suárez (2002)
*Daucus carota* – Lucio (1985), Lane *et al.* (1999)
*Erygium* (syn. *Eryngium*) sp. – Gil-Lletget (1945)
*Pimpinella* sp. – Chernel (1899)
*Thapsia villosa* – Lucio (1985)
*Torilis nodosa* – Bravo *et al.* (2016)
**Primulaceae**
*Anagallis arvensis* – Bravo *et al.* (2016)
*Primula elatior* – Gooch *et al.* (2015)
**Plumbaginaceae**
*Limonium gmelini* – Faragó & Csatári (1993)
**Convolvulaceae**
*Convolvulus* sp. – Gil-Lletget (1945), Bravo *et al*. (2016)
*Convolvulus arvensis* – Chernel (1899), Palacios *et al.* (1975), Lucio (1985), Lane *et al.* (1999), Suárez (2002), Bravo *et al.* (2012)
**Boraginaceae**
**Boraginaceae** – Gooch *et al.* (2015)
*Alkanna lutea* – Lucio (1985)
*Anhusa azurea* – Bravo *et al*. (2016)
*Echium* sp. – Lucio (1985), Bravo *et al*. (2016)
*Echium plantagineum* – Lane *et al.* (1999), Bravo *et al*. (2016)
*Heliotropium europaeum* – Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al*. (2016)
*Lithospermum* sp. – Bravo *et al*. (2016)
*Myosotis* sp. – Lucio (1985), Lane *et al.* (1999)

**Lamiaceae (Labiatae)**

*Lamium amplexicaule* – Bravo *et al.* (2012), Bravo *et al.* (2016)
*Salvia verbenacea* – Bravo *et al.* (2016)

**Solanaceae**

*Solanum nigrum* – Lucio (1985), Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al.* (2016)

**Scrophulariaceae**

*Kickxia spuria* – Bravo *et al.* (2012)
*Veronica* sp. – Gooch *et al.* (2015), Bravo *et al.* (2016)
*Veronica hederifolia* – Lucio (1985), Lane *et al.* (1999), Bravo *et al.* (2016)
*Veronica triphyllos* – Lane *et al.* (1999)

**Orobanchaceae**

*Parentucellia latifoia* – Lane *et al.* (1999)

**Rubiaceae**

*Asperula cf. arvensis* – Palacios *et al.* (1975)
*Galium* sp. – Suárez (2002)
*Galium tricornutum* – Bravo *et al.* (2012), Bravo *et al.* (2016)
*Sherardia arvensis* – Bravo *et al.* (2016)

**Plantaginaceae**

*Plantago* sp. – Jourdain (1948), Cramp & Simmons (1980), Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al.* (2016)
*Plantago coronopus* – Palacios *et al.* (1975), Lane *et al.* (1999)
*Plantago lanceolata* – Mansfeld (1958), Fodor *et al.* (1971), Palacios *et al.* (1975), Lucio (1985), Lane *et al.* (1999), Gooch *et al.* (2015)
*Plantago major* – Mansfeld (1958), Fodor *et al.* (1971)
*Plantago media* – Mansfeld (1958), Fodor *et al.* (1971)

**Valerianaceae**

*Valerianella* sp. – Hennicke (1905), Jourdain (1948)

**Dipsacaceae**

*Cephalaria syriaca* – Lane *et al.* (1999)
*Scabiosa* sp. – Lane *et al.* (1999)
*Scabiosa stellata* – Bravo *et al.* (2016)

**Campanulaceae**

*Jasione montana* – Suárez (2002)

**Asteraceae (Compositae)**

*Achillea ageratum* – Bravo *et al.* (2012)
*Achillea millefolium* – Mansfeld (1958), Fodor *et al.* (1971)
*Anacyclus clavatus* – Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al.* (2016)
*Andryala integrifolia* – Lane *et al.* (1999), Bravo *et al.* (2012), Bravo *et al.* (2016)
*Anthemis* sp. – Palacios *et al.* (1975), Lucio (1985)
*Anthemis arvensis* – Lane *et al.* (1999)
*Anthemis cotula* – Palacios *et al.* (1975)
*Apargia* sp. – Jourdain (1948)

*Arnoseris* sp. – Cramp & Simmons (1980)
*Bellis perennis* – Lane *et al.* (1999)
*Carduus tenuiflorus* – Bravo *et al.* (2012)
*Carthamus lanatus* – Lane *et al.* (1999), Bravo *et al*. (2016)
*Chondrilla juncea* – Bravo *et al.* (2012)
*Cichorium intybus* – Bravo *et al.* (2012)
*Cirsium* sp. – Bravo *et al*. (2016)
*Cirsium arvense* – Nečas & Hanzl (1956), Glutz *et al.* (1973), Cramp & Simmons (1980), Lucio (1985)
*Cnicus benedictus* – Bravo *et al*. (2016)
*Conyza canadensis* – Bravo *et al.* (2012)
**Corimbiferae** – Palacios *et al.* (1975)
*Crepis* sp. – Jourdain (1948), Cramp & Simmons (1980), Lucio (1985), Gooch *et al.* (2015)
*Crepis virens (capillaris)* – Lucio (1985)
*Filago* sp. – Bravo *et al*. (2016)
*Filago pyramidata* – Lane *et al.* (1999)
*Galinsoga parviflora* – Mansfeld (1958), Fodor *et al.* (1971)
*Hedypnois cretica* – Suárez (2002)
*Hedypnois polymorpha* – Palacios *et al.* (1975)
*Hieracium* sp. – Jourdain (1948), Cramp & Simmons (1980), Gooch *et al.* (2015)
*Hieracium aurantiacum* – Gooch *et al.* (2015)
*Hyoseris* sp. – Jourdain (1948)
*Hypochaeris* (syn. *Hypohoesris*) sp. – Palacios *et al.* (1975), Cramp & Simmons (1980)
*Hypochaeris* (syn. *Hypohoeris*) *glabra* – Palacios *et al.* (1975)
*Lactuca serriola* – Bravo *et al.* (2012)
*Lactuca viminea* – Lane *et al.* (1999)
*Lapsana communis* – Gooch *et al.* (2015)
*Leontodon* sp. – Jourdain (1948), Glutz *et al.* (1973), Cramp & Simmons (1980)
*Leontodon taraxacoides* – Bravo *et al.* (2012)
*Leontodon hispidus* – Gooch *et al.* (2015)
cf. *Leucanthemum* – Palacios *et al.* (1975)
*Leucanthemum vulgare* – Gooch *et al.* (2015)
*Mantisalca salmantica* – Bravo *et al.* (2012)
*cf. Podospermum* sp. – Palacios *et al.* (1975), Cramp & Simmons (1980)
*Podospermum laciniatum* – Palacios *et al.* (1975)
*Scolymus* sp. – Palacios *et al.* (1975)
*Scorzonera* sp. – Dolgushin (1962), Isakov & Flint (1989), Bravo *et al*. (2016)
*Senecio* sp. – Palacios *et al.* (1975), Gooch *et al.* (2015)
*Senecio vulgaris* – Lane *et al.* (1999)
*Sonchus* sp. – Lucio (1985), Suárez (2002)
*Sonchus arvensis* – Lucio (1985)
*Sonchus oleraceus* – Glutz *et al.* (1973), Cramp & Simmons (1980), Lucio (1985), Suárez (2002), Bravo *et al.* (2016)

*Tanacetum vulgare* – Mansfeld (1958), Glutz *et al.* (1973), Cramp & Simmons (1980)
*Taraxacum* sp. – Palacios *et al.* (1975), Cramp & Simmons (1980), Lucio (1985), Isakov & Flint (1989), Lane *et al.* (1999)
*Taraxacum officinale* – Mansfeld (1958), Fodor *et al.* (1971), Glutz *et al.* (1973), Palacios *et al.* (1975), Lucio (1985), Bravo *et al.* (2012), Gooch *et al.* (2015), Bravo *et al*. (2016)
*Thrincia* sp. – Palacios *et al.* (1975), Cramp & Simmons (1980)
*Thrincia hispida* – Palacios *et al.* (1975)
*Thrincia hirta* – Palacios *et al.* (1975)
*Tolpis (Hieracium) barbata* – Lane *et al.* (1999), Bravo *et al*. (2016)
cf. *Tragopogon* sp. – Dolgushin (1962), Palacios *et al.* (1975), Isakov & Flint (1989)
*Tripleurospermum perforatum* – Gooch *et al.* (2015)
Tubiflorae – Palacios *et al.* (1975)

**Monocotyledonopsida**

**Colchicaceae**

*Muscari* sp. – Bravo *et al.* (2016)
*Muscari comosum* – Lane *et al.* (1999)
*Muscari racemosum (neglectum)* – Palacios *et al.* (1975), Lane *et al.* (1999)
*Ornithogalum umbellatum* – Rörig (1900), Glutz *et al.* (1973), Cramp & Simmons (1980)

**Alliaceae**

*Allium* sp. – Glutz *et al.* (1973)
*cf. Allium longicuspis* – Dementiev & Gladkov (1951)

**Juncaceae**

*Luzula sylvatica* – Lucio (1985)

**Poaceae (Gramineae)** – Thaisz (1899), Sterbetz (1977), Cramp & Simmons (1980), Faragó (1981), Faragó & Csatári (1993), Bravo *et al.* (2012)
*Aegilops* sp. – Palacios *et al.* (1975), Bravo *et al*. (2016)
*Aegilops ovata* – Palacios *et al.* (1975)
*Agropyron repens* – Glutz *et al.* (1973), Cramp & Simmons (1980)
*Aira caryophyllea* – Palacios *et al.* (1975)
*Antinoria agrostidea* – Lane *et al.* (1999)
*Avena fatua* – Lucio (1985)
*Avena sterilis* – Bravo *et al*. (2016)
*Brachypodium pinnatum* – Lucio (1985)
*Bromus* sp. – Fodor *et al.* (1971), Lucio (1985), Lane *et al.* (1999), Bravo *et al*. (2016)
*Bromus diandrus* – Lane *et al.* (1999)
*Bromus rubens* – Lane *et al.* (1999)
*Bromus squarrosus* – Bravo *et al*. (2016)
*Bromus tectorum* – Palacios *et al.* (1975)
*Cynodon dactylon* – Bravo *et al*. (2016)
*Dactylis glomerata* – Lucio (1985)
*Echinochloa crus-galli* – Fodor *et al.* (1971)
*Festuca* sp. – Sterbetz (1977), Isakov & Flint (1989)
*Festuca pseudovina* – Fodor *et al.* (1971), Faragó & Csatári (1993)

*Hordeum asperum* – Lane *et al.* (1999)
*Hordeum murinum* – Fodor *et al.* (1971), Lane *et al.* (1999), Bravo *et al*. 2016
*Lolium perenne* – Lucio (1985)
*Lolium rigidum* – Bravo *et al*. (2016)
*Mibora minima* – Lane *et al.* (1999)
*Phalaris* sp. – Palacios *et al.* (1975), Lucio (1985)
cf. *Phleum* sp. – Palacios *et al.* (1975)
*Phleum pratense* – Lane *et al.* (1999)
*Poa* sp. – Palacios *et al.* (1975), Lucio (1985)
*Poa annua* – Lucio (1985), Lane *et al.* (1999)
*Poa bulbosa* – Palacios *et al.* (1975), Lane *et al.* (1999)
*Poa pratensis* – Fodor *et al.* (1971), Lucio (1985)
*Setaria* sp. – Bodnár (1924)
*Taeniatherum caput-medusae* – Bravo *et al*. (2016)
*Tragus recemosus* – Dolgushin (1962)
*Vulpia* sp. – Palacios *et al.* (1975), Lane *et al.* (1999)
*Vulpia myuros* – Palacios *et al.* (1975), Lucio (1985)

**Animal diet of Great Bustard**

**Annelida**
**Oligochaeta** – Rocha *et al*. (2005)
  **Lumbricidae** – Jourdain (1948), Gewalt (1959), Cramp & Simmons (1980)
  *Lumbricus terrestris* – Fodor *et al.* (1971)
**Arthropoda**
**Crustacea**
**Isopoda** – Gewalt (1959), Cramp & Simmons (1980)
**Chilopoda** – Rocha *et al*. (2005)
  *Scolopendra* sp. – Palacios *et al.* (1975)
**Diplopoda** – Rocha *et al*. (2005)
  *Julus* sp. – Suárez (2002)
**Insecta**
**Mantidea**
  **Mantidae** – Rocha *et al*. (2005)
  *Mantis* sp. – Spangenberg (1951), Rjabov & Ivanova (1971), Bravo *et al*. (2012)
  *Mantis religiosa* – Palacios *et al*. (1975), Suárez (2002)
**Orthoptera**
  **Acrididae** – Spangenberg 1951, Dementiev & Gladkov (1951), Dolgushin (1962), Rjabov & Ivanova (1971), Palacios *et al*. (1975), Cramp & Simmons (1980), Rocha *et al*. (2005), Bravo *et al.* (2014)
  *Acheta* sp. – Palacios *et al*. (1975)
  *Calliptamus italicus* – Palacios *et al*. (1975), Isakov & Flint (1989)
  *Decticus verrucivorus* – Gewalt (1959)

**Gryllidae** – Dolgushin (1962), Cramp & Simmons (1980), Rocha *et al.* (2005)
*Gryllus campestris* – Jourdain (1948), Spangenberg (1951), Gewalt (1959), Fodor *et al.* (1971), Sterbetz (1977)
*Gryllotalpa gryllotalpa* – Jourdain (1948), Spangenberg (1951), Gewalt (1959), Fodor *et al.* (1971), Palacios *et al.* (1975), Cramp & Simmons (1980)
**Oedipodinae** – Palacios *et al.* (1975)
*Pachytylus migratorius* – Spangenberg (1951), Fodor *et al.* (1971)
*Platystolus surcularius* – Palacios *et al.* (1975)
**Tettigonidae** – Jourdain (1948), Dementiev & Gladkov (1951), Rjabov & Ivanova (1971), Cramp & Simmons (1980), Isakov & Flint (1989), Rocha *et al.* (2005)
*Tettigonia* (syn. *Phasgonura*) *viridissima* – Gewalt (1959), Palacios *et al.* (1975), Sterbetz (1977)
**Dermaptera** – Jourdain (1948), Cramp & Simmons (1980)
*Forficula* sp. – Spangenberg (1951), Sterbetz (1977)
*Forficula auricularia* – Fodor *et al.* (1971)
**Coleoptera** – Dolgushin (1962)
*Agriotes lineatus* – Fodor *et al.* (1971)
**Alleculidae** – Bravo *et al.* (2016)
*Amphimallon solstitialis* – Gewalt (1959), Fodor *et al.* (1971), Sterbetz (1977)
*Anisoplia* sp. – Palacios *et al.* (1975)
*Anisoplia austriaca* – Kistjakinskij (1957)
*Anomala* sp. – Rörig (1900), Hennicke (1905)
*Anomala vitis* – Sterbetz (1977)
*Apion* sp. – Mansfeld (1958)
*Aromia* sp. – Jourdain (1948)
*Aromia moschata* – Hennicke (1905)
*Asida* sp. – Palacios *et al.* (1975), Lucio (1985)
**Asidae** – Palacios *et al.* (1975)
*Blittophaga opaca* – Mansfeld (1958)
*Blittophaga undata* – Rörig (1900), Mansfeld (1958), Gewalt (1959)
*Brachycerus barbarus* – Palacios *et al.* (1975), Suárez (2002)
**Brachyderinae** – Palacios *et al.* (1975)
**Buprestidae** – Rocha *et al.* (2005)
**Calandrynae** – Palacios *et al.* (1975)
*Calosoma* sp. – Jourdain (1948)
*Calosoma sycophanta* – Hennicke (1905)
*Calosoma denticolla* – Kistjakinskij (1957)
**Cantharidae** – Bravo *et al.* (2016)
*Cantharis* sp. – Suárez (2002)
*Capnodis tenebricosa* – Palacios *et al.* (1975)
**Carabidae** – Nečas & Hanzl (1956), Kistjakinskij (1957), Dolgushin (1962), Rjabov & Ivanova (1971), Palacios *et al.* (1975), Cramp & Simmons (1980), Isakov & Flint (1989), Lane *et al.* (1999), Rocha *et al.* (2005), Bravo *et al.* (2012), Bravo *et al.* (2016)

*Carabus* sp. – Rörig (1900), Hennicke (1905), Fodor *et al.* (1971)
*Carabus auratus* – Niethammer (1942), Gewalt (1959), Glutz *et al.* (1973)
*Carabus nitens* – Niethammer (1942), Gewalt (1959)
*Cassida* sp. – Jourdain (1948), Lucio (1985)
*Cassida nebulosa* – Rörig (1900), Hennicke (1905), Gewalt (1959)
*Cassida subferruginea* – Kistjakinskij (1957)
**Cerambicidae** – Dolgushin (1962), Rocha *et al*. (2005), Bravo *et al*. (2016)
*Cetonia aurata* – Huszthy (1781), Nečas & Hanzl (1956), Dolgushin (1962)
*Chrysomela* sp. – Lucio (1985)
*Chrysomela banksi* – Suárez (2002)
*Chrysomela fastuosa* – Gewalt (1959)
*Chrysomela polita* – Gewalt (1959)
*Chrysomela sanguinolenta* – Rörig (1900)
**Chrysomelidae** – Dolgushin (1962), Cramp & Simmons (1980), Lucio (1985), Lane *et al.* (1999), Rocha *et al*. (2005), Bravo *et al*. (2012), Bravo *et al*. (2016)
*Cleonus* sp. – Rörig (1900), Hennicke (1905), Bodnár (1924), Jourdain (1948)
*Cleonus nigrivittis* – Kistjakinskij (1957)
*Cleonus piger* – Glutz et al. (1973)
*Cleonus punctiventris* – Kistjakinskij (1957)
*Coccinella septempunctata* – Palacios *et al.* (1975), Lucio (1985), Suárez (2002)
**Coccinellidae** – Lane *et al.* (1999)
*Coniocleonus* sp. – Palacios *et al*. (1975), Suárez (2002)
*Cryptocephalus* sp. – Lucio (1985)
*Cryptocephalus sericeus* – Gewalt (1959)
**Curculionidae** – Hennicke (1905), Nečas & Hanzl (1956), Dolgushin (1962), Rjabov & Ivanova (1971), Palacios *et al.* (1975), Cramp & Simmons (1980), Lucio (1985) Isakov & Flint (1989), Lane *et al.* (1999), Rocha *et al*. (2005), Bravo *et al*. (2012), Bravo *et al*. (2014), Bravo *et al*. (2016)
*Cycloderes* sp. – Palacios *et al.* (1975), Suárez (2002)
*Dorcadion aethiops* – Fodor *et al.* (1971), Sterbetz (1977)
*Dorcadion fulvum* – Nečas & Hanzl (1956), Fodor *et al.* (1971), Sterbetz (1977)
*Dytiscus* sp. – Jourdain (1948)
*Elater* sp. – Jourdain (1948)
**Elateridae** – Chernel (1899), Hennicke (1905), Mansfeld (1958), Gewalt (1959), Palacios *et al.* (1975)
Epuraea sp. – Lucio (1985)
**Erodiinae** – Palacios *et al.* (1975)
*Eusomus* sp. – Bodnár (1924)
*Geotrupes* sp. – Rörig (1900), Hennicke (1905), Jourdain (1948), Palacios *et al.* (1975)
*Geotrupes cf.* stercorarius – Palacios *et al.* (1975)
*Geotrupes laevigatus* – Suárez (2002)
*Geotrupinae* – Dolgushin (1962), Isakov & Flint (1989)
*Haltica* sp. – Jourdain (1948)

*Haltica oleracea* – Hennicke (1905)
*Hellopatus* sp. – Lucio (1985)
**Helopinae** – Palacios *et al.* (1975)
**Histeridae** – Lane *et al.* (1999)
*Hister fimetarius* – Glutz *et al.* (1973)
*Hypera* sp. – Palacios *et al.* (1975), Suárez (2002)
**Hylobiinae** – Palacios *et al.* (1975)
*cf. Labidostomis* sp. – Palacios *et al.* (1975)
*Lachnaea sexpunctata* – Palacios *et al.* (1975)
*Larinus* sp. – Palacios *et al.* (1975)
*Larinus buccinator* – Suárez (2002)
*Leptinotarsa decemlineata* **–** Gewalt (1959), Fodor *et al.* (1971), Glutz *et al*. (1973), Sterbetz (1977), Cramp & Simmons (1980)
*Leucosomus pedestris* – Nečas & Hanzl (1956)
*Meloë* sp. – Vasvári (1942), Nečas & Hanzl (1956), Kistjakinskij (1957), Palaus Soler (1960), Dolgushin (1962), Palacios *et al.* (1975), Lucio (1985)
*Meloë collaris* – Lucio (1985)
*Meloë* (syn. *Physomeloe*) *corallifer* – Palacios *et al.* (1975), Lucio (1985)
*Meloë hungarus* – Greschik (1939)
*Meloë* (syn. *Berberomeloe*) *majalis* – Entz (1904), Palacios *et al.* (1975), Lucio (1985), Suárez (2002), Sánchez-Barbudo *et al*. (2012)
*Meloë proscarabeus* – Vasvári (1942), Palacios *et al.* (1975)
*Meloë rugosus* – Vasvári (1942)
*Meloë tuccius* – Palacios *et al.* (1975), Suárez (2002)
*Meloë variegatus* – Vasvári (1942), Lucio (1985)
*Meloë violaceus* – Greschik (1939), Vasvári (1942), Lucio (1985)
*Meloë violaclur* – Vasvári (1942)
**Meloidae** – Palacios *et al.* (1975), Lane *et al.* (1999), Rocha *et al*. (2005), Bravo *et al*. (2014), Bravo *et al*. (2016), Heneberg (2016)
*Melolontha* sp. – Jourdain (1948)
*Melolontha melolontha* – Nečas & Hanzl (1956), Mansfeld (1958), Fodor *et al*. (1971), Glutz *et al*. (1973), Sterbetz (1977)
**Melolonthinae** – Isakov & Flint (1989)
**Melyridae** – Lane *et al.* (1999), Rocha *et al*. (2005)
*Microlarinus* sp. – Suárez (2002)
*Micrositus* sp. – Lucio (1985)
*Mylabris quadripunctata* – Kistjakinskij (1957)
**Nitidulidae** – Rocha *et al*. (2005)
*Opatrum sabulosum* – Fodor *et al*. (1971), Sterbetz (1977)
*Otiorrhynchus* sp. – Rörig (1900), Hennicke (1905), Bodnár (1924), Jourdain (1948)
*Oxythyrea funesta* – Palacios *et al.* (1975)
**Phalacridae** – Rocha *et al*. (2005)
*Phyliam* sp. – Lucio (1985)

*Phyliam abreviatus.* – Lucio (1985)
*Phytodecta formicata* – Fodor *et al.* (1971)
*Phytodecta variabilis* – Suárez (2002)
*Phytonomus variabilis* – Fodor *et al.* (1971)
*Pimelia* sp. – Palaus Soler (1960), Palacios *et al.* (1975), Suárez (2002)
*Pimelia rugulosa* – Palacios *et al.* (1975)
*Pimelia baetiva* – Lucio (1985)
*Pimelia punctata* – Lucio (1985)
*Psilothrix cyaneus* – Palacios *et al.* (1975)
*Rhizortogus aequinoctialis* – Fodor *et al.* (1971)
Rhynchiitinae – Palacios *et al.* (1975)
*Rhytidoderes* sp. – Palacios *et al.* (1975)
**Scarabaeidae** – Cramp & Simmons (1980), Lucio (1985), Lane *et al.* (1999), Rocha *et al.* (2005), Bravo *et al*. (2012), Bravo *et al*. (2014), Bravo *et al*. (2016)
*Scarabaeus* sp. – Fodor *et al.* (1971), Sterbetz (1977)
*Sepidium bidentatum* – Palacios *et al.* (1975), Lucio (1985)
*Silpha* sp. – Jourdain (1948), Suárez (2002)
*Silpha atracta* – Hennicke (1905)
*Silpha obscura* – Gewalt (1959)
*Silpha reticulata* – Hennicke (1905)
**Silphidae** – Cramp & Simmons (1980)
Staphylinidae – Palacios *et al.* (1975), Lane *et al.* (1999), Rocha *et al*. (2005)
*Staphylinus* sp. – Suárez (2002)
*Stenus* sp. – Suárez (2002)
*Subcoccinella vigintiquatuorpunctata* – Fodor *et al.* (1971)
**Tenebrionidae** – Dolgushin (1962), Rjabov & Ivanova (1971), Palacios *et al.* (1975), Cramp & Simmons (1980), Lucio (1985), Isakov & Flint (1989), Lane *et al.* (1999), Rocha *et al*. (2005), Bravo *et al*. (2012), Bravo *et al*. (2012), Bravo *et al*. (2014), Bravo *et al*. (2016)
*Tentyria* sp. – Suárez (2002)
*Tentyria bassil* – Lucio (1985)
*Timarcha* sp. – Suárez (2002)
*Tropinota hirta* – Palacios *et al.* (1975), Lucio (1985)
*Tropinota squalida* – Suárez (2002)
*Zabrus tenebrioides* – Fodor *et al.* (1971), Sterbetz (1977)
*Zonabris (Mylabris)* sp. – Palacios *et al.* (1975)

**Hymenoptera**
*Formica* sp. – Palacios *et al*. (1975)
Formicidae – Dementiev & Gladkov (1951), Fodor *et al.* (1971), Isakov & Flint (1989), Rocha *et al*. (2005), Bravo *et al*. (2012), Bravo *et al*. (2014), Bravo *et al*. (2016)
cf. Braconidae – Palacios *et al.* (1975)

**Diptera** – Jourdain (1948), Bravo *et al*. (2012), Bravo *et al*. (2016)

  **Brachycera** – Palacios *et al.* (1975)
  *Musca* sp. – Gewalt (1959)
**Lepidoptera** – Rjabov & Ivanova (1971), Palacios *et al.* (1975), Cramp & Simmons (1980), Rocha *et al.* (2005), Bravo *et al.* (2012), Bravo *et al.* (2016)
  *Agrestis* sp. – Bodnár (1924)
  **Cuculliinae** – Palacios *et al.* (1975)
  *Hyles* (syn. *Deilephila, Celerio*) *euphorbiae* – Gewalt (1959)
  *Hamestra* sp. – Bodnár (1924)
  **Noctuidae** – Gewalt (1959), Palacios *et al.* (1975)
  **Noctuinae** – Palacios *et al.* (1975)
  *Papilio machaon* – Gewalt (1959)
  **Pieridae** – Gewalt (1959), Palacios *et al.* (1975)
  *Pieris brassicae* – Gewalt (1959)
**Hemiptera** – Bravo *et al.* (2014)
  **Heteroptera** – Hennicke (1905), Niethammer (1942), Gewalt (1959)
  *Carpocoris fuscispinus* – Suárez (2002)
  *Eurydema* sp. – Fodor *et al.* (1971), Sterbetz (1977), Lucio (1985)
  *Eurydema ornatum* – Suárez (2002)
  *Eurygaster* sp. – Fodor *et al.* (1971), Sterbetz (1977), Lucio (1985)
  *Eurygaster austriaca* – Suárez (2002)
  *Eurygaster maura* – Kistjakinskij (1957), Suárez (2002)
  *Nabis* sp. – Suárez (2002)
  **Pentatomidae** – Palacios *et al.* (1975), Bravo *et al.* (2016)
  *Reduvius personatus* – Suárez (2002)
  **Scutellaridae** – Glutz *et al.* (1973)
  *Stolia* sp. – Suárez (2002)
**Homoptera** – Isakov & Flint (1989)
**Arachnoidea**
  **Areaneidea** – Jourdain (1948), Gewalt (1959), Dolgushin (1962), Palacios *et al.* (1975), Bravo *et al.* (2012), Bravo *et al.* (2016)
  **Araneae** – Rocha *et al.* (2005)
**Solifuga** – Rocha *et al.* (2005)
**Mollusca**
**Gastropoda**
  *Agriolimax agrestis* – Jourdain (1948), Fodor *et al.* (1971), Cramp & Simmons (1980)
  *Helix pomatia* – Fodor *et al.* (1971), Cramp & Simmons (1980)
**Vertebrata**
**Amphibia** – Jourdain (1948), Cramp & Simmons (1980)
  *Hyla arborea* – Gewalt (1954), Rjabov & Ivanova (1971)
  *Bufo viridis* – Rjabov & Ivanova (1971)
  *Rana arvalis* – Gewalt (1954)
**Reptilia** – Jourdain (1948), Dementiev & Gladkov (1951), Dolgushin (1962), Cramp & Simmons (1980)

*Lacerta* sp. – Spangenberg (1951), Nečas & Hanzl (1956)
*Lacerta agilis* – Rjabov & Ivanova (1971)
*Podarcis hispanicus* – Gil-Lletget (1945)
**Aves** – Spangenberg (1951), Fodor *et al.* (1971)
*Alauda arvensis* – Chernel (1899), Jourdain (1948), Cramp & Simmons (1980)
*Alaudidae* juv. – Dolgushin (1962)
*Melanocoripha yeltonensis* juv. – Dementiev & Gladkov (1951), Spangenberg (1951)
*Motacilla flava* juv. – Rjabov & Ivanova (1971)
*Numenius arquata* ov. – Gewalt (1954), Cramp & Simmons (1980)
*Oenanthe oenanthe* juv. – Rjabov & Ivanova (1971)
**Mammalia**
*Lagurus lagurus* – Glutz *et al.* (1973)
*Lepus europaeus* (juv.) – Jourdain (1948), Fodor *et al*. (1971), Cramp & Simmons (1980)
*Microtus arvalis* – Chernel (1899), Gewalt (1959), Cramp & Simmons (1980)
*Microtus agrestis* – Jourdain (1948)
*Microtus* (syn. *Pitymys*) *duodecimcostatus* – Palacios *et al.* (1975)
*Microtus socialis* – Dolgushin (1962)
**Muridae** – Dolgushin (1962), Rjabov & Ivanova (1971), Sterbetz (1977)
*Mus* sp. – Fodor *et al.* (1971)

### Other ingredients in the stomach of Great Bustard

For digestion, the Great Bustard swallows pebbles and quartz pieces so-called *gastrolits* even as chicks. Besides, Hennicke (1905) mentioned coins, Gewalt (1959) mentioned metal pieces and relatively large pieces of rubber. According to Nečas and Hanzl (1956), some other indigestible objects such as glass splinters, pieces of china also occur in the Great Bustard's stomach regularly. According to Moltoni (1968) in the county of Vicenza, Italy, the stomach of a shot-down young male Great Bustard also included a piece of ceramics, and a strongly corroded German 2 Pfennig coin. Sterbetz (1977) found gastrolits in the stomach of three bustards out of 16. In one of these, there was a tile fragment with three cm diameter, in the other there were 2 pebbles of 6 and 10 mm and in the last one a pebble of 30 mm showed up. We conclude that the gastrolits assist in digestion by the fragmentation of the food.

## Discussion

We have detected 272 plant and 217 animal, altogether 489 taxa as Great Bustard diet based on data received from 9 (10) countries for *Otis tarda tarda* area: (Portugal, Spain, United Kingdom, Germany, Austria, Slovakia, Hungary, Ukraine, Kazakhstan, former Soviet Union). Out of 272 plant taxa, there were 40 cultivated plants, 232 wild plants and weeds. From the latter, 43 taxa were monocotyledons and 189 were dicotyledons.

The families of wild plants and weeds taken, in succession were as follows: dicotyledons (30 families) – Asteraceae/Compositae (59 taxons), Fabaceae/Papillionaceae (26), Brassicaceae

(22), Cariophyllacae (11), Apiaceae/Umbelliferae (9), Boraginaceae (8), Poligonaceae (5), Plantaginaceae (5), Chenopodiaceae (4), Geraniaceae (4), Scrophulariaceae (4), Rubiaceae (4), Dipsacaceae (3), Ranunculaceae (2), Papaveraceae (2), Rosaceae (2), Primulaceae (2), Convolvulacae (2), Lamiaceae/Labiatae (2), Fagaceae (2), Amaranthaceae (1), Resedaceae (1), Linaceae (1), Euphorbiaceae (1), Malvaceae (1), Onagraceae (1), Plumbaginaceae (1), Solanaceae (1), Orobanchaceae (1), Valerianaceae (1), Campanulaceae (1). Monocotyledons (4 families) – Poaceae/Gramineae (36 taxons), Colchicaceae (4), Alliaceae (2), Juncaceae (1).

Animal food is shared among Annelida (3 taxa), Arthropoda (189) Mollusca (2) and Vertebrata (23) phyla. Arthropods are mostly represented with Insecta (181), Arachnoidea (3), Chilopoda (2), Diplopoda (2), and Crustacea (mostly Isopoda) (1) classes.

The orders of Insects based on the regularity of taxon-numbers are as follows: Coleoptera (134), Orthoptera (12), Lepidoptera (10), Hemiptera (13), Mantidea (3), Dermaptera (3), Hymenoptera (3), Diptera (2), Homoptera (1).

The phylum of Vertebrates is represented by all the four terrestrial classes: Mammalia (8 taxa), Aves (7), Amphibia and Reptilia (4–4).

Considering the high number of 489 taxa taken as food, we definitely *need to regard Great Bustard as a generalist species.* The Bustard's great adaptation ability is the base and evidence of the wide spectrum of the consumed plant and animal taxa.

The cited, detailed publications also have shown that the volume of certain taxa in total, seasonally and also in various age-groups were different. This means that the inner rates of diet components constantly change.

Young Great Bustard chicks, but even older ones, consume fresh shoots, crops and seeds of plants. During the period of reproduction of female Great Bustards, „grazing" cannot be observed, which in contrast, is a charasteristic type of behaviour in males. However, they consume more insects. During mating season, male Great Bustards feed on animals in a large proportion. Hens can very often digest rough plant parts and seeds. They defecate them even without digestion (Gewalt 1959).

In Spain, according to the examinations of Palacios *et al.* (1975), 90.2% of the volume of *spring* was plant food. Most of plant diet was represented by the families of Compositae/Asteraceae (51.3%), a Fabaceae (11.4%), a Cruciferae/Brassicaceae (11.4%) and Gramineae/Poaceae (9.3%). In diet composition made up by Arthropoda, coleopterans (Scarabaeidae, Curculionidae, Tenebrionidae and from the Meloidae family) dominated by 95.50%. In the *summer diet*, the importance of green plant parts was decreasing, however, seeds of grains and Arthropods increased (Mantidae, Orthoptera and Formicidae). In the *autumn* aspect, comparing the summer one, there was no significant difference, but the consumption of cultivated plants was increasing. The rate of Orthoptera in the diet remained unchanged at the same time (Locustidae, Gryllidae), just like in the case of Hymenoptera (Formicidae). In the *winter* period, similarly to that of spring, the green plant parts dominated, though the animal diet was practically missing.

Based on the investigation of stomach content and summer/winter faeces, Lucio (1985) analysed the diet of Great Bustard, collected at the Duero Basin. During the whole year, alfalfa played an important role, though at the end of summer and in winter the seeds of winter wheat and winter barley, grapes and Papilionaceae dominated the diet. Besides cultivated plants, he detected the presence of 35 species belonging to the following families: Compositae/Asteraceae (8 species), Gramineae/Poaceae (8 species), Cruciferae/ Brassicaceae (6 species), Boraginaceae (3 species), Caryophyllaceae (2), Ranunculaceae (2), Plantaginaceae (1), Euphorbiaceae (1), Scrophulariaceae (1), Umbelliferae (2) és Juncaceae (1). In the *spring* season, most of the animal food in the investigated stomachs was Coleoptera (97.16%) – within that mostly Tenebrionidae, Meloidae, Chrysomelidae – and Heteroptera. Out of the faeces collected during the *summer* period, coleopteras, hymenopteras and heteropteras were shown to be present with 20–47% frequency, though in *winter* Arthropoda was only possible to make out in one out of ten faeces.

The diet spectrum of a Northwest Spanish Great Bustard population was analysed based on faeces investigation by Lane *et al.* (1999). The analysis considering the data of the whole year, detected 65 plant species – some of them lacking in earlier analyses – in the course of consumption of summer, winter and autumn. The ratio of green plant parts referring to dry material was 48.4%, and seeds in August 10.6%. In the second half of summer, there were seeds of winter wheat and winter barley in the faeces. In the course of the whole year, alfalfa was the most chosen food component and types of grass were preferred to a lesser extent only. Besides plant food, the specimens of 8 Insect orders were found in the faeces, out of which Coleoptera, Hymenoptera and Orthoptera were available in the largest number and ratio. They consumed coleopteras during the whole year although ortopteras were eaten, in a smaller amount than they were disposable. Hymenopteras in May were of less significant, they were consumed mostly in September and November.

Based on the investigation of stomach content of young bustards, Bravo *et al.* (2012) concluded, that diet – referring to dry material – was 33% arthropods, 30% green plant material and 23% seed. Gastrolits in stomachs were only be found in summer and autumn. Food components changed by aspects. In summer, they consumed mostly arthropods (50%), green plant parts mostly in wintertime (56%). The volume and the average size of the Arthropod component – in the case of males – were larger than that of females, but there was no significant difference between sexes. In winter, weeds, Papilionaceae, seeds of cultivated plants dominated, although grain types were preferrably consumed and the seeds of these (wheat, barley) were of great importance during autumn and winter.

Based on faeces samples of 299 hens and 320 cocks, Bravo *et al.* (2016) investigated if there was a sex-specific difference between the food spectrum, diversity and the degree of overlaps of food spectra and size of Arthropod preys, working at 9 Spanish Great Bustard sites. They confirmed that both sexes were mainly herbivorous and they particularly consumed papilionaceous plants, if available. Males fed on less Arthropod diet than females, but at the same time, the size of those are significantly larger than in the case of females. The diet of males shows a bigger diversity than that of the hens, though except for the period after mating. The overlap in food between sexes was found to b 0.7, which is one of the smallest rates in the case of birds. The investigation has shown that in relation with the sexual dimorphism of particular scales, the difference between the sexes' dietary niche can be explained by the dissimilar reproduction role of Great Bustard males and females.

In southwest England, Gooch *et al.* (2015) examined the diet of the reintroduced Great Bustards on free territories, both in the time of without feeding and in the time of supplementary feeding (October-December). In the course of the investigation of the faeces sample, they used the method of microhystology. The ingredients of the food were formed in the function of plant availability and the period of phenology. Animals of lower orders were rarely made evident as food. The main food were green part and seeds of cultivated plants such as rape, mustard, barley, at the same time the monotocyledonous and dicotyledonous weeds were only of second importance (25%).

Benchmark investigations were made in Kazakhstan (Rjabov & Ivanova 1971) – adult (n = 25) and juveniles (n = 12) birds – analysing stomach content. Among the listed taxa, there were 25 plant species; considering one stomach, it was usually dominated by 2–3 species and 25 specimens, on average.

The great value of the investigation is that it provided the relations of volume as well. Accordingly, in the case of adult birds the relation of animal and plant food was found to be 37.8 : 62.2 volume %, though in the case of chicks it is 96.5 : 3.5 volume %. They have shown that from May to August, Great Bustards shifted from the dominance of plant materials to insect food, gradually. One of the reasons of this is that in nature, the availability of insects is increasing and that of plant decreasing, however, before migration (on the investigated area the Great Bustard is a regular migratory bird) the organism is required to accumulate protein and fat. At the same time, there is an interesting statement by declaring that with the increase of nutritional value, the fullness rate of the stomach was decreasing. *The Great Bustard's ability to subsidize the inefficient quality of food with quantity is regarded to be positive adaptation ability by the authors.* When the bird consumes food of low energy value (plants) it consumes a large quantity of that. From food of big nutritional value they consume only moderately. The mixed food makes it possible for Great Bustards to turn from food of one type into another one and they are capable of doing so quite quickly. The animal food for Great Bustards contains protein of 13–30%, though in the case of plants it is 3.5–5.3%. By aging, protein consumption for the body volume is decreasing; at the end of growing protein consumption nearly stops and in the case of adult specimens nitrogen-balance comes into place. It might be observed that out of the feeding birds with different ages, younger ones rather have animal, older ones plant food. The diversified component of these diet guarantees all the amino-acids needed for protein-synthesis.

To summarize, we can declare that in the food of young Great Bustards animal food, in the older ones plant food is dominating. *The component of diet is possibly not related to selection, rather to the abundance of it and the change of availability recepectively to the ever present demand for animal food.*

Simultaneously, it is important to concluce that it can de explained with a wide plant and animal food spectrum (richness) that Great Bustards even in intensive agricultural habitats can find food with indispensable quantity and quality. This is improved by the fact that neither in Europe (Kollar 1996, Nagy 2009, Alonso 2014) nor regional (Kollar 2001, Faragó 2004, Bankovics 2005, Alonso & Palacín 2009, Spakovszky *et al.* 2011, Raab *et al*. 2014, Vadász & Lóránt 2014, Faragó 2018) level can we find the lack of food among the endangaring factors for the globally threatened species as opposed e.g. to Grey Partridge *(Perdix perdix)* for instance (Potts 1986, 2012).

## Request

Neither the resource list nor the diet list gained from it can be complete, so the author wishes to be informed about references concerning missing data.

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# Diurnal feeding strategies of the Ferruginous Duck *(Aythya nyroca)* in Lake Tonga (Northeastern Algeria)

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**Abstract** Although the Ferruginous Duck *(Aythya nyroca)* has thoroughly been studied, the foraging behaviour of this species is still not completely known. In the present paper we studied the diurnal feeding behaviour of ducks. We monitored the annual cycle of birds through two fieldtrips per month. The instantaneous behaviour of birds was recorded in regular 30-minute intervals from 7 a.m. to 4:30 p.m., amounting a total of 456 observation hours. Food searching activity corresponds to a quarter of the total diurnal time budget of the Ferruginous Duck. Foraging behaviour was classified into five categories dominated by the "diving", which is almost 45.61% of the total search time. Foraging activities at the water surface considered to be secondary activities, including feeding by "bill", "neck and head", and "beak and head" in a rate of 19.86%, 14.53%, and 13.98%, respectively. The "toggle" remains a minor activity and represents only 5.99% of foraging time. The feeding behaviour of this species correlated to several environmental parameters (rainfall, temperature and wind velocity), and linked to the group size of ducks visiting the lake. Regarding the food intensity, our results show the highest values for "bill and head" behaviour. "Diving" has the longest feeding interval (16.16±14.1 minutes), while foraging by "bill" has the shortest (0.69 ± 0.48 minutes).

Keywords: El-kala, foraging behaviour, near threatened species, energy budget, Anatidae, wildfowl

**Összefoglalás** Annak ellenére, hogy a cigányrécével *(Aythya nyroca)* számos tanulmány foglalkozott, táplálkozási szokásai kevésbé ismertek. Jelen tanulmányban a faj nappali táplálékszerzéssel kapcsolatos viselkedését vizsgáltuk. A madarak éves táplálkozási ciklusának monitorozása havonta két terepbejárással történt. Az adott viselkedési mintákat 30 perces időintervallumokban rögzítettük: reggel 7 óra 30 perctől délután 16 óra 30 percig, összesen 456 megfigyeléssel töltött órában. A táplálék keresésével töltött idő hozzávetőlegesen a réce napi aktivitásának negyedét teszi ki. A táplálékszerzéssel kapcsolatos viselkedési mintákat öt kategóriába soroltuk: „merülés" (kereséssel töltött idő 45,61%-a), másodlagos táplálékszerzés a vízfelszínről, a „csőr a felszín alatt" (19,86%), a „nyak és fej a felszín alatt" (14,53%,) „csőr és fej a felszín alatt" (13,98%), valamint a „tótágast állva" történő táplálékszerzés, mely az idő 5,99%-át teszi ki. E faj táplálkozási szokásai számos környezeti paraméterrel (csapadék, hőmérséklet és szélsebesség) függnek össze, és a tavat látogató récék csoportmérete is befolyásoló tényező. A táplálékforrás intenzitásának tekintetében a legmagasabb értékeket a „csőr és fej a felszín alatt" viselkedési mintára kaptuk. A „merülés" mutatta a leghosszabb időintervallumot (16,16±14,1 perc), míg a legrövidebbet (0,69 ± 0,48 perc) a "csőr a felszín alatt" viselkedési minta.

Kulcsszavak: El-kala, táplálékszerzés, mérsékelten fenyegetett fajok, energiaforgalom, Anatidae, vízimadarak

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## Introduction

Understanding foraging strategies that animals use when balancing energy budgets can lead to a clearer view of potential constraints to populations, as well as species' behavioral scope, when responding to environmental changes (Pyke 1984). The allocation of time into foraging varies among taxa and individuals and may have important implications for meeting energy requirements (Bautista *et al.* 1998). When facing with food or energetic deficits, the ability to adjust foraging time and strategies allows animals to maintain the necessary rate of energy gaining. For obligate diurnal foragers, day length forces strict limits on available foraging time. The Ferruginous Duck *(Aythya nyroca)* is a shy and cautious diving duck widely distributed in Asia, Africa, and Europe. During the wintering season, this species is a regular visitor in El-Kala wetlands. It is also reported as nesting species in North Africa since the beginning of the 20th century. Its nesting was observed for the first time in 1972 in Algeria (François 1975). During the last decades, nesting populations in this region have suffered serious declines, as well as changes in their distribution (Ali & Ripley 1978, Perennou *et al*. 1994, Callaghan 1997, Lopez & Mundkur 1997, Grimmett *et al*. 1999, Robinson & Hughes 2003).

According to the Red List of Threatened Species (IUCN 2015), the Ferruginous Duck occupies the 'near threatened' status. In Algeria, this species is protected by decrees N°83-509 of 20th August 1983 and N°06-05 of 15th July 2006, relating to the protection and preservation of some critically threatened species. *A. nyroca* has also been presented as a priority species in 4 prominent international conservation treaties: the European Union Bird Directive, the Bern Convention, the Bonn Convention, and the African Eurasian Migratory Waterbird Agreement (Robinson & Hughes 2003).

The Ferruginous Duck is omnivorous. In Uzbekistan, stomach content analysis reveals 78% of sprouts and freshwater plant seeds and 22% of aquatic insects during the nesting period (Kashkarov & Mukhina 1997). In Bulgaria, this duck feeds mostly on seeds and other aquatic plants such as pondweeds (*Potamogeton* spp.), sedges (*Carex* spp.), hornworts (*Ceratophyllum* spp.) and bulrushes (*Scirpus* spp.) (Ayaichia *et al.* 2017). However, animal material can dominate locally or temporarily and includes invertebrates such as chironomids (Chironomidae), snails (gastropods), coleopteran beetles and also small fish and frogs (Phillips 1923, Dementiev & Gladkov 1952, Sterbetz 1967, Cramp & Simmons 1977, Amat & Soriguer 1982, Paspaleva *et al*. 1984, Patrikeev 1996, Green 1998). In addition to the measurement of the total time spent in foraging, which has been rather widely discussed in several studies (Green 1998, Ayaichia *et al*. 2017), understanding feeding methods used by ducks may also enquire on constraints beared by populations. We already know that feeding only with submerged bill may be linked to the choice of feeding in shallower zones, but could also be a response to a need of maintaining activity that requires alertness (remaining eyes above the surface) where predation risks and disturbance are the highest (Guillemain *et al.* 2002). Moreover, the increasing of foraging depth during winter reflects a gradual depletion of resources (Guillemain & Fritz 2002), even a change in consumed prey types (Guillemain *et al.* 2000). In birds, foraging is a limiting process which allows energetic gain. A good wintering season in foraging terms would permit the reconstitution of endogen reserves mobilised during migration and/or to finish moulting (Heitmeyer 1988). Foraging also influences breeding, which is a costly phenomenon on nutritive elements, and can require not only the lepidic reserves but either the stocked tissue proteins (Heitmeyer 1988, Owen & Black 1990). In Anatidae, species often reproduce early, the clutch size and the date of laying depend on the cumulated reserves before arrival on the nesting sites (Ankney & MacInnes 1978, Pattenden & Boga 1989). During the migration journey to the wintering sites, birds forage intensively to reconstitute energetic reserves (Landys *et al.* 2004). Foraging behaviour is determined by foraging niche and depends generally on certain factors of climatic zones and charging capacity (Ankney & MacInnes 1978, Krapu 1981, Drobney 1982, Pattenden & Boag 1989).

In this study, we tried to understand why Ferruginous Duck changes its foraging methods. First, we searched factors, which affect the processes via feeding behaviour. We examined the relation between feeding methods and some environmental factors (temperature, rainfalls, and wind speed). We also considered the relationship between the choice of a foraging method and the ducks' group sizes present at the Lake Tonga (influence of the competition).

## Materials and Methods

Field work was conducted over an annual cycle, from January to December in 2013 with two surveys per month. Two classical methods were implemented: The Scan Sampling and Focal Individual Sampling. Scan sampling requires that the behaviour of individuals in the sample is being recorded instantaneously (Altmann 1974). Many waterfowl activity budget studies, utilizing scan sampling, involve surveying the entire local population at the time of sampling, i.e. all birds on a pond (Skead 1977, Norman *et al.* 1979, O'Donoghue & O'Halloran 1994, Adair *et al.* 1996). In some instances, the study site is too large to be sampled from one point (Campbell 1978). A solution to this problem is to divide the site into non-overlapping sections that are observed separately. Then, data needs to be weighted according to the number of birds observed in the different sections (Hepworth & Hamilton 2001). In our case, it took approximately 1 h to sample the entire pond. The different behaviours of the monitored ducks were identified using binoculars, scanning from left to right (Hepworth & Hamilton 2001). To facilitate the sampling, the pond was divided into 5 sections. Antagonistic behaviour was excluded because of its infrequency. All of the different types of feeding behaviour by submersion of the beak, the head, the beak and head, the head and neck or by diving were considered as feeding activities. The aim of this sampling was to estimate the number of individuals in each activity category, on each sampling occasion. These numbers would then be used to estimate the proportion (or percentage) of individuals in each category. Focal observations (10 mins, Altmann 1974) were conducted on feeding individuals chosen at chance; each change in behaviour was recorded. Observations took place in the site twice monthly between 7 a.m. and 4:30 p.m., for a total of 24 study days. Thereby, a total of 456 scans were performed. Data was recorded by the same observers throughout the study. Presumed repetition of observations on the same individual were removed (Altmann 1974). Analyses were restricted to the temporal organization of behaviour during foraging, successions of feeding bouts and interruptions, where birds were standing or swimming in an upright position (head-up vigilance bouts, hereafter scans). We considered foraging to be terminated by any activity other than feeding or scanning (Cézilly & Brun 1989). Foraging methods were classified into five categories: feeding by diving (the whole body was in the water), feeding by bill (only bill was in the water), feeding by bill and head, (bill and head were in the water), feeding by neck and head (diving with head and neck in the water) and feeding by upending (only tail remains out of water). We collected environmental data during each time block. Air temperature (°C, recorded every 10 mins) and wind velocity (km/h, recorded continuously). We were unable to conduct systematic nocturnal surveys due to dense vegetation in the control treatments, distances from blinds to study plots, and logistical constraints.

### Study site

Our study area is located in North-eastern Algeria, in the National Park of El-Kala, on the Lake Tonga (in Ramsar since 1983). This lake is ca. 2,500 ha (Belhadj *et al*. 2007) and it is one of the most significant wetlands of North Africa. Lake Tonga provides important habitats of extensive beds of aquatic plants and nesting sites for several rare and globally threatened waterbirds. It is a significant breeding area for such rare waterfowl as Ferruginous Duck, White-headed Duck *(Oxyura leucocephala)*, Common Pochared *(Aythya ferina)* and Marbled Teal *(Marmaronetta angustirostris)*. It attracts a rich and varied population of many birds of prey (Smart & Hollis 1990). The abundant aquatic vegetation of this lake plays a fundamental role in the distribution of waterbirds offering both shelter and food. It is mainly composed by islets of lesser bulrush *(Thypha angustifolia),* yellow iris *(Iris pseudoacorus),* lakeshore bulrush *(Scripus lacustris),* cosmopolitan bulrush *(Bolboschoenus maritimus),* Australian phragmite *(Phragmites australis),* Mediterranean willow *(Salix pedicellate),* and simplestem bur-reed *(Sparganium erectum).* In spring, we witness the immergence and flowering of very invasive hydrophytes of free-water species, white nenuphar *(Nymphaea alba)* (Abbaci 1999).

### Statistical analyses

We calculated food intensity of each foraging cycle according to the following formula: IA = A / (A+R), where IA = feeding intensity, A = duration of feeding phase, and R = duration of breathing phase (Allouche & Tamisier 1984, Campredon 1984). We used Pearson's test for correlations, Mann-Whitney's test for comparison between seasons of feeding activities, and packages 'ade4' and 'ade4TkGUI' in the free software R v3.0.3 (R Core Team 2014) for factorial analysis of correspondences (FAC).

## Results

Results show that the Ferruginous Duck spends the quarter (25.40%) of the diurnal time with foraging, 30.08% of the time with swimming, and with comfort activities (preening, resting and sleeping) predominated at a rate of 44.52%. Parade activities and flight recorded only a minimal part of diurnal activity rhythms and thus, have been removed from the analyses.

Diurnal feeding activities indicated two important peaks: the first one in February with a value of 44%, followed by another in April with a value of 59.94%. The lowest values of the diurnal foraging are recorded between the months of June and September, less than 30% *(Figure 1)*.

The most frequent foraging method observed is feeding by diving (46.61% of food cycle). Other activities, feeding by "bill" by "neck and head" and by "bill and head" are secondary activities and are represented 19.86%, 14.53% and 13.98%, respectively. Up-ending is a minimal activity and represents only 5.99% of the foraging cycle.

Except feeding by neck and head ($U = 13$, $n = 12$, $p = 0.47$), all other feeding behaviours differ between wintering periods (January-April then November-December) and summer period that spreading between May and October (diving: $U = 0$, $n = 12$, $p < 0.01$; toggle: $U = 3$, $n = 12$, $p < 0.05$; beak: $U = 3$, $n = 12$, $p < 0.05$; beak and head: $U = 3$, $n = 12$, $p < 0.05$) *(Figure 2)*.

FAC demonstrates 78% of information in axe 1 and 2. Toggle, neck and head, and beak and head are grouped in positive side of axe 2 while diving (negative side) and beak (positive side) are positioned separately in axe 1 *(Figure 3)*. The first group is associated with April and September, peak with May to August and October. Diving is associated with

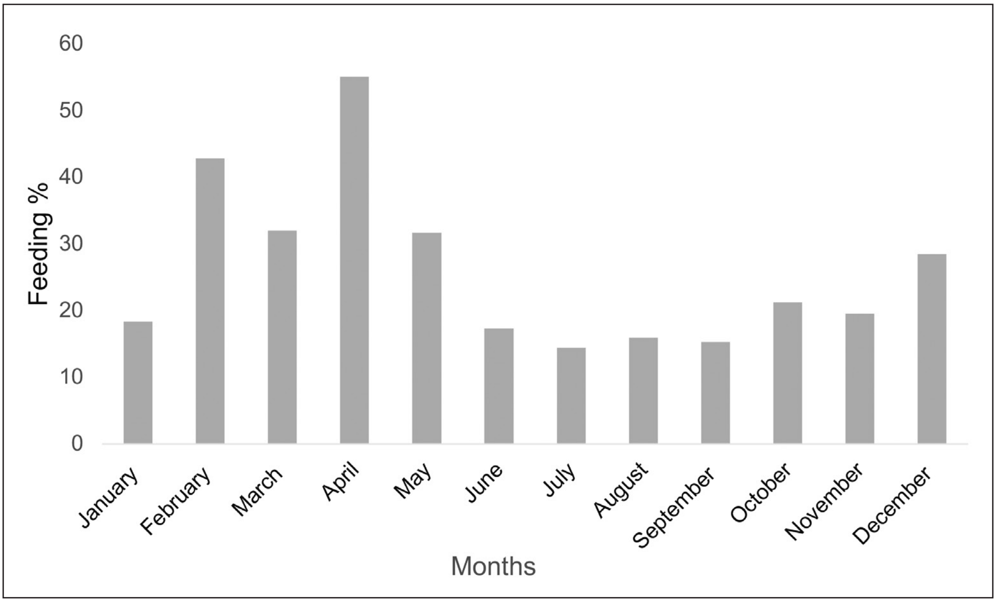

*Figure 1.* Annual foraging activity of Ferruginous Duck
*1. ábra* A cigányréce éves táplálkozási aktivitása

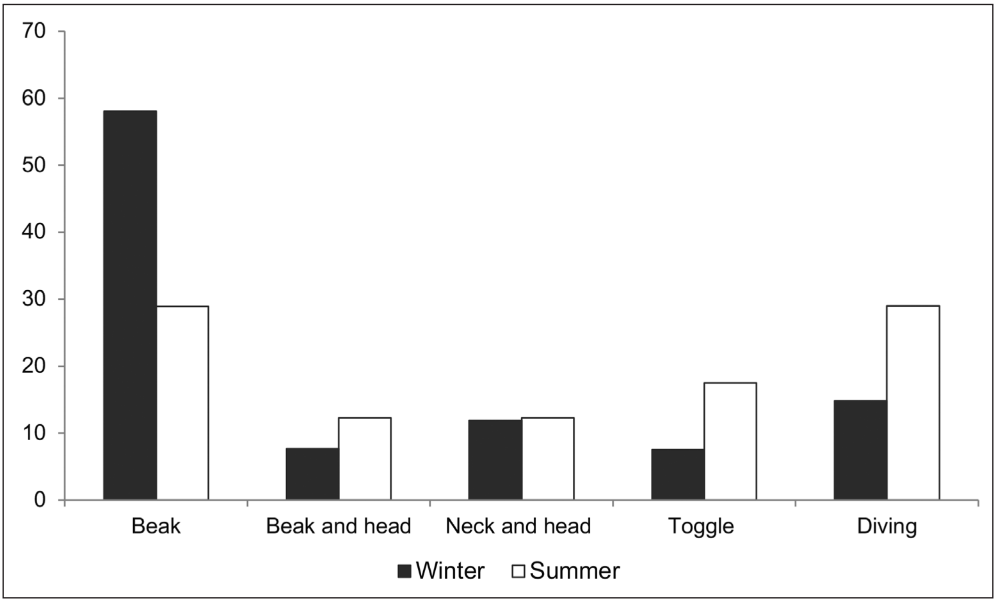

*Figure 2.* Seasonal differences of foraging activities
*2. ábra* A táplálkozásmód évszakonkénti változása

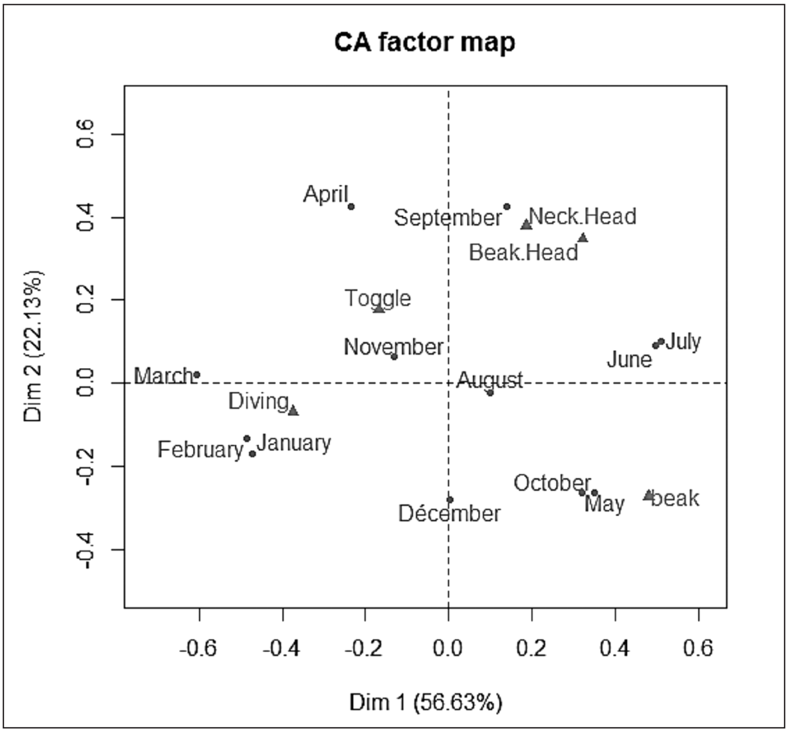

*Figure 3.* FAC results of *foraging* activities
*3. ábra* A táplálkozási aktivitás FAC eredményei

months from January to March and November.

Feeding intensity is significantly and negatively correlated with the studied factors: rainfall (test of Pearson, p < 0.002, r = – 0.93), temperature (p < 0.001, r = – 0.74), wind speed (p < 0.001, r = – 0.98).

Feeding activities linked to the surface are significantly and negatively correlated to the number of ducks on the surface and also to the number of diving ducks. However, foraging activity linked to the depth is significantly and positively correlated to the number of ducks on the surface *(Table 1).*

*Table 1.* Correlation between foraging method and bands' sizes
*1. táblázat* A táplálkozásmód és a csoportméret összefüggései

| **Activities** | **number of diving ducks** | **number of surface ducks** |
|---|---|---|
| Surface feeding | *r* = – 0.002<br>*p* = 0.99 | *r* = – 0.096<br>*p* = 0.019 |
| Feeding in depth | *r* = 0.019<br>*p* = 0.95 | *r* = 0.85<br>*p* = 0.0004 |

*Table 2.* Feeding intensity by foraging method
*2. táblázat* A táplálkozás intenzitása az egyes táplálkozásmódok esetében

| **Feeding type** | **A (in sec.)** | **R** | **IA** |
|---|---|---|---|
| Diving | 16.16 ± 14.1 | 15 ± 12.36 | 0.56 ± 0.28 |
| Up-ending | 3.26 ± 1.12 | 3.63 ± 3.69 | 0.46 ± 0.24 |
| Bill and Head | 5.25 ± 5.2 | 4.45 ± 3.73 | 0.47 ± 0.28 |
| Head and Neck | 9.97 ± 8.38 | 9.95 ± 7.01 | 0.57 ± 0.26 |
| Bill | 0.69 ± 0.48 | 1.82 ± 0.87 | 0.33 ± 0.12 |

*Table 2* shows that diving is the longest foraging behaviour with also a long breathing phase. The shortest behaviour is feeding by bill with a short breathing phase compared to other behaviours. Concerning food intensity, "head and neck" and diving behaviours recorded the highest values.

## Discussion

The results show that the Ferruginous Duck exhibits an important diurnal comfort rate. Our results are supported by other studies. Diurnal resting and other comfort activities in Anatidae represent one of the best ways for rearrangement of energy reserves with a view of migratory for wintering populations (Hill & Ellis 1984, Rave & Baldassare 1989, Hohman & Rave 1990, Green *et al*. 1999, Tamisier & Dehorter 1999), as well as, ensure the reproductive success for nesting populations (Hill & Ellis 1984, Hohman & Rave 1990, Green *et al.* 1999). Swimming is an essential activity for ducks, it is often associated with foraging. Individuals of the studied species fatten up by moving. It takes the second place in the total balance of diurnal activities of this species. Prevalence of this activity is basically observed in the beginning of the day and toward the end of the wintering period. Numerous factors determine importance of diurnal foraging. At northern latitudes, birds allocate 80 to 100% of the diurnal period for feeding (Goss-Custard 1969, 1979), while in more temperate areas, even tropical, this rate is lower, for instance, ranged between 25 and 87% in Africa (Puttick 1984, Fasola & Biddau 1997). This is notably explained by upper energy needs for colder temperature. According to Campredon (1984), granivorous or omnivorous ducks devote 35% of their feeding diurnal time while diving ducks of the genus *Aythya* generally spend less than 30% of their diurnal time with feeding (Nilsson 1970). For example, this proportion is 23% for the Ferruginous Duck in Bulgaria (Petkov 2003), 21% for Tufted Duck *(Aythya fuligula)* in Switzerland (Pedroli 1982), and 17% for the Common Pochard *(Aythya ferina)* (Sabir 2004).

Many ducks, including the Ferruginous, are known to exhibit feeding peak early in the morning and late in the evening (Rodway 1998, Aissaoui *et al.* 2011). Ferruginous Ducks prefer to forage at night and continue feeding diurnally. The diurnal feeding maxima at the beginning and the end of the day is probably the continuation of the night feeding activity that compensates increase of energy needs spent in thermoregulation. One of the most significant decrease in diurnal foraging, recorded in this study, was observed during nesting period. One of the reasons that may explain this pattern, is the continuous monitoring of chicks against predators – mainly the Western Marsh Harrier *(Circus aeruginosus),* requiring a continuous presence of adults close to their nests. This decrease could also be a result of increasing temperatures during the day. In fact, the heat stress is a key factor that influences ducks' health and which enhances during hot seasons and in hot regions (Zhu *et al*. 2014). We believe that the daily heat during summer period forces ducks to decrease their diurnal feeding activity. This loss of time will be compensated by an intensive foraging rate by the end of the day or during the night with temperature decrease This kind of bimodal declining and fluctuating activity pattern, driven by food availability, temperature or the presence of predators, was also recorded by other authors, such as Tanmay (2014), who studied diurnal feeding behaviour of the Ferruginous Duck in Turkey (see also Rodway 1998, Aissaoui *et al*. 2011).

During winter, we observed that individuals search food more actively by decreasing their moves and their vigilance, essentially during cold days. Poor environmental conditions in this period, combined with the increased number of competitors arriving for winter are force this species to spend more time foraging to maintain thermoregulation/energy supplies. Feeding rate increases also before reproduction period translating the need to accumulate more fat as well as other nutrients essential to female's breeding.

Food resources are generally distributed heterogeneously, both in time and space, and foraging animals show flexible responses to this heterogeneity. This flexibility is expressed at different levels: animals can occupy a new habitat, select a different patch within the same habitat, and select different items within a patch (reviews in Stephens & Krebs 1986, Hughes 1993, Sutherland 1996). Another kind of behavioral adjustment involves switching search methods (Stephens & Krebs 1986). Short-term switches or the short-term changes in food searching methods were observed and analysed in numerous animal groups as a rapid and reversible adaptation response to different conditions of food availability (Thomas 1974, Davies 1977, Recher *et al*. 1983, Formanowicz & Bradley 1987, Grant & Noakes 1987, Village 1990, Bell 1991, Nakano *et al.* 1999). The Ferruginous Duck is an excellent diver, but we have also highlighted other feeding methods less frequent than diving, but have crucial importance in the subventions of nutritional needs. For the Ferruginous Duck, diving remains the most efficient feeding technique because by this method it gathers the most rentable preys in term of energy, which are generally animal materials (benthic macro-invertebrates) (Phillips 1923, Dementiev & Gladkov 1952, Sterbetz 1969, Cramp & Simmons 1977, Amat & Soriguer 1982) or certain plants such as sago pondweed *(Potamogeton* *peetinatus),* small pondweed *(P. panormitanus),* and bulrush *(Schoenoplectus litoralis),* abundant in the benthos. Alternative feeding techniques are dominated by the usage of bill. This technique occurs essentially in shallow waters where vegetation is available at water surface. We believe that this technique also allows ducks to maintain a certain level of vigilance while foraging. This capacity in combination between vigilance and food seeking might be a crucial importance for species whose type and/or energy needs necessitate daily, long foraging. Effectively, individuals may be unable to compensate the loss of the feeding time if vigilance is reached only by "head up", in a time period where feeding is impossible (Martin & Katzir 1999). Feeding by bill and so other feeding behaviour linked to the surface are generally used to collect insects such as chironomids or submerged seeds (Cramp & Simmons 1977).

According to Poysa (1983), two reasons may explain the choice of ducks' feeding method; 1) water depth; 2) distribution of prey. In winter, diving ducks are mostly feeding on benthic macro-invertebrates (Nilsson 1972, Stott & Olson 1973, Bellrose 1980, Jones & Drobney 1986, Poulton *et al*. 2002). This kind of prey with high energy can only be obtained by "diving". Depletion of surface resources, presence of great number of several wintering duck species also force the studied species to look for food in the depth. Increase in the rate of foraging activities linked to the surface in summer time may be explained by the abundance of sufficient food resources on the surface to supply energy needs, and also by the need to maintain more vigilance due to presence of chicks during this period (see previous section).

Numerous authors linked foraging behaviour to environmental factors. For instance, Paulus (1984) has studied the Gadwall *(Mareca strepera)* in Louisiana in October 1977 and in April 1978, and found a negative relationship between ducks' feeding rate and temperature fluctuation. Gaston and Nasci (1989) report that temperature decrease provokes an increase of food seeking. Thompson *et al.* (1991) found negative correlations between wind speed and foraging rate of four duck species: Blue-winged Teal *(Anas discors)*, Northern Shoveler *(A. clypeata)*, Northern Pintail *(A. acuta)*, and the American Wigeon *(A. americana)*. Results of the present study show a clear decrease in foraging during rainy days. We assumed that ducks have difficulties to reach submerged vegetation because of the increase of water depth, but also of their incapability to locate surface preys due to water turbulence by rains. Our study also shows the negative influence of wind speed on feeding activity. Thompson *et al*. (1991) emphasizes that wind speed would have more influence on duck's foraging than may have any other climatic parameters. In fact, we noticed that formation of waves on water surface disturbs feeding activity and sometimes completely interrupts it, since wind also disturbs the movements of insects (such as chironomids), which generally depend on the surface vegetation. Furthermore, the influence of temperature, especially thermal stress in hottest or coldest periods, forces ducks to limit their feeding and increase comfort behaviour in order to reduce energy use.

At Lake Tonga, the Ferruginous Duck cohabits with several bird species, especially the Common Pochard, the Northern Shoveler, the Eurasian Teal *(Anas crecca),* and the Eurasian Coot *(Fulica atra)*. Various studies on habitat use by community of ducks showed separation of niches between species in horizontal dimensions, such as size of wetlands, vegetation characteristics, and chemical characteristics of water (Bengston 1971, Weller 1975, Toft *et al*. 1982, Anderson & Ohmart 1988, Monda & Ratti 1988, Bergan & Smith 1989, Nummi & Poysa 1993, Nudds *et al.* 1994). Ferruginous Duck is belonging to the omnivore diving ducks according to diet composition and feeding methods (Pecsics *et al.* 2017). Some studies demonstrate the presence of vertical partitioning in foraging methods in the depths of water column. Amat (1984) suggested that the Red-crested Pochard *(Netta rufina)* and the Common Pochard use different habitats with the same foraging strategy in winter, however, they share the same habitat but use different feeding methods in spring. In the present case, results demonstrated clearly that feeding behaviour of Ferruginous Ducks is highly modulated by presence of competitors. In order to optimize its food supply, this species adopts different food-seeking strategies to be able to face the competitiveness. When group size of surface ducks become a constraint, either for consumption intensity of the surface preys or because of prey's disturbance which generate an increase foraging time, it forces this species to dive as the most efficient strategy. Competitiveness with other diving ducks obliges certain individuals to choose surface feeding as a mean to face this constraint. We also noticed interferences between ducks on the same supply spot, which can be manifested in aggressive behaviour of dominant ducks, forcing some individuals to change the foraging site.

Behaviour linked to surface foraging are the shortest in terms of time; this may be explained by the fact that these postures put ducks in position of weakness facing predators, while having eyes under water and the rest of the body exposed. Shortening or fragmenting those phases of foraging seems to be a way to face this constraint. Kramer (1988) discussed that the optimal diving duration are relatively short. Deep, long dives, therefore, will be feasible only with a large reserve in $O_2$. For this, regeneration time would allow fulfilling reserves in $O_2$, which corroborates our results where breathing phases are the longest after diving. During these resting phases, ducks also recover from body heat loss of diving (de Leeuw *et al.* 1998). As it has already been discussed in the previous chapter; diving is a very efficient foraging method during wintering season, diminution of resources (scarce and change of prays distribution) may explain in part the long dives.

### Future perspectives

Unfortunately, data collected in this study are too limited to explain variation of ducks' feeding behaviour in response to the differences in sex and age of individuals but also in response to productivity fluctuation of the study sites. Study of diet of this species and its eventual seasonal variation, different kinds of disturbance (e.g. predators, human presence) can also help the understanding of certain aspects of the foraging behaviour, where more detailed studies of this species at Lake Tonga, and in other sites of its nesting area in Algeria are needed.

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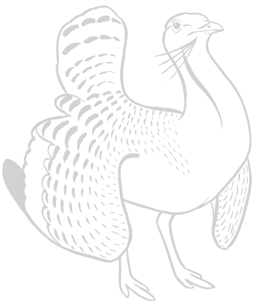

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# Habitat selection of the Common Quail *(Coturnix coturnix)* in an intensively managed agricultural environment

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**Abstract** This study investigated the habitat selection of the Common Quail *(Coturnix coturnix)* during the breeding season of 2014 in an intensively managed agricultural environment (LAJTA Project, North-West Hungary). In order to assess the habitat preferences of the Common Quail, habitat composition around occupied plots were compared with unoccupied control plots. To characterize the habitat, a total of 11 variables related to vegetation structure and diversity, food availability and landscape were quantified. Multivariate methods (PCA and GLMs) were used to distinguish the main factors influencing habitat selection and to model the presence of the Common Quail. Based on our results, in the LAJTA Project, high probability of Common Quail presence can be predicted in plots with higher herbaceous cover and more abundant arthropod communities. The network of ecotone habitats, particularly the proximity to woody habitats, also appeared to have significant importance during the breeding season.

Keywords: Common Quail, plant cover, food availability, field margin, forest belt

**Összefoglalás** Kutatásunkban a fürj *(Coturnix coturnix)* élőhelyválasztását vizsgáltuk intenzív agrárkörnyezetben (LAJTA Project), fészkelési időszakban, 2014-ben. Az élőhely jellemzéséhez a növényzet struktúrájára, az ízeltlábú táplálékkínálatra és a tájszerkezetre vonatkozó változókat számszerűsítettünk. A fürj élőhely-preferenciáinak értékelésére a tényleges territóriumok mellett random kontroll pontok felmérését is elvégeztük, az esetleges elkülönülést és az elkülönülést okozó változókat többváltozós statisztikai módszerekkel (PCA, GLMs) elemeztük. Vizsgálataink alapján a LAJTA Projectben a fürj jelenléte az olyan, erdősávoktól távolabb eső nyílt területeken valószínűsíthető, ahol magasabb a növényborítás és ízeltlábú abundancia. Az ökotonhálózat, ezen belül különösen az erdősávok nem elhanyagolható jelentőségűek.

Kulcsszavak: fürj, növényborítás, táplálékkínálat, táblaszegély, erdősáv

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## Introduction

Understanding the relationships between species and their habitat is a central question in ecology. Habitat defines the available range of resources and living conditions for a species, thus habitat has an important impact on vital rates, such as survival and reproduction (Hall *et al*. 1997). The aim of most habitat selection studies is to understand the roles of different factors, which determine the spatial distribution of individuals (Morris 2003). These diverse components of habitat selection patterns include for example the distribution and availability of food resources, available space (Morris & Davidson 2000), or both intra- and inter-specific interactions (Rosenzweig 1981, Morris 1999). Sometimes, however, individuals can only occupy habitats of lesser quality (Morris 2003). This often happens when the coverage of the suitable habitat is limited due to complete habitat loss or habitat fragmentation. It is widely known that agricultural intensification is one of the main reasons of the decline of farmland bird populations across Europe (e.g. Chamberlain & Fuller 2000, Donald *et al*. 2001, 2006, Báldi 2008, Voříšek *et al*. 2010). However, regional differences in the degree of decline are recognized (Wretenberg *et al*. 2006, Báldi & Faragó 2007, Báldi & Batáry 2011, Tryjanowski *et al*. 2011); therefore more specific population studies are required to better understand the processes. Furthermore, some farmland birds have more habitat flexibility i.e. nesting site or foraging requirements, which could change the patterns of the bird population in the given region (Fuller 2012).

The Common Quail *(Coturnix coturnix)* is widely distributed throughout the Palaearctic region and it is the only long-distance migratory species of Phasianidae (Cramp 1980, McGowan *et al*. 1994). The Common Quail is a typical species of grassland areas, primarily prefers open land, usually without shrubs and trees, either in lowlands or in the mountainous regions. Due to habitat transformations associated with agricultural development, this species became one of the typical species of farmland breeders (Udvardy 1941, George 1990, Guyomarc'h *et al*. 1998). Until the early 1900s, the Common Quail was a common species in Europe, although a slight population decrease was already observed at the end of the 19th century (Glutz von Blotzheim *et al.* 1994). In the 1980s, a large decline in its West-European population was observed (Perennou 2009) and has continued to show a declining trend in most European countries (BirdLife International 2018). In Hungary, the Common Quail is a protected species showing moderate population decline both locally and nationwide (Szép *et al.* 2012, Németh *et al.* 2014, MME 2018). The breeding population is estimated between 74,000 and 90,000 pairs (Hadarics & Zalai 2008, BirdLife International 2018). Studies on Common Quail were mainly carried out in Western Europe (France, Germany, Spain), which were related to its habitat use, movements, hybridization with Japanese Quail *(Coturnix japonica)* or population distribution (e.g. Saint-Jalme & Guyomarc'h 1989, George 1990, 1996, Guyomarc'h 2003, Puigcerver *et al.* 1999, 2007). Common Quail is a less studied species in Hungary, research on its ecology is poorly represented in the Hungarian avian literature (i.e. Keve *et al.* 1953), while mostly faunistic papers have been published (e.g. Szűts 1898, Barthos 1917, Külley 1924, Bán & Igmándy 1939, Keve 1955, Rapos 1957, Kovács 1965, Debreceni *et al.* 1990, Kovács 2005, Faragó 2012b).

The main goal of this study was to assess the habitat selection of the Common Quail in a human-transformed habitat. Our aim was to find out which parameters influence the habitat selection the most in an intensively managed agricultural environment.

## Material and Methods

### Study area

The study was carried out in the area of the LAJTA Project, which covers 3,065 ha of land in the Kisalföld (Little Hungarian Plain), North-West Hungary *(Figure 1)*. Until 1995, the area had been managed exclusively by the Lajta-Hanság Co. However, in 1995, due to compensations/privatization, 50% of the area was transferred to the hands of smallholders. This area has a continental climate (mean annual temperature is 9.6 °C, annual precipitation is 504 mm, mean relative humidity is 73%) where mainly cereals, corn, alfalfa, rape and maize are cultivated. About 94% of the farming is large scale (Lajta-Hanság Joint Stock Company, average field size 40 ha) and 6% is small scale (small holders, average field size 2.5 ha). In both cases, there is intensive technology which, from the point of view of mechanization and the use of chemicals, has not changed in the past few decades. Fields are separated from each other by forest belts (110 ha), tree rows (8 ha) and hedgerows (1 ha) (Faragó 2012a). Pasturing did not take place in the Project territory and the fodder demand of animal husbandry was supplied by growing alfalfa and silo maize.

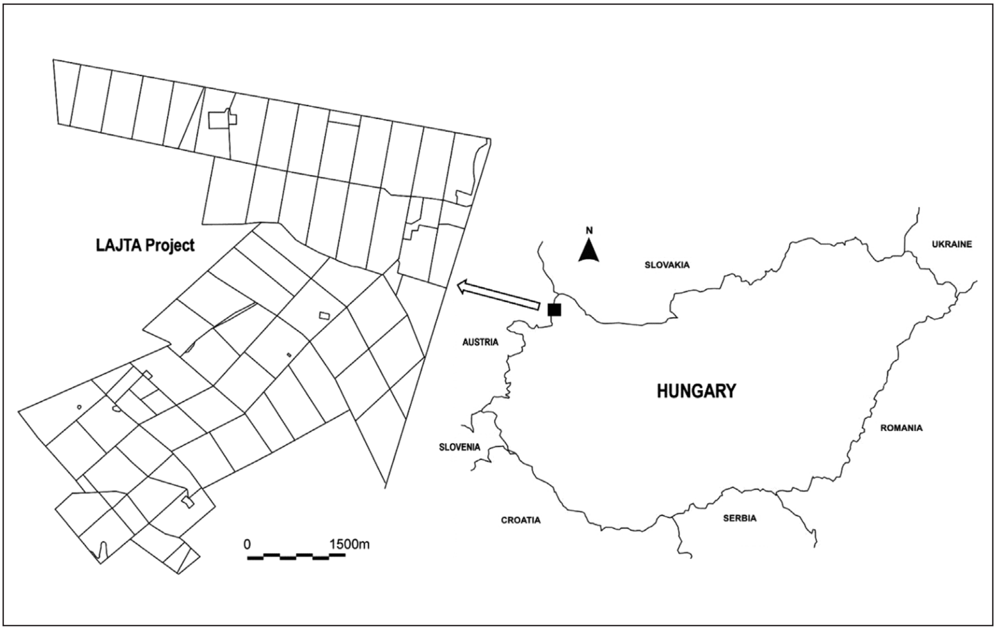

*Figure 1.* Map of the study area (LAJTA Project)
*1. ábra* A vizsgálati terület (LAJTA project)

## Field surveys

In Hungary, no specific survey technique has been proposed for the Common Quail, the used survey method is therefore roughly based on the guidance provided by Rodríguez-Teijeiro *et al*. (2010). Calling Common Quail males were counted during the breeding season between late April and August (28 survey days in total, 11 of which were in the beginning of the breeding season) in the entire study area by listening to the calls and crowing of the territory holding males. Surveys were carried out under favourable weather conditions, starting at dawn and lasting about 2.5–3 hours. At every survey point, during the first two minutes of stay we detected and counted the number of singing males. After this first step of detection, a digital bird caller (model NEWGOOD Speaker-92A) was used to play the female call lasting 20–25 seconds to stimulate silent males. The approximate position of each detected males were recorded by walking in the direction of the singing male until the bird rose up. The place from where quails delivered their first spontaneous calls at dusk has been regarded as the centre of activity. We considered a territory occupied if we documented multiple detections.

In order to assess the habitat preferences of the Common Quail, habitat composition for a total of 18 occupied territories were compared with 18 unoccupied control plots randomly selected in the study area. To characterize the habitat around territories, a total of 11 variables were quantified related to vegetation structure and diversity, food availability and landscape. Since the core daily activity area was described as a 1.5–2 ha (Perennou 2009), a 75 m radius plot was chosen for the determination of the following variables: plant species richness (Plant_S), plant diversity (Plant_Div), plant cover (Plant_Cov), arthropod number (Arth_N), arthropod dry weight (Arth_W) and arthropod diversity (Arth_Div). Furthermore, a 500 m radius plot was chosen to account for the following landscape characteristics: total length of woody ecotones like forest belts, tree rows, hedgerows (Wood_Lgth) and distance from the nearest one (Wood_Dist), total length of grassy field margins (Margin_Lgth) and distance from the nearest one (Margin_Dist); and total length of roads (Road_Lgth). With respect to grassy field margins, only those that appeared separately from woody ecotones were considered. For botanical analysis, species list and cover were recorded in randomly selected 5×5 m quadrats (N = 5). For measuring arthropod food availability, pitfall trapping was conducted. In each quadrat, a Barber trap (plastic cup of 300 ml capacity, with 80 mm diameter and 120 mm depth) was placed fitted with aluminium roofs to prevent trapping small vertebrates (e.g. lizards, rodents, shrews). For preserving solution 5% formaldehyde was used. Barber traps were installed following the detection and localization of the quails, and were operated for two months, roughly covering both the incubation and rearing periods. Traps were emptied in every two weeks.

## Data analysis

Principal Component Analysis (PCA) was used to describe the habitat structure based on data of both the Common Quail occupied and non-occupied control plots and to distinguish the main factors influencing habitat selection. Only PCA factors with eigenvalues more than 1.0

were selected (Kaiser Criterion). Factor loadings were rotated with a varimax raw transformation. Mean factor scores between the occupied and control plots were compared by using *t*-test. Normality and homogeneity of variances were tested for all parameters, and in case of necessity, transformed to fit the assumptions of parametric tests.

Generalized linear models (GLMs) were used to evaluate the presence of Common Quails, based on the obtained principal components (PCs). Since territory occupation by quails was considered as a binary response variable (presence – 1, absence – 0), the logistic link functions was applied with binomial error structure. Forward stepwise (likelihood ratio) method was applied to select the final variable in the model. Each variable was tested for significance and only those contributing significantly ($p<0.05$) to the model were retained. The performance of the GLMs was assessed using Cohen's Kappa statistics, describing the proportion of the correctly classified predictions after the probability of chance agreement has been removed (Cohen 1960). According to Landis and Koch (1977), strength of agreement can be considered slight to fair for κ values 0–0.4, moderate for 0.4–0.6, substantial for 0.6–0.8 and almost perfect for 0.8–1.0, respectively. Statistical analyses were computed using SPSS ver. 20 (IBM Corp. Released, 2011) and SAS statistical package ver. 9.1 (SAS 2012).

## Results

The PCA performed on the habitat variables yielded four new variables with eigenvalues higher than 1.0 that together explain 87.85% of the total variance *(Table 1)*. The first component (PC1) accounted for 36.85% of the total variance and it is principally governed by variables connected with herbaceous cover (Plant_Cov) and diversities (Plant_S, Plant_Div). Other major contributors to PC1 are the abundance of arthropods (Arth_N) and distance from the nearest woody ecotone (Wood_Dist). Mean factor scores on this axis differ significantly between the Common Quail occupied and non-occupied control plots (*t* test, $t = 5.023$, $p < 0.01$). The second component (PC2) accounted for 22.36% of the total

*Table 1.* Factor loadings after varimax rotation for the principal components in PCA on the habitat variables used

*1. táblázat* Az élőhelyváltozókon végzett főkomponens analízis (PCA) eredménye: komponens-együtthatók mátrixa varimax forgatás után

| | **Principal component** | | | |
|---|---|---|---|---|
| | **PC1** | **PC2** | **PC3** | **PC4** |
| Plant_S | **0.514** | 0.183 | 0.319 | 0.264 |
| Plant_Div | **0.603** | –0.098 | 0.290 | –0.119 |
| Plant_Cov | **0.863** | 0.244 | –0.180 | 0.096 |
| Arth_N | **0.667** | 0.340 | –0.187 | 0.022 |
| Arth_W | –0.231 | **0.801** | –0.196 | –0.231 |
| Arth_Div | –0.214 | **0.870** | 0.144 | 0.097 |
| Wood_Lgth | 0.311 | –0.372 | **0.796** | 0.159 |
| Wood_Dist | **–0.696** | –0.313 | 0.134 | 0.221 |
| Margin_Lgth | 0.319 | **0.576** | 0.276 | –0.202 |
| Margin_Dist | –0.361 | –0.344 | **–0.625** | –0.033 |
| Road_Lgth | 0.193 | –0.209 | 0.220 | **–0.678** |
| Eigenvalues | 4.054 | 2.460 | 1.920 | 1.229 |
| Explained variance % | 36.85 | 22.36 | 17.46 | 11.17 |
| Cumulated variance % | 36.85 | 59.22 | 76.68 | 87.85 |

*Table 1.* Summary of GLMs for the probability of presence of Common Quail

2. táblázat Az általánosított lineáris modell (GLMs) eredménye a fürj jelenlétének predikciójára

| Factors | β | SE | $\chi^2$ | p |
|---|---|---|---|---|
| (intercept) | 2.018 | 0.747 | 7.114 | 0.008 |
| PC1 | 0.076 | 0.017 | 34.073 | 0.000 |
| PC3 | –0.625 | 0.210 | 3.988 | 0.047 |
| Residual deviance | 17.963 | | | |

variance, with loadings large for arthropod diversity (Arth_Div) and weight (Arth_W); and total length of field margins (Margin_Lgth). On this axis, no significant difference has been observed between the mean factor scores of occupied and control plots (*t* test, *t* = 0.892, NS). The third component (PC3), accounted for an additional 17.46% of the total variance, is determined by the woody ecotone length (Wood_Lgth) and distance from the nearest field margin (Margin_Dist). No significant difference was observed among the Common Quail and control plots on this axis (*t* test, *t* = 1.873, NS). The fourth component (PC4), accounted for 11.17% of the total variance, was mainly governed by the total length of roads (Road_Lgth). Nevertheless, mean factor scores showed no significant difference on this axis (*t* test, *t* = 1.516, NS).

A summary of the final GLM model is presented in *Table 2*. PC1 showed a positive influence (β = 0.076) on Common Quail presence probability, and it was the most influential new variable ($\chi^2$ = 34.073) derived from the PCA. PC3 was less influential ($\chi^2$ = 3.988) and showed a negative relationship (β = –0.625) to the presence probability of quails. The model performed better in correctly predicting Common Quail habitat where presence occurred (70.4%) than in correctly classifying unoccupied habitat (62.6%). According to the κ statistic (0.341) the model had only fair agreement with the testing dataset.

## Discussion

In Hungary, the Common Quail once inhabited grasslands and wooded steppes (Faragó 2002). Nowadays, significant part of the population is breeding in agricultural environments, systematically choosing open land (Németh *et al.* 2014), usually preferring areas with a dense herb layer (Perennou 2009). Based on our results, in the LAJTA Project, two key components of the environment that positively affected the occurrence of Common Quails were protective cover and food availability. This dual requirement has been shown to be equally important for several other farmland bird species including the Grey Partridge *(Perdix perdix)* or Eurasian Skylark *(Alauda arvensis)*. The dense herbaceous cover provides nesting site, more protection against rough weather conditions and predators (Rands 1986, Green & Stowe 1993, Eggers *et al.* 2011). According to Capdevila *et al.* (2016), plant height may also have importance because taller vegetation has better suitability for hiding nests from predators. This is also demonstrated by the fact that in the course of crop harvesting the Common Quail moves to new, more suitable habitats with taller vegetation, as demonstrated by Rodríguez-Teijeiro *et al.* (2010) and Németh and Winkler (2017). As previously reported, the Common Quail did not avoid large arable fields with permanent crops (George 1990, Michailov 1995, Broyer 1996, Aunins & Priednieks 2003). Moreby and Aebischer (1992) and Panek (1997) supposed that permanent cover tends to increase the number of insects, which is an essential food supply for gamebird chicks (e.g. partridges, quails) and maintains higher reproductive success of birds. Our results showed that arthropod abundance plays a crucial role in habitat selection, while diversity and biomass of arthropod prey seem to have less importance. Although seasonal variations occur in the diet of quails (Gál & Marosán 2003), invertebrate species represent a significant proportion of Common Quail food during the breeding season (Keve *et al.* 1953, Combreau & Guyomarc'h 1992). During the first few weeks after hatching, the chicks are feeding mainly on insects therefore growth is mainly determined by the available invertebrate food resources (Combreau & Guyomarc'h 1989, Guyomarc'h *et al.* 1998). As the Common Quails also feeds on a wide range of seeds, apart from the plant cover the diversity of herbaceous vegetation seems to have great importance in the LAJTA Project, as indicated by the results of PCA. Managed cereal field, where the most Common Quail territories were found, usually support lower seed resources than field margins (Wilson *et al.* 1999, Vickery *et al.* 2002, Holland *et al.* 2012). Nevertheless, some cultivated fields (e.g. winter wheat, phacelia) in the LAJTA Project are characterized by considerable herbaceous cover and species richness, not reaching, however the conditions observed in the field margins. In our study, we found only slight effect of field margins. Capdevila *et al.* (2016) found that female quails preferred to nest near field margins, which might be related to the greater food resources and more suitable nest cover. Although a number of studies have emphasized the higher probability of predation risk in field margins (e.g. Paton 1994, Batáry & Báldi 2004), Capdevila *et al.* (2016) found no edge effect in Common Quail nest predation probability. Apart from grassy strips, previous studies in Europe emphasized the role of woody ecotones (e.g. hedges, shrubs, forest shelterbelts) in relation to certain farmland birds (e.g. Jánoska 1998, Hinsley & Bellamy 2000, Batáry *et al*. 2010, Faragó *et al.* 2012, Morelli 2013). In the LAJTA Project, the network of woody ecotones proved to have a non-negligible impact on Common Quail habitat selection through breaking the continuity of large fields. As the results revealed, the Common Quail showed avoidance of the forest belts and was mainly detected far from their edges, which is in good agreement with observations conducted in similar environments (e.g. Panek 1998, Perennou 2009).

Our results in the LAJTA Project indicate that the Common Quail is likely to occur in large-scale farming landscape, which can be classified as intensively managed agricultural environment. The importance of adequate vegetation structure (permanent, tall and dense) identified as protective rather than obstructive cover for farmland birds (e.g. Erdős *et al*. 2009, Eggers *et al*. 2011), has also been confirmed for Common Quail by our study.

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# Assessment of the breeding and wintering sites of Eurasian Woodcock *(Scolopax rusticola)* occurring in Hungary based on ringing recovery data

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**Abstract** Using the latest dataset of the Hungarian Bird Ringing Centre, the aims of this study were to describe the monthly spatial pattern of woodcock occurrence and to assess the main wintering and breeding areas of the birds associated with Hungary in the last decade. Descriptive analyses were performed regarding the annual number of detections (ringing, recaptures and recoveries), and the relation between the annual number of woodcock ringers and the number of ringed birds was tested. Minimum convex polygons (MCP) were calculated for the detections of each month, and the variation of the monthly MCP size was evaluated. Distances of all detection locations were measured from the geographical central point of Hungary, and the distributions of these distances were compared among the months. The annual number of ringed birds increased, however it was not in relation with the number of people involved in ringing. The rate of recoveries was 7.5%. Two types of the recovery circumstances were registered: 89.9% by hunting, 10.1% found dead. MCPs were calculated for eight months. Each MCP overlapped with Hungary, to varying degrees, however remarkable differences were found in the MCP sizes among the different months. The largest areas were covered in December, January and February, while the areas in September and October were less than half of that size. The shortest distances to the country were registered in March, April, October, and November. Moderate distances were recorded in May and September, and the longest distances were found in December, January and February. Large amount of data is available about the wintering areas, and a wide wintering zone can be estimated. In contrast, there is no or only very little information about the areas covered in summer.

Keywords: Eurasian Woodcock, migration, ringing, recoveries, spatial analysis

**Összefoglalás** A vizsgálat célja a Magyarországon jelölt vagy megkerült erdei szalonkák szezonális előfordulásának elemzése, és az alapján a fő telelő- és költőterületek lehatárolása volt a Magyar Madárgyűrűzési Központ adatainak felhasználásával. Leíró jellemzéssel értékeltem az előfordulások (gyűrűzések, megkerülések és visszafogások) számát, és vizsgáltam a gyűrűzést végző személyek száma és a gyűrűzött egyedek száma közötti kapcsolatot. Az előfordulási helyek alapján minimum konvex sokszögekkel (MKP) előfordulási területeket határoztam meg havi bontásban, és a területek méreteit összevetettem. Az előfordulási helyek Magyarország geometriai középpontjától mért távolságait havi bontásban értékeltem. A szalonka gyűrűzések száma az elmúlt tíz évben jelentős mértékben nőtt, ez azonban nem függött össze a gyűrűzést végző személyek számának alakulásával. A megkerülések aránya 7,5% volt, ebből 89,9% vadászathoz, míg 10,1% egyéb okból történt elhulláshoz köthető. Nyolc hónap pontjai alapján lehetett MKP-t lehatárolni. Ezek mindegyike érintette az ország területét, viszont méreteikben jelentős eltérés mutatkozott. A legnagyobb méretű területeket december, január és február hónapok esetében találtam, míg a szeptemberi és októberi területek kisebb, mint fele akkorának bizonyultak. Az ország középpontjához legközelebb a március, április és október hónapok, legtávolabbra pedig a decemberi, januári és februári előfordulási helyek estek. A nagy mennyiségű téli időszakból származó előfordulási hely alapján egy széles, nagy kiterjedésű telelőterület határolható le, ezzel szemben a nyári előfordulásról semmilyen közvetlen információval nem rendelkezünk.

Kulcsszavak: erdei szalonka, vonulás, gyűrűzés, megkerülés, térbeli elemzés

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## Introduction

Ringing data of Eurasian Woodcock *(Scolopax rusticola)* is the most reliable source of information available to date in Hungary about the migration movements of this cryptic and difficult-to-observe species. However, due to the difficulties of capturing, there was a very low amount of data gathered until a methodological change in the last decade. The most effective way to capture woodcock is night trapping with dip nets (Gossmann *et al.* 1988). The method aims to capture individual birds feeding on the ground on open fields (grazed meadows or agricultural lands). Birds are detected and approached silently using spot lamps, and then they are covered with a bell-shaped net (~1 m diameter), which is attached to a 4–8 meter long rod (bamboo or plastic). The capturing method is especially selective, not only for the species but in some cases, even for individuals (Bub 1996). It has been used successfully for capturing other species as well, like Nightjars (Forero *et al.* 2001), Pheasants (Labisky 1959) or sandgrouse (Benítez-López *et al.* 2010). The method was introduced in our country with the kind help of French ringers in 2005 (Fluck 2011). Before that, most captures occurred unintentionally, during the captures of passerines with mist nets. Capturing with mist nets combined with visual and audio lures proved to be successful in special circumstances recently (Heward *et al.* 2017), especially for males during the breeding season, although its importance is still lower.

Thanks to the effectiveness of dip nets, the number of Woodcocks ringed multiplied in the last decade (Schally 2015), therefore now it is possible to assess seasonal spatial distribution of the species.

Using the latest available dataset, the aims of this study were (1) to describe the monthly spatial pattern of woodcock occurrence based on ringing and recovery locations between 2005 and 2017, and (2) to assess the main wintering and breeding areas of the birds associated with Hungary.

## Material and Methods

The official data of the Hungarian Bird Ringing Centre was used for all analyses. In total, 732 records of detections (ringing, recapture and recovery) were available from the period between 1913 and 2017, from which the number of birds ringed in Hungary was 475. As 90% (429 records) of the whole dataset belonged to the period 2005–2017, I decided not to use older data for further analyses. This may have also decreased the chance of bias caused by possible long-term changes in the migration patterns. Descriptive analyses were performed regarding the annual number of detections (ringing, recaptures and recoveries), and the relation between the annual number of woodcock ringers (who reported at least one ringed bird in a given year) and the number of birds ringed was tested with Pearson linear correlation.

The location of each detection was displayed on a map, and minimum convex polygons (MCP – an area bordering all points by connecting the most outer ones) were calculated for each month, then the variation of the monthly MCP size was evaluated.

Distances of all detection locations were measured from the geographical central point of Hungary, and the distributions of these values were also compared among different months.

Spatial analyses were performed with Quantum GIS (v2.14) and statistical analyses were conducted using R software (v3.3.1).

## Results

### Descriptive analysis

The annual number of ringed birds increased during the study period *(Figure 1)*, however it was not in relation with the number of people involved in ringing (r = 0.432 NS). It should be noted, that the number of people was relatively low during the whole period (Mean = 9.846; SD = 3.105).The rate of recoveries compared to the total number of birds ringed (only in the case of woodcocks ringed in Hungary) was 7.5% (32 records). Two types of the recovery circumstances were registered during the study period: 89.9% by hunting, 10.1% found dead. The rate of recaptures compared to the total number of birds ringed was similar to recoveries (29 records – 6.8%). While most recoveries occurred abroad (27 records – 84.4%), there was only one recapture that was not registered at the exact same ringing site, but 1,132 km further.

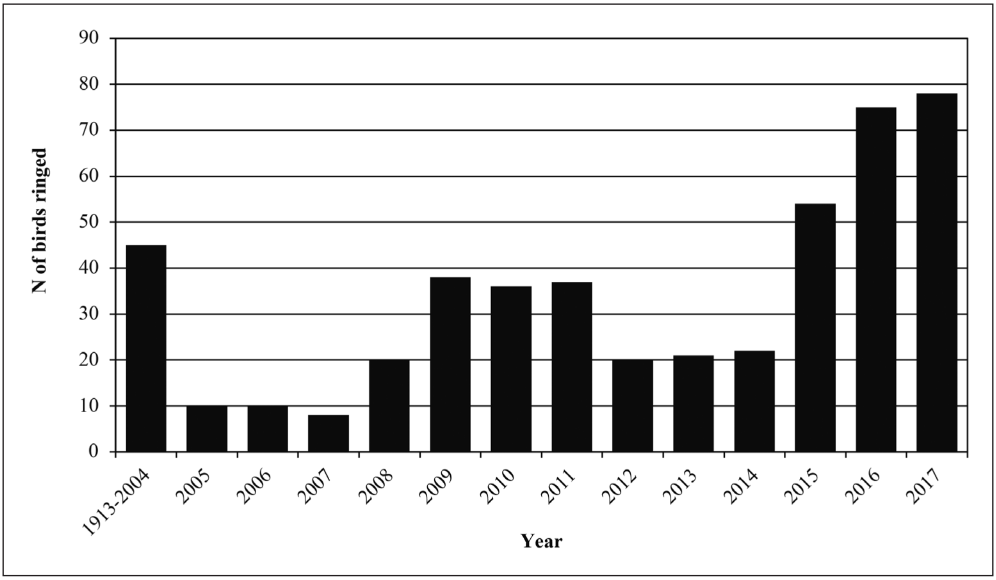

*Figure 1.* Annual number of the ringed Eurasian Woodcock in Hungary (1913–2017)
*1. ábra* Az erdei szalonka gyűrűzések évenkénti számának alakulása Magyarországon (1913–2017)

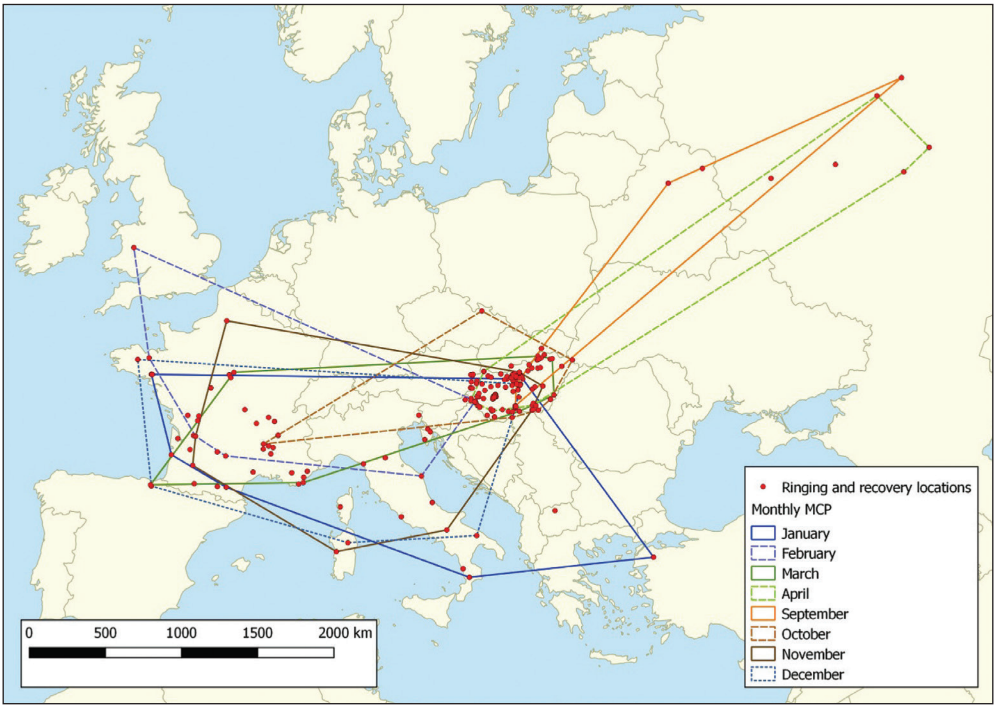

*Figure 2.* Locations of Eurasian Woodcock ringing and recovery (2005–2017)
*2. ábra* Az erdei szalonka gyűrűzések és megkerülések térbeli eloszlása (2005–2017)

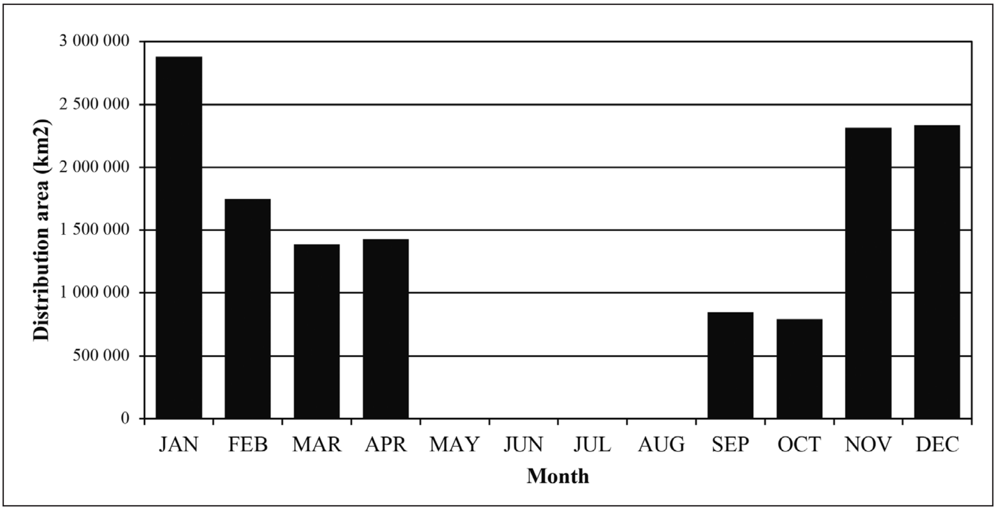

*Figure 3.* Monthly variation in the size of distribution areas represented by minimum convex polygons
*3. ábra* A minimum konvex sokszögek által határolt elterjedési területek méretei az egyes hónapokban

### MCP sizes

MCPs were calculated for eight months. It was not possible to calculate for June, July, and August, due to the complete lack of data from those months. May was also excluded because of the small amount of points (3 detections). Each calculated MCP overlapped with Hungary, to varying degrees *(Figure 2)*, however remarkable differences were found in the MCP sizes among the different months *(Figure 3)*.

The largest areas were covered in winter (December, January and February – Mean = 2,321,267.26 km$^2$, SD = 566,788.78 km$^2$), while the areas in September and October were less than half of that size (Mean = 817,365.86 km$^2$, SD = 38,407.38 km$^2$).

### Distance from the country centre

Large difference was found among the months regarding the distances of detection locations measured from the central point of Hungary. However the data did not fit the assumptions of either normality, nor the similarity of distributions, therefore no statistical comparisons were performed *(Figure 4)*. According to the distributions of the monthly data, three different groups could be identified: The shortest distances to the country were registered in March, April, October, and November. Moderate distances were recorded in May and September. The longest distances were found in December, January and February.

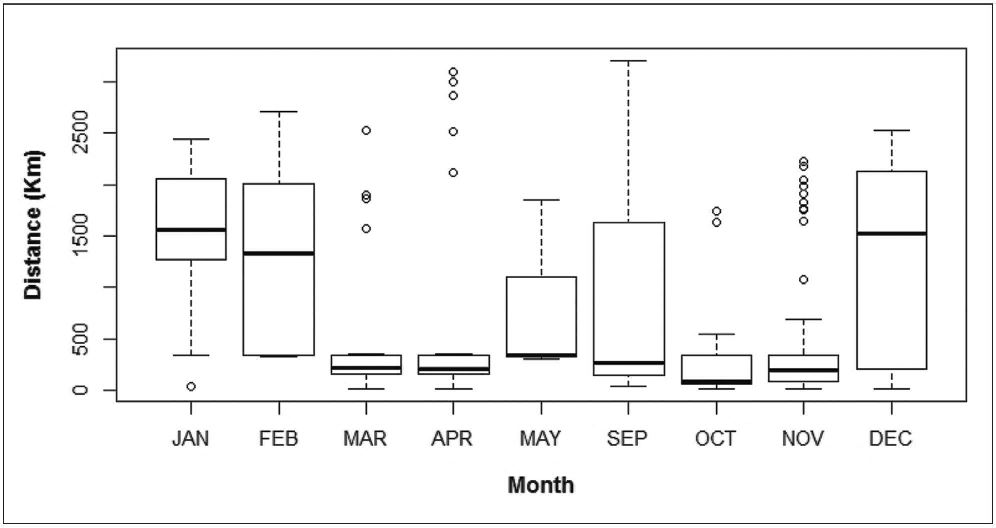

*Figure 4.* Monthly variation in the distance of ringing and recovery locations to the central point of Hungary

*4. ábra* A gyűrűzések és megkerülések helyszíneinek Magyarország geometriai középpontjától mért távolságainak alakulása az egyes hónapokban

## Discussion

Large amount of data is available about the wintering areas, and a wide wintering zone can be estimated. In contrast, there is no or only very little information about the areas covered in May, June, July or August. We can only guess these locations by the zones assessed using the points of April and September, and by older ringing data (Faragó 2006). Regarding the dominance of hunting among the recovery circumstances, the results might be strongly influenced by regional and seasonal differences in hunting activity. In most countries, hunting seasons are established in winter, and there are some in spring, but not one of course in summer (Ferrand & Gossmann 2009). Therefore, one possible way to get the missing information is raising the activity of ringing in the areas, where woodcocks are most probably breeding according to our knowledge. Ringing activity is also higher in wintering areas, e.g. in France more than 6,000 individuals are ringed annually (Rest *et al.* 2017). Fortunately, the activity has been raised recently also in Russia (Fokin & Fokina 2017). Although finding and ringing of broods would be necessary, recent studies showed that it also has serious drawbacks: finding nests or chicks requires much effort and time, and the incubating females are very likely to abandon their nests even after their first detection (Fokin & Fokina 2017). Capturing in summer might also be more difficult, because the habitat use of the birds might change during warm and dry periods, and they do not leave the forests to search for food on open grounds (Hoodless & Hirons 2007).

The largest areas were covered in winter, which can be surprising. One might expect that the birds are usually moving from large breeding areas to smaller, narrower wintering areas. The results however do not support this assumption. High genetic diversity and weak population structuring was found in the birds associated with Hungary (Schally *et al.* 2018), which can also be explained by a relatively large breeding area.

It is also surprising, that even with the largest maximum monthly distance values, still the detections of April and September generally fell closer to the centre of the country than the detections in winter. Satellite telemetry studies have shown that some birds might breed further as previously stated based on ringing recovery data (Arizaga *et al.* 2015, Rest *et al.* 2018), thus this difference is very likely to be caused only by the lack of data. Another possible cause of this result can be the individual variance in the timing of migration. However, based on the results, the assumption that most woodcocks might breed relatively close to the Carpathian Basin, cannot be excluded. For example, in France, beside a local breeding population (Ferrand *et al.* 2003), stable isotope studies revealed that the Baltic–Western European Russia and the Central-European regions are the most important origins of the birds in that country (Hobson *et al.* 2013).

## Conclusion

Although the woodcock ringing activity has raised in many countries in the last decade, there is still a lack of sufficient information about the origins of birds that occur in the country. Despite the low chance of successful detection, woodcock ringing efforts in the summer in Hungary should be improved in order to have more reliable information, but a more proper assessment of the main breeding areas could be best aided by a satellite telemetry project.

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# Analysis of skull morphometric characters in diurnal raptors (Accipitriformes and Falconiformes)

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**Abstract** Diurnal birds of prey (Accipitriformes and Falconiformes) has traditionally been known as comprising a single order. Recently, this classification has been used in the non-taxonomic sense as referring to a convergent group of birds that are largely classified as predatory birds. Although these birds are similar in their morphology, the species differ in their foraging methods and prey preference. The cranial shape and the physical attributes determine the efficiency of the resource use. The aim of this study is to increase our knowledge of the relationship between skull shape, prey preference, and foraging habits. A geometric morphometric approach was used to analyse two-dimensional cranial landmarks. We used principal component (PC) analyses on measurements that may be related to prey preference and foraging habits. The PCs are resulted described the relative height of the skull and beak, the variation in the relative size, the orientation and robustness of the lacrimal bone, the variation in the relative size of the *neurocranium* compared to the *viscerocranium*, and the orientation of the palatine bone. The dietary categories significantly overlap. The skull morphology reflects more on foraging habits than diet or prey preference.

Keywords: cranial morphology, morphometric, anatomy, jaw, skull, shape, convergent evolution, diurnal predator, prey preference

**Összefoglalás** A nappali ragadozó madarakat (Accipitriformes és Falconiformes) ma is szokás egy csoportként kezelni, bár nem rendszertani értelemben. Külső jegyeiket és megjelenésüket tekintve nagyon hasonlóak, ám a fajok eltérnek a táplálkozás-mechanizmust és a prédaállatokat illetően. Mindezek a koponyán is megfigyelhető adaptációt mutatnak. Tanulmányunkban e madarak cranialis jegyeinek elemzésével a táplálékpreferencia, a táplálkozásmód és a morfológiai jellemzők közötti lehetséges összefüggéseket kerestük. A vizsgálat során kétdimenziós landmarkok használatával főkomponens-analíziseket végeztünk. A főkomponensek a koponya és a csőr relatív magasságát, a könnycsont nagyságát, helyzetét és robuszticitását, az agy- és arckoponya egymáshoz viszonyított nagyságát, valamint a *palatinum* relatív nagyságát és helyzetét magyarázzák. Az egyes táplálkozási csoportok nagymértékben átfednek egymással. A koponyamorfológia sokkal inkább tükrözi a táplálékszerzés módját, mint a táplálékpreferenciát.

Kulcsszavak: koponya-sajátosságok, morfometria, anatómia, állkapocs, koponya, alak, konvergens evolúció, nappali ragadozó, táplálékpreferencia

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## Introduction

Birds of prey are small to large raptors which hunt and feed on other animals. Many species of these birds are apex predators in the food chain. There are insectivores, piscivores, avivores, mammalivores, scavengers, and we can find both generalist and highly specialized species (Bijleveld 1974, Cramp 1980).

Traditionally, this group includes the diurnal and the nocturnal predators. The diurnal birds of prey are formally classified into five families of three orders: Accipitridae (hawks, eagles, buzzards, harriers, kites and Old World vultures), Pandionidae (Osprey – *Pandion haliaetus*), Sagittariidae (Secretary Bird – *Sagittarius serpentarius*), Falconidae (falcons, caracaras and forest falcons) and Cathartidae (New World vultures) (Yuri *et al.* 2013, Jarvis *et al*. 2014).

Diurnal birds of prey have traditionally been treated as comprising a single order. However, as relationships between different higher taxa are uncertain and the whole assemblage is polyphyletic, that is why the phrase "diurnal bird of prey" should be used in non-taxonomic sense as referring to a convergent group of predatory birds (Helbig *et al*. 1994). Recent analyses show that the traditional raptor families Accipitridae (hawks, eagles, kites, Old World vultures) and Falconidae (falcons, caracaras) are not sister taxa (Barker *et al.* 2004, Cracraft *et al*. 2004, Hackett *et al*. 2008, McCormack *et al*. 2013, Jarvis *et al*. 2014, Prum *et al*. 2015). Currently, Accipitriformes is the order including hawks, eagles, and kites (Nagy & Tökölyi 2014), and Falconiformes are reserved for the falcons, falconets, forest falcons, and caracaras (Mindell *et al*. 2018).

Although the number of morphological similarities is great, ultimately the groups differ in their foraging methods. The foraging performance and the cranial morphology are functionally linked in a number of vertebrate taxa (Anderson *et al*. 2008). The cranial shape and the physical attributes determine the efficiency of the resource use (Dumont 2003). The feeding methods provide an example of the link between morphological modification and performance (Benkman 2003). Numerous vertebrate taxa show that cranial dimensions are related to the amount of bite force (Csermely *et al.* 1998, Ward *et al.* 2002, McBrayer 2004, Van der Meij & Bout 2004, Anderson *et al*. 2008, Sustaita & Hertel 2010). The feeding system of most vertebrates produces bite force by the musculoskeletal system of the head (Herrel *et al*. 2005).

The feeding strategies are highly diverse and the morphological adaptations for feeding are a notable feature of avian evolution (Zweers *et al.* 1994). The oral apparatus is comprised of musculoskeletal and neural systems. The avian skull shows a great variety of morphological variation (Zusi 1993). Larger animals generally have access to larger prey due to their greater muscular power and size. These factors are further related to allometry. Allometry has a key role in craniofacial form across a range of bird clades (Marugán-Lobón & Buscalioni 2006, Kulemeyer *et al*. 2009, Fabbri *et al*. 2017).

There are numerous physical similarities in the prey preference of some groups (e.g. hawks and falcons) but there are notable differences in hunting strategies (Cade & Digby 1982). For example, accipiters are known for using their legs and talons. The grip force has a clear implication and connectedness to the ability to subdue and kill prey (Csermely *et al.* 1998, Csermely & Gaibani 1998). Different characteristics of the talons are also seen to have important roles. The morphology and talon size are related to grasp and killing the prey (Csermely & Rossi 2006, Fowler *et al.* 2009). Compared to the accipiters, falcons subdue their prey with their feet, but ultimately kill the prey with their beaks. Their jaws deliver powerful bites to the prey's neck and kill the prey by breaking the cervical bones, producing damage to the nerves and spinal cord (Hertel 1995, Csermely *et al.* 1998, Sustaita & Hertel 2010).

The bird-eaters have wide skulls and beaks, while the scavenger birds have narrow beaks with greater curvature (Hertel 1995, Ladyguin 2000, Jones *et al.* 2007, Sustaita & Hertel 2010).

In most avian lineages, male to male competition for females has led to an increase in male size due to sexual selection; therefore the males are larger than females (Andersson 1994, Colwell 2000). However, in some groups like raptors and owls reversed size dimorphism exists and females are the larger sex (Mueller 1990, Owens & Hartley 1998) with the exception of the New World vultures (Graves 2017). Reversed sexual dimorphism (RSD) increases with prey size, consistent with the small-male hypothesis (Andersson & Norberg 1981, Møller & Garamszegi 2012). The intrasexual dimorphism is visible in the case of numerous vertebrate taxa. In kestrels, the directional selection on a particular size may be under contrasting pressures by the environment, and in breeding females, the advantages of large size can be counterbalanced during harsh environmental conditions (Massemin *et al.* 2000). However, morphological differences in shape between males and females are undetectable (Verwaijen *et al.* 2002).

The morphology of the skull, the maxillary and mandibular characteristics and the important details of the skull structure are determinants of the different foraging groups. These two dimensional methods allow size and shape to be considered independently, preserve geometric information, and offer techniques for studying in form (Adams *et al.* 2004). A previous study in a 2-D geometric morphometric work explored the relationship among skull shape and ecology in scavenging raptors, which reflected the size and structure of the jaw muscles but did not provide further information on other trophic guilds (Si *et al.* 2015).

In this study, we investigated the cranial and morphological diversity among the different groups. Our objective was to increase our knowledge on the relationship between skull shape and foraging habits of diurnal raptors, to find those characters that are related to diet and prey preference, and to find the possible convergent attributes. The differences in force acting on the beak during feeding may be related to skull geometry and jaw musculature. If there is a significant overlap in skull geometry between the species, it would suggest that skull geometry has evolved along similar pathways and has the same mechanical demands. The differences between the species may reflect selection pressures related to the different foraging habits. To investigate the morphological diversity of the skulls between the species, we used landmark-based morphometric methods.

## Materials and methods

### Specimens

This study is based on 142 skulls of 81 species. All skulls are from adult specimens of raptors and belong to the collection of Eötvös Loránd University (Budapest, Hungary), the collection of the Hungarian Natural History Museum (Budapest, Hungary), and the digital archives of Wageningen University (Wageningen, Netherlands) and Canterbury Museum (Christchurch, New Zealand). No bird has been killed to get its skull; all birds died either of natural causes, accidental death or died in captivity.

### Groups and diet

Before the analyses, we created seven groups, which represent the following diet categories (Hertel 1995, Guangdi *et al*. 2015). This study seeks to test that the different prey preference may have an effect on skull morphology.

- A: Avivores (Newton 1978, Lindberg & Odsjö 1983, Hinsley *et al.* 1995, Dixon *et al.* 2018)
- B: Mammalivores (Korpimäki 1985, Puzović 2008, Pomichal *et al.* 2014, Kotymán *et al.* 2015)
- C: Generalists (Bielefeldt *et al.* 1992, Graham *et al.* 1995, Tóth 2014)
- D: Herpetivores (Bakaloudis *et al.* 1998)
- E: Piscivores (Gende *et al.* 1997, Sulkava *et. al* 1997)
- F: Scavengers (Brown & Plug 1990, Moreno-Opo *et al.* 2010)
- G: Insectivores (Itämies & Mikkola 1972, Palatitz *et al.* 2015, Szövényi 2015).

### Landmarks and procedures

The variation of cranial morphology is analysed using landmark-based geometric morphometry. In our former study, we used conventional morphometric variables which were selected *a priori* (Pecsics *et al.* 2017), however in this case the meaningful variables are discovered by the analysis presented in a more recent study (Pecsics *et al.* 2018). We should not choose them before the analysis. We tried to find landmarks for this analysis to cover the geometric form of the skull. The landmarks provide a comprehensive sampling of morphology and the features of biological significance can be explored. The ideal landmarks are discrete and noticeable anatomical features, do not alter their topological positions relative to other landmarks, and provide adequate coverage of the morphology (Zelditch *et al.* 2004). The landmarks were taken from high resolution (1200×1600 pixels) photos. We took 3 photographs from each specimen (lateral, ventral, and dorsal) with closed jaws and without lower jaw. Images were standardised for the *foramen magnum occipitale* and the tip of the beak. We investigated the repeatability of the measurements by Spearman's correlation. The test was between two separate digital measures performed on skull photos ($n = 20$). For each specimen, 12 fixed landmarks *(Table 1)* were recorded in ventral view

*Table 1.* Number and description of landmarks. Terminology according to (Baumel 1993, Sun *et al.* 2018)

*1. táblázat* Az egyes landmarkok száma és leírása. Terminológia Baumel (1993) és Sun *et al.* (2018) alapján

| Number of landmark | Description of landmark |
|---|---|
| 1 | tip of the maxilla |
| 2 | the lateral associating point of palatine and maxilla |
| 3 | the most anterior-lateral point of pars lateralis |
| 4 | the most posterior-lateral point of pars lateralis |
| 5 | processus pterygoideus of palatine |
| 6 | articulation point of palatine and maxilla |
| 7 | articulation point pf pterygoid and quadrate |
| 8 | articulation of quadrate and jugal |
| 9 | most lateral point of opisthotic |
| 10 | prominentia cerebellaris |
| 11 | most caudal point of foramen magnum |
| 12 | most caudal point of condylus occipitalis |

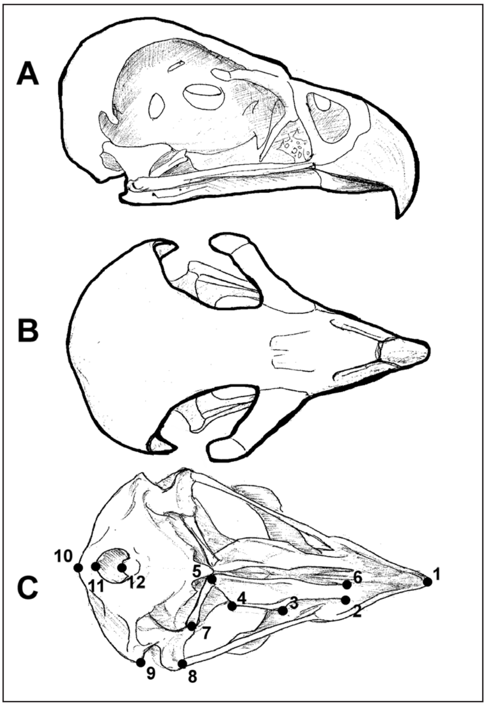

*Figure 1.* Position and number of landmarks. A: whole skull shape in lateral view, B: whole skull shape in dorsal view, C: the shape fixed landmarks in ventral view (numbers correspond to *Table 1*)

*1. ábra* A vizsgálatban használt landmarkok száma és pozíciója. A: a teljes koponya oldalnézetből, B: a teljes koponya felülnézetből, C: fix landmarkok alulnézetből (a számok megnevezését lásd az *1. táblázat*ban)

(Guangdi *et al*. 2015, Sun *et al.* 2018). We used 800 sliding landmarks to examine the shape of the whole skull in dorsal and lateral view *(Figure 1)*. These landmarks were allowed to slide along their corresponding curve due to the minimalization of the bending energy. The coordinates of the landmarks were digitised using TpsDig 2.16 software (Rohlf 2010) and were transformed using the Procrustes superimposition method. Consensus configurations and relative warps were conducted. Variability in shape was assessed using the scores obtained for each individual on the first two relative warps. We conducted principal component analyses (PCA) on these morphological variables. The relative warps correspond to the principal components (PCs) and define the shape space in which individuals are replaced. We used PAST v.1.7 software (Hammer *et al.* 2001) to perform principal component analysis and extract deformation grids. We only considered those PCs which explain >10% of the variance.

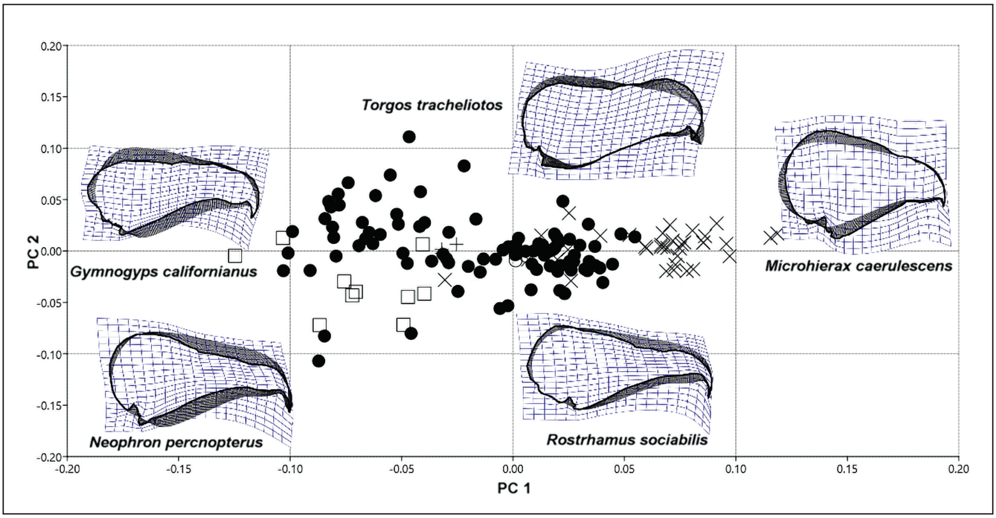

*Figure 2.* Graphical output of PCA performed on the two-dimensional landmark data (lateral view). PC1-PC2 biplot. The first PC axis described the relative height of the skull (PC1). The second PC axis described the relative highness of the beak (PC2). Thick black areas show the differences compared to the computer generated mean shape
● Accipitridae, × Falconidae, ☐ Cathartidae, ○ Pandionidae, + Sagittaridae

*2. ábra* A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (oldalnézet). Az első főtengely a koponya relatív magasságát magyarázza (PC1). A második főtengely a csőr relatív magasságával hozható kapcsolatba (PC2). A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja
● Accipitridae, × Falconidae, ☐ Cathartidae, ○ Pandionidae, + Sagittaridae

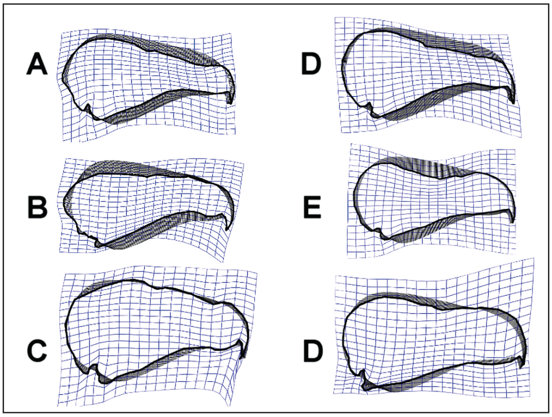

*Figure 3.* Various vulture species sharing very similar convergent attributes. A: Black Vulture *(Coagyps atratus)*, B: Californian Condor *(Gymnogyps caliornianus)*, C: King Vulture *(Sarcoramphus papa)*, D: Hooded Vulture *(Necrosyrtes monachus)*, E: White-backed Vulture *(Gyps africanus)*, F: Rüppell's Griffon Vulture *(Gyps rueppelli)*

*3. ábra* Az egyes keselyűfajok hasonló konvergens bélyegeket hordoznak. A: Hollókeselyű *(Coagyps atratus)*, B: Kaliforniai kondor *(Gymnogyps caliornianus)*, C: Királykeselyű *(Sarcoramphus papa)*, D: Csuklyás keselyű *(Necrosyrtes monachus)*, E: Fehérhátú keselyű *(Gyps africanus)*, F: Karvalykeselyű *(Gyps rueppelli)*

## Results

Our measures were significant, irrespective of measuring mode (all $r > 0.97$, all $P < 0.0001$).

The first analysis focused on the whole skull from lateral view *(Figure 2)*. We used sliding landmarks (800) to describe the cranial shape of the raptors. The first two PCs explained 59% and 17% of the variance in skull shape. The first PC axis described the relative height of the cranium (PC1). The Old World and New World vultures have long narrow head with relatively long beaks, while falcons and falconets have broad and round *neurocraniums* with short beaks. The second PC axis described the relative highness of the beak (PC2). Species like Lappet-faced Vulture *(Torgos tracheliotos)*, Cinereous Vulture *(Aegypius monachus)*, Philippine Eagle *(Pithecophaga jefferyi)* and Steller's Sea Eagle *(Haliaeetus pelagicus)* have high beaks and longer culmens. The Snail Kite *(Rosthramus sociablis)*, Black Vulture *(Coragyps atratus)*, Hooded Vulture *(Necrosyrtes monachus)* and Egyptian Vulture *(Neophron percnopterus)* have a very narrow and slender beak. Old World vulture and New World vulture species share similar morphology *(Figure 3)*.

During the second analysis we used sliding landmarks (800) to describe the skull in dorsal view. The first two PCs explained 63% and 21% of the variance in shape *(Figure 4)*. The first PC axis described variation in the relative size of the lacrimal bone and the beak (PC1). The

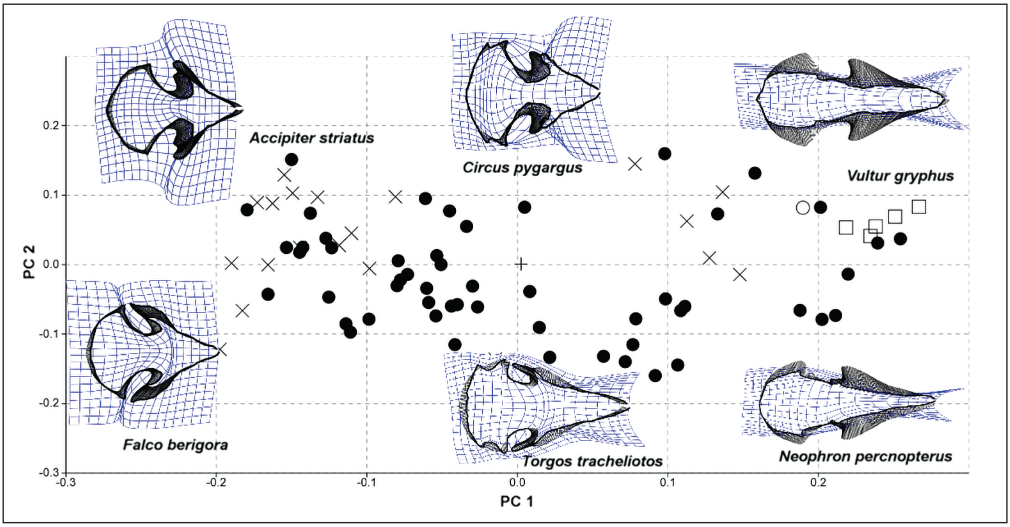

*Figure 4.* Graphical output of PCA performed on the two-dimensional landmark data (dorsal view). PC1-PC2 biplot. The first PC axis described variation in the relative size of the lacrimal bone and the beak (PC1). The second PC axis described differences in the orientation and robusticity of the lacrimal bone (PC2). Thick black areas show the differences compared to the computer generated mean shape

● Accipitridae, × Falconidae, ☐ Cathartidae, ○ Pandionidae, + Sagittaridae

*4. ábra* A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (felülnézet). Az első főtengely (PC1) a könnycsont és a csőr relatív nagyságát, a második főtengely a könnycsont relatív helyzetét és robuszticitását magyarázza. A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja

● Accipitridae, × Falconidae, ☐ Cathartidae, ○ Pandionidae, + Sagittaridae

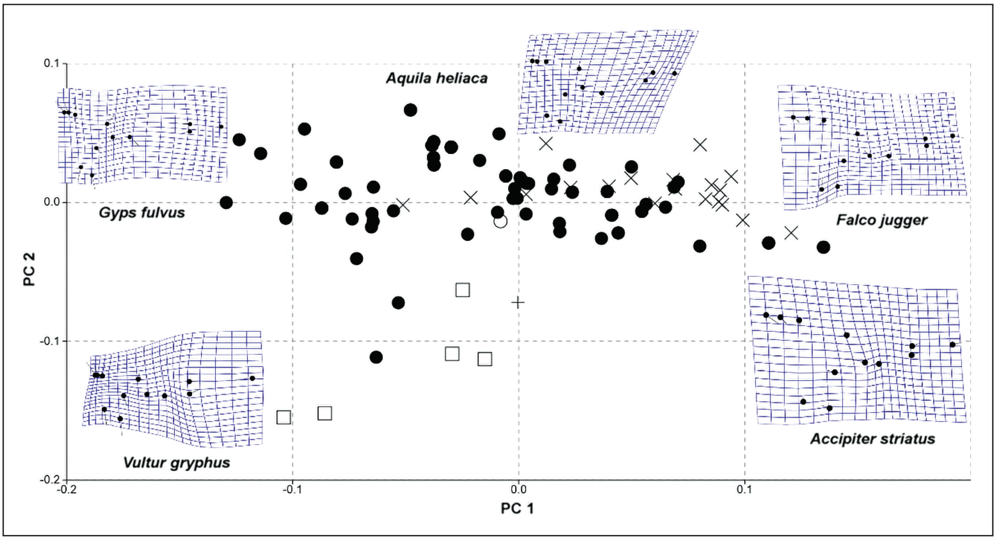

*Figure 5.* Graphical output of PCA performed on the two-dimensional landmark data (ventral view). PC1-PC2 biplot. The first PC axis described variation in the relative size of the *neurocranium* compare to the *viscerocranium* (PC1). The second reflects the relative size of the palatine bone and its distance from the tip of the beak (PC2). Thick black areas show the differences compared to the computer generated mean shape

● Accipitridae, × Falconidae, ☐ Cathartidae, ○ Pandionidae, + Sagittaridae

*5. ábra* A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (felülnézet). A PC tengelyek a *neurocranium* és a *visceroscranium* relatív nagyságát (PC1), valamint a *palatinum* relatív nagyságát és távolságát mutatják a csőrhegytől (PC2). A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja

● Accipitridae, × Falconidae, ☐ Cathartidae, ○ Pandionidae, + Sagittaridae

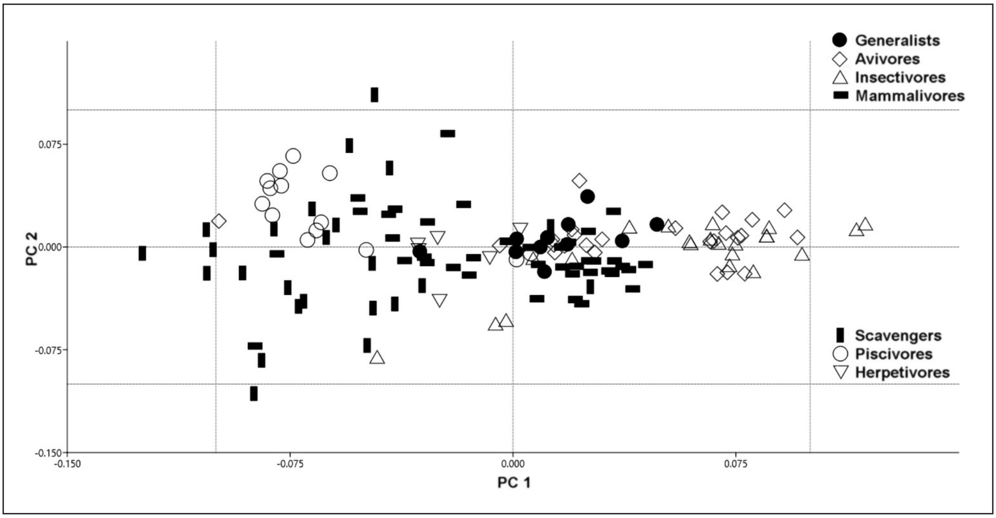

*Figure 6.* The species of different diet categories combined with the cranial shape in ventral view

*6. ábra* Kombinált ábra az egyes fajok oldalnézeti koponyaalakja és táplálékbázisa megjelenítésével falcons and *Accipiter* species have long lacrimal bones and shorter beaks compared with vultures with very tiny lacrimal bones and long beaks. The second PC axis (PC2) described differences in the orientation and robustness of the lacrimal bone *(Figure 4)*.

The third analysis tried to describe the shape of the *cranium* fixed landmarks (12) in dorsal view. The first two PCs explained 52% and 21% of the variance in shape. The first PC axis described variation in the relative size of the *neurocranium* compare to the *viscerocranium* (PC1) and the second reflected to the relative size of the palatine bone and its distance from the tip of the beak (PC2). The analysis showed that New World vulture species differ considerably from other raptors *(Figure 5)*.

In every case, the generalist species are in the middle of the morphospace.

We tried to identify the differences between the diet categories *(Figure 6)*. There are no clear differences between the categories, as different groups are overlapping.

## Discussion

We found that in the lateral view there are differences in the shape of the relative height of the cranium and the beak. Larger species have longer beaks compared to the *neurocranium*. The allometric head growth reflected variation in head length. It can explain some of the differences between species because the smaller species usually have bigger *neurocranium* and smaller *viscerocranium*. Allometric patterns within populations do not necessarily parallel interspecific allometry (Grant *et al.* 1985). The shape of the skull of vulture species (e.g. Andean Condor) strongly differs from the skull of small raptors like falconets (e.g *Microhierax caerulescens*) and small accipitrids *(Accipiter nisus)*. But at the similar size, for example Egyptian Vulture *(Neophron percnopterus)* and bigger falcons *(Falco cherrug, Falco rusticolus)*, species also strongly differ due to the variant foraging habits and mechanical demands. Smaller and slender beaks allow the bird to deftly collect small food items from difficult to reach places. The Snail Kite *(Rosthramus sociablis)*, Black Vulture *(Coragyps atratus)*, Hooded Vulture *(Necrosyrtes monachus)* and Egyptian Vulture *(Neophron percnopterus)* have very narrow and slender beak. Molluscivore Snail Kite extracts the food with a highly specialized bill from the snail shell (Bergmann *et al.* 2013). Smaller vulture species have similar bills due to the same conditions. These species are scavengers that feed primarily on carrions, collecting the small meat pieces from between the ribs, bones, and holes. This action demands a very similar beak shape. Larger vulture species have even larger and more hooked bills. Only the largest species (Lappet-faced Vulture and Cinereous Vulture) can tear open a big carcass, later allowing smaller vulture species to access the innards (Kruuk 1967, Schüz & König 1983, Hille *et al.* 2016, Ballejo *et al.* 2018). Steller's Sea Eagle, Philippine Eagle and Harpy Eagle *(Harpia harpyja)* have also high beaks and long culmens similar to the larger vulture species. The diets of these predators' consist primarily of live prey. While tearing the prey, the bigger and stronger beak is necessary due to the larger size of their prey. Sometimes raptors swallow the prey animal whole but larger prey size demands that the raptor possess stronger beaks and requires them to use their feet and claws to tear apart their prey, enabling them to swallow the pieces bit by bit.

Without big claws, larger scavengers need stronger adductor and neck muscles (Kulemeyer *et al.* 2009). In our analyses, the extinct Haast's Eagle *(Harpagornis moorei)* was morphologically closer related to vultures and sea eagles. The fossil data and remains suggest that the giant eagle was an active avivore hunter (Brathwaite 1992). Accipitrid raptor's feet and claws have a key role in immobilizing, killing and treating the prey (Csermely & Gaibani 1998, Fowler *et al.* 2009). The skull morphology is reflecting more on foraging habits than diet or prey preference. The falcons have shorter and stronger beaks because these species are killing their prey with their bite (Hull 1991, Sustaita & Hertel 2010). Like other bird taxa, the strong and tapered beak is in positive correlation with bite performance (Van der Meij & Bout 2004, Herrel *et al.* 2005). As a result of convergent evolution, different scavengers share very similar morphology. These species have slender and lower skulls, longer bills, small sideward orbits, and caudally positioned quadrates. New World vultures can be distinguished by their large nostrils, narrow crania, and small orbits, and the nostrils are not divided by a septum.

The second analysis showed obvious differences between the Sharp-shinned Hawk *(Accipiter striatus)* and Andean Condor *(Vultur gryphus)*. The orbit size is associated with the mobility and the size of prey. Scavengers have small orbits with very tiny lacrimal bones, due to dead and immobile prey. Orbits of other groups of raptors are even larger. The pursuit-hunter insectivores and avivores have very large orbits with long lacrimal bones which correspond with acute vision and broad visual field (Martin 2007). More evolved binocular vision enables them to examine environments without moving the neck (Jones *et al.* 2007). The orbits of these species are larger and more anterior in position (Heesy 2004). While flying, pursuit-hunters always catch prey by initiating quick, stooping attacks above prey animals (O'Rourke *et al.* 2010). The larger species also have large, round cranium which suggests that these species should have excellent flying and maneuvering skills.

Mammalivore species bear a reduced attachment area for the adductor muscles, a relatively large palatine, long maxilla, and caudally positioned quadrate (Sun *et al*. 2018). The caudally positioned quadrate can increase the bite force (Van der Meij & Bout 2004). The herpetivore species have very similar attributes as mammalivore raptors due to the same mechanical demands. The mammalian and reptilian prey animals may have tougher skin (Hertel 1995).

The third analysis showed differences in the relative length of the cranium. Larger species have longer bills and more caudally positioned quadrate bone and *foramen magnum occipitale*. *Aquila* and *Haliaeetus* species have large palatine with wide quadrate bone. The other big raptors (Harpy and Philippine Eagle) share similar attributes. Convergent evolution and similar ecological demands allow that hawk and eagle-like species evolved in different subfamilies (Haring *et al.* 2007). We also found in our analyses that Caracara species are very close to buzzards and closer to the smaller vulture species in morphospace. These scavengers largely differ from the other falcon species. The New World vultures showed extremities with relative long and narrow craniums but relatively short and divided palatine bones with long maxilla. This could be due to the highly developed nasal region of these species; it is a well-known fact that these birds have excellent sense of smell whereas the Old World vultures find carcasses only by sight (Houston 1986).

The study showed that the generalist species are in the middle of the morphospace, which corresponding with the relatively high degree of overlap in skull shape and diet. These non-specialised raptors are very successful and have a wide range in prey spectrum and distribution.

In future studies, it would be interesting to perform combined analyses with cranial shape and attributes of the leg and talons. Similarities in the skull shape can reflect also the phylogenetic relation. In this study, we did not investigate the effect of phylogeny. The phylogenetic control would be necessary in a further analysis.

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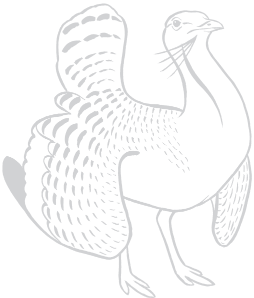

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# Pigeons, sandgrouse, cuckoos, nightjars, rollers, bee-eaters, kingfishers and swifts in the European fossil avifauna and their osteological characteristics

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**Abstract** In the article, the author describes the presence of fossil records of the pigeons (Ord. Columbiformes, Fam. Columbidae), sandgrouse (Ord. Pteroclidiformes, Fam. Pteroclididae), cuckoos (Ord. Cuculiformes, Fam. Cuculidae), nightjars (Ord. Caprimulgiformes, Fam. Caprimulgidae), rollers (Ord. Coraciiformes, Fam. Coraciidae), bee-eaters (Ord. Coraciiformes, Fam. Meropidae), (Ord. Coraciiformes, Fam. Upupidae), kingfishers (Ord. Coraciiformes, Fam. Alcedinidae) and swifts (Ord. Apodiformes, Fam. Apodidae) in Europe, particularly the Carpathian Basin, during the Tertiary and Quaternary, as well as their osteological characteristics. These orders generally contain a small number of species in Europe, most of them consisting of thermophilic, migratory species. Their fossil and subfossil remains provide precious information about the climatic conditions of their respective areas of origin.

The text is supplemented by 15 figures and 2 tables.

Keywords: Carpathian Basin, Tertiary, Quaternary, avian fauna

**Összefoglalás** A tanulmányban a szerző bemutatja a galambok, pusztai tyúkok, kakukkok, lappantyúk, szalakóták, gyurgyalagok, jégmadarak és sarlósfecskék jelenlétét a harmad- és negyedidőszak európai, benne a Kárpát-medencei fosszilis madárvilágban, és ismerteti csonttani jellegzetességeiket. A kevés európai fajjal rendelkező rendek többségükben melegkedvelő, vonuló fajokat foglalnak magukban, így maradványaik a lelőhelyeik éghajlatára nézve is értékes információkat szolgáltatnak. Csonttani jellegzetességeik eltérőek.

A szöveget 15 ábra és 2 táblázat egészíti ki.

Kulcsszavak: Kárpát-medence, harmadidőszak, negyedidőszak, madár fauna

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## Introduction

These orders and families are usually represented by merely a few species amongst the European fossilized and recent avian fauna, but are also representative of certain dry land habitats considering their lifestyles, diets and nesting habits.

Most of them are insectivorous, thus are only present as summer guests in Europe, but as such, they provide a reference point regarding climate characteristics of the respective eras to which their remains belong.

Their skeletal remains are typically easy to distinguish from species of other orders. In the following, we will describe these characteristics, and illustrate them on plates. For every discussed skeletal part, the anatomical terminology (after: Lambrecht 1933, Ballmann 1976, Baumel *et al.* 1979, Gilbert *et al.* 1981, Jánossy 1985, Kessler 2013) and method of measurement (von den Driesch 1976, Gál 2002, Kessler 2013) of the bone is given. Arrows indicate the morphological characteristics *(Figure 1)* and the method of measurement *(Figure 2)*.

According to skeletal parts, their characteristics are the following:

1. *Mandibula (Figure 3)*
a. the tip of the beak is:
– very short: *Columba, Streptopelia, Syrhaptes;*
– short: *Cuculus;*
– long: *Coracias, Merops;*
– very long: *Alcedo, Upupa;*
b. the recess between the stems is:
– ovoid: *Coracias, Syrhaptes;*
– ovoid, with recess in the middle: *Alcedo, Cuculus, Merops;*
– pointed: *Columba, Streptopelia, Upupa;*
c. the stem is:
– very long: *Columba, Streptopelia, Syrhaptes*;
– long: *Alcedo, Coracias, Merops, Upupa;*
– with spur: *Cuculus;*

2. *Coracoideum (Figure 4)*
a. the *processus acrocoracoidalis* is:
– rounded: *Alcedo*, *Caprimulgus, Coracias, Upupa;*
– hooks: *Columba, Merops, Streptopelia, Syrrhaptes;*
– cut-off: *Apus, Cuculus;*
b. the *processus procoracoidalis* is:
– missing: *Caprimulgus;*
– mixed with a *processus acrocoracoidalis*: *Alcedo, Upupa;*
– long: *Cuculus, Syrrhaptes*;
– short: *Apus, Columba, Coracias, Merops, Streptopelia*;
c. the medial end of the sternal part is:
– short and pointed: *Upupa;*
– long and pointed: *Caprimulgus, Merops, Syrrhaptes;*
– cut-off and pointed: *Alcedo;*
– short and rounded: *Apus, Cuculus;*
– long and rounded: *Columba, Coracias, Streptopelia;*
d. the lateral end of the sternal part:
– curves downward sharply: *Apus, Upupa;*
– curves upward: *Columba, Coracias, Merops, Streptopelia;*
– cut-off straight: *Caprimulgus;*

– straight: *Cuculus, Syrrhaptes;*
– rounded: *Alcedo;*

3. *Scapula (Figure 5)*
a. the lateral projection is:
– cone-shaped: *Apus, Coracias, Merops, Streptopelia;*
– rounded: *Alcedo, Columba, Upupa;*
– cut-off end: *Caprimulgus*, *Cuculus;*
b. the dorsal projection is:
– cone-shaped: *Apus, Columba, Streptopelia;*
– rounded: *Caprimulgus, Coracias, Cuculus;*
– forked: *Alcedo, Merops, Upupa;*

4. *Humerus (Figure 6–7)*
a. the *crista biccipitalis* is:
– rounded: *Caprimulgus, Columba, Coracias, Merops, Streptopelia, Upupa;*
– cone-shaped: *Alcedo, Cuculus, Syrrhaptes;*
– cut-off: *Apus;*
b. the *crista pectoralis* is:
– rounded: *Alcedo, Caprimulgus, Coracias, Cuculus;*
– cone-shaped: *Merops, Syrhaptes, Upupa;*
– curves downward: *Columba, Streptopelia;*
– cut-off end: *Apus;*
c. the *processus supracondylaris* dorsalis is:
– rounded: *Caprimulgus, Merops;*
– slightly protruding cone shape: *Coracias, Cuculus;*
– missed: *Alcedo, Apus, Columba, Streptopelia, Syrrhaptes, Upupa;*
d. the *processus flexorius* is:
– cone-shaped: *Columba, Coracias, Cuculus;*
– rounded: *Alcedo, Apus, Caprimulgus, Merops, Streptopelia, Upupa, Syrrhaptes;*

*5. Ulna (Figure 8–9)*
a. the *olecranon* is:
– pointed cone: *Alcedo, Apus, Caprimulgus, Coracias, Merops, Upupa, Syrrhaptes;*
– blunt cone: *Columba, Cuculus, Streptopelia;*
b. the *cotyla dorsalis* is:
– blunt cone: *Alcedo, Apus, Caprimulgus, Columba, Coracias, Cuculus, Merops, Streptopelia, Syrrhaptes, Upupa;*
c. the *tuberculum carpale* is:
– rounded: *Alcedo, Apus, Merops, Streptopelia;*
– pointed cone: *Syrrhaptes;*
– blunt cone: *Caprimulgus, Columba, Coracias, Cuculus, Upupa;*

6. *Radius (Figure 10)*
   a. the *corpus radii* is:
   – slightly curved: *Alcedo*, *Caprimulgus, Coracias, Merops, Upupa;*
   – straight: *Apus, Columba, Cuculus, Streptopelia, Syrrhaptes;*
   c. *tuberculum aponeurosis ventralis*:
   – pointening: *Apus, Caprimulgus, Cuculus, Upupa;*
   – blunted: *Alcedo, Coracias, Columba, Merops, Streptopelia, Syrrhaptes;*
   d. *tuberculum aponeurosis dorsalis*:
   – pointening: *Upupa;*
   – with double point: *Apus;*
   – rounded: *Alcedo, Columba, Merops, Streptopelia, Syrrhaptes;*
   – curved: *Caprimulgus, Coracias, Cuculus;*

7. *Carpometacarpus (Figure 11)*
   a. the *spatium intermetacarpalis* is:
   – narrow: *Apus;*
   – large: *Columba, Streptopelia, Syrrhaptes;*
   – very broad: *Cuculus, Upupa;*
   – medium wide: *Alcedo, Caprimulgus, Coracias, Merops;*
   b. the *facies articularis digiti major* is:
   – straight: *Apus, Caprimulgus, Syrrhaptes;*
   – oblique cone shaped: *Columba, Coracias, Cuculus, Streptopelia, Upupa;*
   – with protruding end: *Alcedo, Merops;*
   c. the *distal end of the metacarpus major* is:
   – pointed cone shape*: Apus;*
   – blunt cone: *Caprimulgus, Columba, Cuculus, Streptopelia, Syrrhaptes;*
   – rounded: *Alcedo*, *Coracias, Merops, Upupa;*

8. *Phalanx proximalis digiti majoris (Figure 12)*
   a. the proximal end is:
   – wavy: *Alcedo;*
   – straight: *Merops, Upupa;*
   – rounded: *Apus, Caprimulgus;*
   – oblique: *Columba, Coracias, Cuculus, Streptopelia, Syrrhaptes;*
   b. the distal end is:
   – rounded: *Cuculus, Merops;*
   – protruding: *Alcedo, Apus, Columba, Caprimulgus, Coracias, Streptopelia, Syrrhaptes;*
   – protruding dorsal: *Upupa;*
   c. the dorsal side is:
   – rounded: *Caprimulgus, Columba, Coracias, Merops, Streptopelia, Syrrhaptes;*
   – wavy: *Alcedo, Cuculus;*
   – straight: *Upupa;*
   – oblique: *Apus;*

9. *Femur (Figure 13)*
a. the *trochanter femoris* is
– protruding: *Caprimulgus, Columba, Streptopelia, Syrrhaptes;*
– not protruding: *Alcedo, Apus, Coracias, Cuculus, Merops, Upupa;*

The morphological homogeneity is significant in the case of this skeletal part.

10. *Tibiotarsus (Figure 14)*
a. the *crista fibularis* is:
– well-developed: *Alcedo, Apus, Columba, Coracias, Streptopelia, Upupa;*
– undeveloped: *Caprimulgus, Cuculus, Merops, Syrrhaptes;*
b. the *incisura intercondylaris* is:
– deep: *Alcedo, Apus*;
– medium developed: *Caprimulgus, Columba, Coracias, Cuculus, Streptopelia, Syrrhaptes;*
– poorly developed: *Merops, Upupa;*

Homogeneity is significant in the case of this skeletal part.

11. *Tarsometatarsus (Figure 15)*
a. the *corpus metatarsi* is:
– narrow: *Upupa;*
– medium thick and straight: *Caprimulgus, Columba, Coracias, Cuculus, Streptopelia, Syrrhaptes;*
– thick, short and straight: *Alcedo, Apus;*
– thick and curved: *Merops;*
b. the *trochlea metatarsi* II. is:
– pointed: *Apus, Cuculus, Merops, Upupa;*
– rounded: *Alcedo, Caprimulgus, Columba, Coracias, Streptopelia, Syrrhaptes;*
c. the *trochlea metatarsi* III. is:
– protruding: *Apus, Merops, Upupa;*
– not protruding: *Alcedo, Caprimulgus, Columba, Coracias, Cuculus, Streptopelia, Syrrhaptes;*
d. the *trochlea metatarsi* IV. is:
– semicircular: *Merops, Streptopelia;*
– cone shape: *Apus, Syrrhaptes, Upupa;*
– protruding: *Alcedo, Caprimulgus, Columba, Coracias, Cuculus;*

This bone is the most typical skeletal part of these orders. *Figure 2*. helps understand the size charts *(Table 1–2)*.

## Systematics

The presence of fossil species in Europe and the occurrence of recent genera and species at sites of the Carpathian Basin and Europe, and symbols for fossilized species from the Carpathian Basin are as follows:

**Abbreviations: Q1-Q2 –** Lower Pleistocene; **Q3 (Q3/I-Q3/II) –** Middle Pleistocene; **Q4/I –** Upper Pleistocene; **Q4/II –** Holocene; † – extinct/fossil species.

**Ord. Columbiformes (Latham, 1790)**
**Fam. Columbidae (Illiger, 1811)**
Representatives of the family are only known since the early Miocene across Europe. Their oldest occurrences are *Columba omnisanctorum* Ballmann, 1976 and *C. pisana* Portis, 1889 from the early and middle Pliocene of Italy (MN 14-15, MN 15-16) (Portis 1889, Ballmann 1976).

Pigeons are only known on the recent genus level from the Neogene of Europe: *Columba* sp. from Vǎršec, Bulgaria and Sandalja, Croatia (MN 17).

**– *Columba* (Linnaeus, 1758)**
**– *Columba livia* (Gmelin, 1789)**
**Q1:** Beremend 17 (Hungary) (Jánossy 1992, 1996); **Q4/I:** Velika pec na Lipi (Croatia) (Malez-Bačić 1979, V. Malez 1984,); **Q4/II:** Legény Cave (Hungary) (Lambrecht 1913); from the Quaternary of Europe: **Q1-2:** France, Italy; **Q3:** Azerbaijan, Croatia, France, Georgia, Greece, Russia, Ukraine; **Q4:** Austria, Bosnia-Herzegovina, Croatia, Czech Republic, France, Georgia, Germany, Greece, Ireland, Italy, Montenegro, Portugal, Russia, Spain, Ukrajne, United Kingdom (Tyrberg 1998).
**– *Columba palumbus* (Linnaeus, 1758)**
MN 16: Betfia 13 (Romania) (Kessler 1975, Gál 2002); **Q2:** Nagyharsány Hill 1–4 (Hungary) (Lambrecht 1916, 1933, Jánossy 1979a); **Q3/I:** Hundsheim (Austria) (Jánossy 1971, 1974); **Q4/I:** Bajót, Baits Cave (Jánossy 1979b); Bajót, Jankovich Cave (Lambrecht 1933, Jánossy 1979a); Budapest, Remetehegy Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979a, 1986); Cserépfalu, Subalyuk Cave (Jánossy 1979a); Pilisszántó, I. Shelter Cave (Lambrecht 1915, 1933, Jánossy 1979a, 1986); Tatabánya, Szelim Cave (Jánossy 1979a); Varbó, Lambrecht Kálmán Cave (Jánossy 1979a) (all in Hungary); Körösmart (Râpa, Romania) (Jánossy in Hamar & Csák 1969, Kessler 1974, Gál 2002); **Q4/II:** Bajcsa Castle (Gál 2002); Balatonkeresztúr, Réti-Dűlő (Gál 2007a); Balatonszemes, Bagódomb (Gál 2004, 2007a); Bodajk, Rigólyuk (Kordos 1984); Debrecen, Nyulas (Gál 2007b); Ecsegfalva 23 (Pike-Tay *et al.* 2004, Gál 2007b); Felsőtárkány, Petényi Cave (Jánossy 1979a); Jósvafő, Musztáng Cave (Kessler 2009); Röszke, Ludvár (Jánossy 1985, Gál 2004, 2007b); Tác, Fövénypuszta (Jánossy 1979a, 1979b); Tác-Gorsium (Bökönyi 1984, Jánossy 1985); Tiszaszőlős, Domaháza-puszta (Gál 2007b); Visegrád Castle (Bökönyi & Jánossy 1965, Jánossy 1979a (all in Hungary); Parác (Parţa) (Kessler & Gál 1997, Gál 2004), Remetelórév, Bólyikő Cave (Piatra Boiului) (Kessler 1982); Szegyestel, Drăcoiaia Cave (Sighiștel) (Kessler 1982); Vársonkolyos, Izbîndiş Cave (Şuncuiuș) (Kessler 1977, Gál 2002) (all in

Romania); from the Quaternary of Europe: **Q3:** Austria, France, Greece, Italy, Spain, United Kingdom; **Q4:** Austria, Belgium, Czech Republic, France, Georgia, Germany, Greece, Ireland, Italy, Moldova, Montenegro, Poland, Portugal, Romania, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

**– *Columba oenas* (Linnaeus, 1758)**

**Q4/I:** Hollókő (Jánossy & Vörös 1979, Jánossy 1980); Kőszeg (Lambrecht 1912, 1915, 1933) (all in Hungary); **Q4/II:** Remetelórév, Bólyikő Cave (Piatra Boiului) (Kessler 1982); Révi Caves (Vadu Crișului) (Kessler 1982) (all in Romania); Teufelslucken (Austria) (Soergel 1966); from the Quaternary of Europe: **Q1-2**: Greece; **Q3:** France, Greece, Spain; **Q4:** Austria, France, Greece, Italy, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

**– *Columba* sp. foss. indet.**

**MN 15:** Beremend 26 (Kessler 2010); **MN 15:** Csarnóta 2 (all in Hungary) (Jánossy 1979a: as *Columba livia*);

**– *Columba* sp.**

**Q4/II:** Kőrösbánlak Cave (Bălnaca) (Kessler 1982); Révi Caves (Vadu Crisului, all in Romania) (Kessler 1982).

**– *Streptopelia* (Linnaeus, 1758)**

**– *Streptopelia turtur* (Linnaeus, 1758)**

**Q4/II:** Legény Cave (Hungary) (Lambrecht 1913); Szegyestel, Drăcoiaia Cave (Sighiștel, Romania) (Kessler 1982); from the Quaternary of Europe: **Q3:** Italy; **Q4:** Austria, Czech Republic, France, Italy, Spain, Ukraine (Tyrberg 1998).

**– Columbidae gen. et sp. foss. indet.**

From the middle Miocene of Mátraszőlős 2 (MN 7/8), it was identified to the family level based on the distal fragment of a *tibiotarsus* (Kessler & Hír 2012).

The distal *tibiotarsus* fragment, that had an abraded *condylus,* resembles Columbidae in its main characteristics, but differs from recent *Columba* and *Streptopelia* genera, and shows more similarities with the latter. Its size reflects this as well.

**Fam. Pteroclidae (Bonaparte, 1831)**

Sandgrouse species live in the semi-arid regions of Southern Eurasia and Africa.

Their presence among remains from the Miocene of the Carpathian Basin is somewhat surprising, but they are quite frequently found in the Paleogene and Neogene of the western part of the continent. The bone found in Mátraszőlős may as well come from a migrating specimen.

Their earliest finds come from the Eocene and Oligocene of France (*Archaeoganga pinguis* Mourer-Chauviré, 1992; *A. validus, A. larvatus* Milne-Edwards, 1892), as well as the Miocene (*Leptoganga sepultus* Milne-Edwards, 1892; *Gerandia calcaria* Milne-Edwards, 1867). They are not known from earlier sediments. Recent species are known since the Quaternary.

**– Pteroclidae gen. et sp. foss. indet.**

Site and era: The middle Miocene of Mátraszőlős 1 (MN 7/8) identified from a distal *phalanx* (Kessler 2010).

Typical distal *phalanx* of a sandgrouse:

**– *Syrrhaptes paradoxus* (Pallas, 1773)**
**Q4/I:** Pilisszántó I. Shelter Cave (Hungary) (Lambrecht 1915, 1933, Jánossy 1979a, 1986); from the Quaternary of Europe: **Q4:** Czech Republic (Tyrberg 1998).
**– *Pterocles alchata* (Linnaeus, 1766)**
Only **Q4:** from Italy (Tyrberg 1998).

### Ord. Cuculiformes (Wagler, 1830)

### Fam. Cuculidae (Vigors, 1825)

Cuculidae can be found in the temperate and tropical territories of every continent, apart from the Antarctic, in open, grassy areas, among bushes, or trees.

Their earliest appearance is known from the Eocene represented by the species *Parviculus minor* Harrison & Walker, 1977, described from sites of Burnham-on-Crouch, England (MP 8-9, London Clay) (Harrison & Walker 1977, Harrison 1982), as well as Condé-en Brie, France (MP 8–9) (Mayr & Mourer-Chauviré 2005) from *tarsometatarsus* respectively, as well as from the Eocene and Oligocene of France (*Dynamopterus velox* Milne-Edwards, 1892; *D. boulei* Gailard, 1939), the Eocene of the USA (*Eocucculus cherpinae* Chandler, 1999), this species was also found in the Oligocene of France. *Neococcyx mccorguodalei* Weigel, 1963 from the Oligocene of France. *Veflintopris meini* Ballmann, 1969 from the Miocene of Germany. From the Miocene of Hungary *Cuculus pannonicus* Kessler, 2010 (from the late Miocene of Polgárdi 4 (MN 13) and the late Pliocene of Beremend 15 (MN 16) was described (Kessler 2010), while from the early Pliocene of Csarnóta 2, (MN 15) *C. csarnotanus* was described (Jánossy 1979b). The latter is smaller than the recent European cuckoo, but is a morphologically identical species, while the former is a new species larger than the recent European cuckoo and differs in several morphological characteristics. Representatives of the family are already present in the middle Miocene of Mátraszőlős I, identified as Cuculidae *gent. et sp.*, from a distal phalanx not identifiable from more recent times (Kessler 2010).

The genus was not found elsewhere in the Neogene of Europe. The recent species is known from the lower Pleistocene of Spain (Quibas, Q1) and Czech Republic (Stránská Skála, Q2) outside of the Carpathian Basin. Materials from the Carpathian Basin is thus unique from this era.

**– *Cuculus canorus* Linnaeus, 758**
**Q3/II:** Uppony 6 (Hungary) (Jánossy 1979a); **Q4/I:** Merkenstein (Austria) (Wettstein & Mühlhofer 1938); Pilisszántó I., Shelter Cave (Lambrecht 1915, 1933, Jánossy 1979a, 1986); Tatabánya, Kálvária Cave nr. 4 (all in Hungary) (Gál 2004, 2005); **Q4/II:** Szegyestel, Drăcoiaia Cave (Sighiștel, Romania) (Kessler 1982); Teufelslucken (Austria) (Soergel 1966); from the Quaternary outside the Carpathian Basin **Q3:** Czech Republic, France, Germany; **Q4:** Austria, Czech Republic, France, Italy, Spain (Tyrberg 1998).

### Ord. Caprimulgiformes (Ridgway, 1881)

### Fam. Caprimulgidae (Vigors, 1825)

The order of Caprimulgiformes contains families Steatornithidae, Podargidae, Nyctibiidae, Caprimulgidae and Aegothelidae. They are present on every continent apart from the frigid zones.

The earliest signs of the Caprimulgidae family come from the Eocene of Great Britain, France, Germany and North America (*Eocypselus rowei* Klepsa, *et al.* 2013; *Fluvioviridiavis platyrhamphus* Mayr and Daniels, 2001 from the USA; *Eurofluviridavis robustipes* Mayr, 2005, *Paraprefica kelleri* and *P. major* Mayr, 1999 from Germany; as well as *Archaeotrogon venustus* Milne-Edwards, 1892, A. *nocturnus* Mlíkovský, 2002, *Euronyctibius kurochkini* Mourer-Chauviré, 1989 and *Ventivorus ravei* Mourer-Chauviré, 1989 from the Eocene and Oligocene of France), while recent genera are only known from the Quaternary.

**– *Caprimulgus* (Linnaeus, 1758)**

**– *Caprimulgus europaeus* (Linnaeus, 1758)** / *Caprimulgus* † *capeki* Jánossy, 1977

Site and era: **Q1:** Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1977, Gál 2002, Mlíkovskỳ 2002); **Q4/I:** Tatabánya, Kálvária Cave nr. 4 (Hungary) (Gál 2004, 2005);

W. Čapek described the subspecies *Caprimulgus europaeus* † *fossilis* from the material gathered by Kormos T., modifyed by Jánossy D. as species *C. capeki*. The European nightjar is only known from the early Pleistocene of Europe from Stránská Skála, Czech Republic **(Q2),** and is not too common in the middle and upper Pleistocene either. **Q3:** France, Italy; **Q4:** Croatia, Georgia, Italy, Russia, United Kingdom (Tyrberg 1998).

– ***Caprimulgus ruficollis* (Temminck, 1820)**

The recent species is known outside the Carpathian Basin: **Q3:** France; **Q4:** France (Tyrberg 1998).

### Ord. Apodiformes (Peters, 1940)

Their earliest finds come from the Eocene of Great Britain, *Primapus lacki* Harrison and Walker, 1975; from the Eocene of Denmark: *Scaniacypselus wardi* Harrison and Walker, 1984; from the Eocene of Germany: *S. szarskii* Peters, 1985; *Hassiavis laticauda* Mayr, 1998; from the Eocene and Oligocene of France: *Cypselavus gallicus* Gaillard, 1908; *Procypseloides ignotus* Milne-Edwards, 1871, *P. mourerchauvirae* Mlíkovský, 2002. Recent genera are present from the Miocene. *Apus gailardi* Ennouchi, 1930 is known from the Miocene of France, *A. wetmorei* Ballmann, 1976 from the Pliocene of Italy and Bulgaria, *A. baranensis* Jánossy, 1977 from the Pliocene of Hungary, while *Chaetura baconica* Jánossy, 1977 is known from the Miocene of Hungary. Recent species are known since the Quaternary.

### Fam. Apodidae Olphe-Galliard, 1887

**– *Apus* Scopoli, 1777**

**– *Apus* † *baranensis* (Jánossy, 1977** /*Apus* † *wetmorei* (Ballmann, 1976)

Site and era: Polgárdi 4, upper Miocene (MN 13) (Kessler 2010); Csarnóta 2, lower Pliocene (MN 15) (Kessler 2010); Beremend 5 (Jánossy 1977); Osztramos 20 (Kessler 2010); upper Pliocen (MN 16) (all in Hungary);

It is a fossil species that has typical characteristics of common swifts, but is smaller than recent species. According to its dimensions, Mlikovskỳ defines it as belonging to the species *Apus wetmorei* Ballmann, 1976, described from the late Pliocene of Italy. Bones identified from Csarnóta 2 (MN 15), but mainly from Polgárdi (MN 13), indicate an even smaller species than in Italy, furthermore they predate it as well. Our opinion is that the two species are not identical.

The genus is only known from the middle Miocene of France in Europe, apart from the Carpathian Basin. Recent species are only known from the early Pleistocene.

– ***Apus apus* (Linnaeus, 1758)** / *Apus apus † palapus* (Jánossy, 1974)

**Q2:** Kövesvárad (Hungary) (Kessler 2010); **Q3/I:** Hundsheim (Austria) (Jánossy 1974); Tarkő 1 (Jánossy 1977); **Q4/I:** Hámor, Puskaporos (Lambrecht 1912, 1916, 1933, Jánossy 1986); Szilvásvárad, Istállóskő Cave (Jánossy 1986); **Q4/II:** Felsőtárkány, Petényi Cave (Jánossy 1977) (all in Hungary). From outside the Carpathian Basin, **Q3:** Czech Republic, France, Italy, Russia, Ukraine; **Q4:** Austria, Bulgaria, Czech Republic, France, Germany, Greece, Italy, Poland, Romania, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

The new subspecies was described by Jánossy from the middle Pleistocene find with dimensions matching that of the recent species, and is probably right to be classified into the recent type.

– ***Apus melba* (Linnaeus, 1758)** / *Apus † submelba* (Jánossy, 1972)

**Q3/I:** Tarkő 2, 3, 4 (Jánossy 1972, 1977); **Q3/II:** Uppony 6 (Jánossy 1977); **Q4/I:** Cserépfalu, Subalyuk Cave (Jánossy 1977) (all in Hungary); outside the Carpathian Basin **Q3:** France, Italy; **Q4:** Bulgaria, France, Georgia, Greece, Poland, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

Jánossy describes the material from Tarkő as a more massive, robust species than the recent one, but their dimensions do not differ significantly from the upper values measured in recent specimens. In the absence of morphological characteristics, Mlikovskỳ (2002) classified it as belonging to the recent species.

– ***Apus pallidus* (Shelley, 1855)**

Outside the Carpathian Basin, it is known from the middle Pleistocene **(Q3)** of France (Tyrberg 1998).

**– *Chaetura* (Stephen, 1826)**

**– *Chaetura † baconica* (Jánossy, 1977)**

Site and era: Sümeg, Polgárdi 4, upper Miocene (MN 11-12, MN 13) (Jánossy 1977); Beremend 26, lower Pliocene (MN 15) (all in Hungary) (Kessler 2010);

The fossil species is only known from the Carpathian Basin, as well as the genus from across Europe.

Common swifts are migrating, insectivorous birds with rather typical morphology and lifestyle. Other members of the order live in tropical areas. They spend most of their lives airborne, they only land to nest on ledges of cliffs and rock walls. Although they are quite swift fliers, they might fall prey in the daytime to falcons and in the nighttime to owls.

### Ord. Coraciiformes (Forbes, 1884)

### Fam. Meropidae (Vigors, 1825)

European bee-eaters are typical migrating birds of warm climates, feeding on hymenopterans. They nest in cavities carved into walls of clay any loess. While they have quite conspicuous feathers and live in groups, thus can relatively easily fall prey to predators, we rarely come across their fossilized remains.

**– *Merops* (Linnaeus, 1758)**
**– *Merops † radobojensis* (Meyer, 1865)**
Site and era: Radoboj, middle Miocene (MN 7) (Croatia) (von Meyer 1865, Mlíkovskỳ 1997); Rudabánya, upper Miocene (MN 9) (Hungary) (Kessler 2010). It was originally described as *Fringilla radobojensis* (von Meyer 1865) and Mlikovskỳ redefined it.
**– *Merops apiaster* (Linnaeus, 1758)**
**Q3/I:** Hundsheim (Austria) (Jánossy 1974); the recent species has also been reported from the late Pleistocene **(Q4)** of France (Tyrberg 1998).
**– *Merops* sp. foss. indet.**
**Q1:** Betfia 9 (Romania) (Gál 2002).
**– Meropiidae gen. et sp. foss. indet.**
**MN 6:** Kőalja 2 (Subpiatra 2, Romania) (Kessler & Venczel 2009).

**Fam. Coraciidae** (Vigors), 1825
Rollers are insectivorous with conspicuous feathers, due to this they are migrating summer guests, approximately the size of pigeons. They nest on trees, but live in more open areas. Most of the species live in warm climates.

Representatives of other genera of the family are missing from the Neogene of Europe and extinct genera are known from the Eocene of France (Montmartre, Quercy) and Germany (Messel), represented by the taxa *Cryptornis antiguus* Milne-Edwards, 1871; *Geranopterus alatus* Milne-Edwards, 1892; *G. milneedwardsi* Mayr *et* Mourer-Chauviré, 2000, as well as *Eocoracias brachyptera* Mayr *et* Mourer-Chauviré, 2000 (Milne-Edwards 1869–1871, Mayr & Mourer-Chauviré 2000, Mlikovskỳ 2002). From the Eocene of USA, *Primobucco kistneri* Feduccia, 1973; *Uintornis lucaris* Mars, 1872; *Eobucco brodkorbi* Feduccia and Martin, 1976 were reported.

**– *Coracias* (Linnaeus, 1758)**
**– *Coracias garrulus* (Linnaeus, 1758)**
**Q4/II:** Ecsegfalva (Hungary) (Pike-Tay *et al.* 2004, Gál 2007b);
**– *Eurystomus* (Vieillot, 1816)**
**– *Eurystomus † beremendensis* (Kessler, 2010)**
Described from the early Pliocene of Beremend 26 (MN 15) (Hungary), based on the proximal segment of a *metacarpus* and 2 distal *phalanges* (Beremend, BKAH) (Kessler 2010). It is larger than either the recent species or the find from Betfia.
**– *Eurystomus* sp. foss. indet.**
**Q1:** Betfia 2, 9 (Romania), (Gál 2002).
Finds differ from characteristics of the recent *Coracias garrulus,* but match those of the other genus living in Southern Europe and Africa. Fossilized *Eurystomus* finds are only known from Beremend 26 and Betfia 9, while the recent *Coracias garrulus* species is only known from the early Pleistocene of Ukraine (Tarchankut, **Q1**) (Vojinststven'skyj 1967).

**Fam. Upupidae Bonaparte**

Hoopoes also belong to the group of birds mainly widespread in tropical regions. They are summer guests of the Carpathian Basin, feed on insects and larvae, and nest in tree burrows close to the ground. We rarely come across them among fossilized material.

The family only has two extinct species from the Quaternary: *Upupa antaios* Olson, 1975 from Saint Helena and *U. phoeniculoides* from Austria and Hungary. The recent species is known since the Quaternary.

**– *Upupa* (Linnaeus, 1758)**

**– *Upupa* † *phoeniculoides* (Jánossy, 1974)**

Site and era: upper Pliocene of Beremend 38 (MN 16) (Hungary) (Kessler 2010); Hundsheim, middle Pleistocene **(Q3/I)** (Austria) (Jánossy 1974).

The find shows intermediate characteristics between *Upupa epops* and *Phoeniculus purpureus.* The newer find from Beremend (Kessler 2010), as well as the fact that the recent species is only known from more current material, just like the genus *Upupa* (lower Miocene, Czech Republic, MN 3, the find has only been identified to the genus level), both support the validity of the fossilized species.

The genus is known from the upper Miocene of Czech Republic (*Upupa* sp. – Merkur, MN 3) (Mlikovskỳ 2002), then from the middle Pleistocene of France and Spain.

**– *Upupa epops* (Linnaeus, 1758)**

**Q4/II:** Kevélynyergi-zsomboly (Hungary) (Kessler 2009). From outside the Carpathian Basin: **Q3:** France, Spain; **Q4:** France, Germany, Poland, Spain, Ukraine (Tyrberg 1998).

**Fam. Alcedinidae (Vigors, 1825)**

Kingfishers are widespread in the tropical regions.

Recent Halcyon species are only known from the upper Pleistocene of Israel and China from the Palearctic region, while *Alcedo atthis* is only known from the late Pleistocene of Great Britain, Israel and France. Their earliest known extinct representatives are the *Halcyornis toliapicus* Koenig, 1825 from the Eocene of England and the *Quasisyndactylus longibrachis* Mayr, 2004 from the Eocene of Germany, although their classification is debated.

**– *Halcyon* (Swainson, 1821)**

**– *Halcyon* † sp. foss. indet.**

Site and era: Lucsia Cave, middle Pleistocene **(Q3/I)**, (Romania) (Gál 2002);

**– *Alcedo athis* (Linnaeus, 1758)**

From Europe outside of the Carpathian Basin it is known from upper Pleistocene sites of France and Great Britain (Tyrberg 1998).

## Palaeoecological conclusions

Representatives of the orders and families listed and discussed are typically rarely found among fossilized material, except for pigeons. One reason for this is that they are not present in large numbers even in the recent fauna, and another is that despite their conspicuously colored feathers, they rarely fall prey to predators, especially to owls, to whom we would be able to attribute the accumulation and fossilization of remains due to their pellets. The presented material contains members of two genera that are missing not only from the Carpathian Basin but also most of Europe, apart from the Mediterranean region.

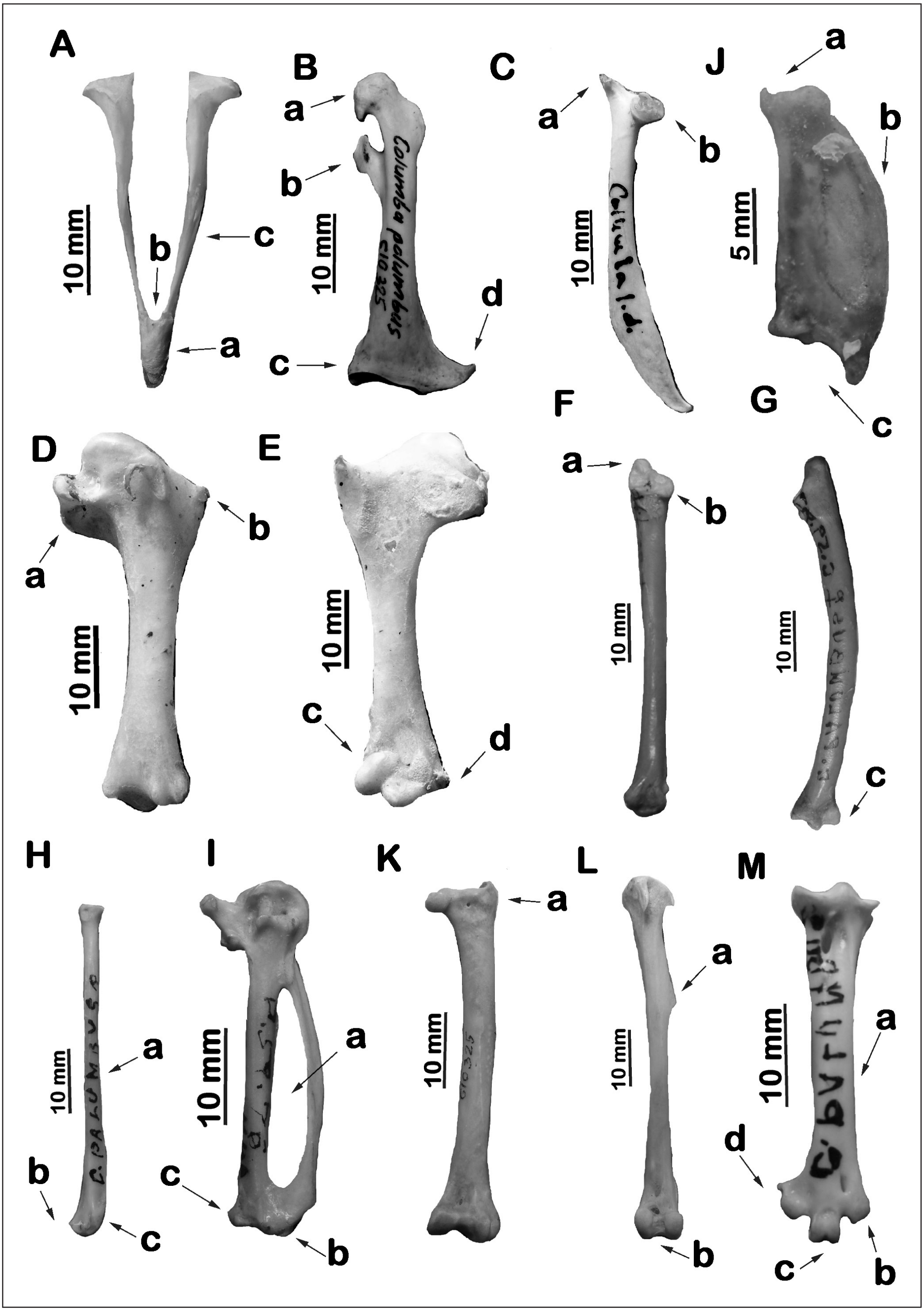
The presence of representatives of the genera *Eurystomus*, but mainly *Halcyon,* in the middle Pleistocene of the Carpathian Basin indicates the climate characteristics of the time, which may have been much milder than those of today, especially since the Lucsia Cave is located on the eastern edge of the Transylvanian mountain chain.

## Acknowledgements

The author wishes to express his deep gratitude to Mihály Gasparik for access to the recent bird bone collection in the Natural History Museum of Hungary, to József Vuts and Lóránd Abos for the language revision.

*Figure 1.* *Columba palumbus* Linnaeus, 1758 osteology characters:
A. *Mandibula* – a. the tip of the beak; b. the recess between the stems; c. the stem;
B. *Coracoideum* – a. *processus acrocoracoidalis*; b. *processus procoracoidalis;* c. the medial end of the sternal part; d. the lateral end of the sternal part;
C. *Scapula* – a. *acromion*; b. *processus articularis humeralis*;
D, E. *Humerus* – a. *crista biccipitalis*; b. *crista deltopectoralis*; c. *processus supracondylaris dorsalis*; d. *epicondylus ventralis*;
F, G. *Ulna* – a. *olecranon*; b. *apophysis glenoidalis interna*; c. *tuberculum carpale*;
H. *Radius* – a. *corpus radii*; b. *tuberculum aponeurosis ventrale*; c. *tuberculum aponeurosis dorsale*;
I. *Carpometacarpus* – a. *spatium intermetacarpale*; b. *facies articularis digitalis major*; c. the distal end of the *metacarpus major*;
J. *Phalanx proximalis digiti majoris* – a. proximal end; b. distal end; c. the dorsal side;
K. *Femur* – a. *trochanter femoris*;
L. *Tibiotarsus* – a. *crista fibularis*; b. *incisura intercondylaris*;
M. *Tarsometatarsus* – a. *corpus metatarsi*; *b. trochlea metatarsi* II.; c. *trochlea metatarsi* III.; d. *trochlea metatarsi* IV.

*1. ábra* *Columba palumbus* Linnaeus, 1758 csonttani jellegek:
A. Alsó állkapocs – a. a csőrhegy jellege; b. a két szár közti mélyedés jellege; c. a szár;
B. Hollócsőrcsont – a. *processus acrocoracoidalis*; b. *processus procoracoidalis*; c. a mellcsonti rész mediális vége; d. a mellcsonti rész laterális vége;
C. Lapocka – a. *acromion*; b. *processus articularis humeralis*;
D, E. Felkarcsont – a. *crista biccipitalis*; b. *crista deltopectoralis*; c. *processus supracondylaris dorsalis*; d. *epicondylus ventralis*;
F, G. Singcsont – a. *olecranon*; b. *apophysis glenoidalis interna*; c. *tuberculum carpale;*
H. Orsócsont – a. *corpus radii*; b. *tuberculum aponeurosis ventrale*; c. *tuberculum aponeurosis dorsale*;
I. Kézközépcsont – a. *spatium intermetacarpale*; b. *facies articularis digitalis major*; c. a *metacarpus major* disztális vége;
J. A nagy (középső) kézujj első ujjperce – a. proximális vég; b. disztális vég; c. dorsalis oldal;
K. Combcsont – a. *trochanter femoris*;
L. Lábszárcsont – a. *crista fibularis*; b. *incisura intercondylaris*;
M. Csüd – a. *corpus metatarsi*; *b. trochlea metatarsi* II.; c. *trochlea metatarsi* III.; d. *trochlea metatarsi* IV.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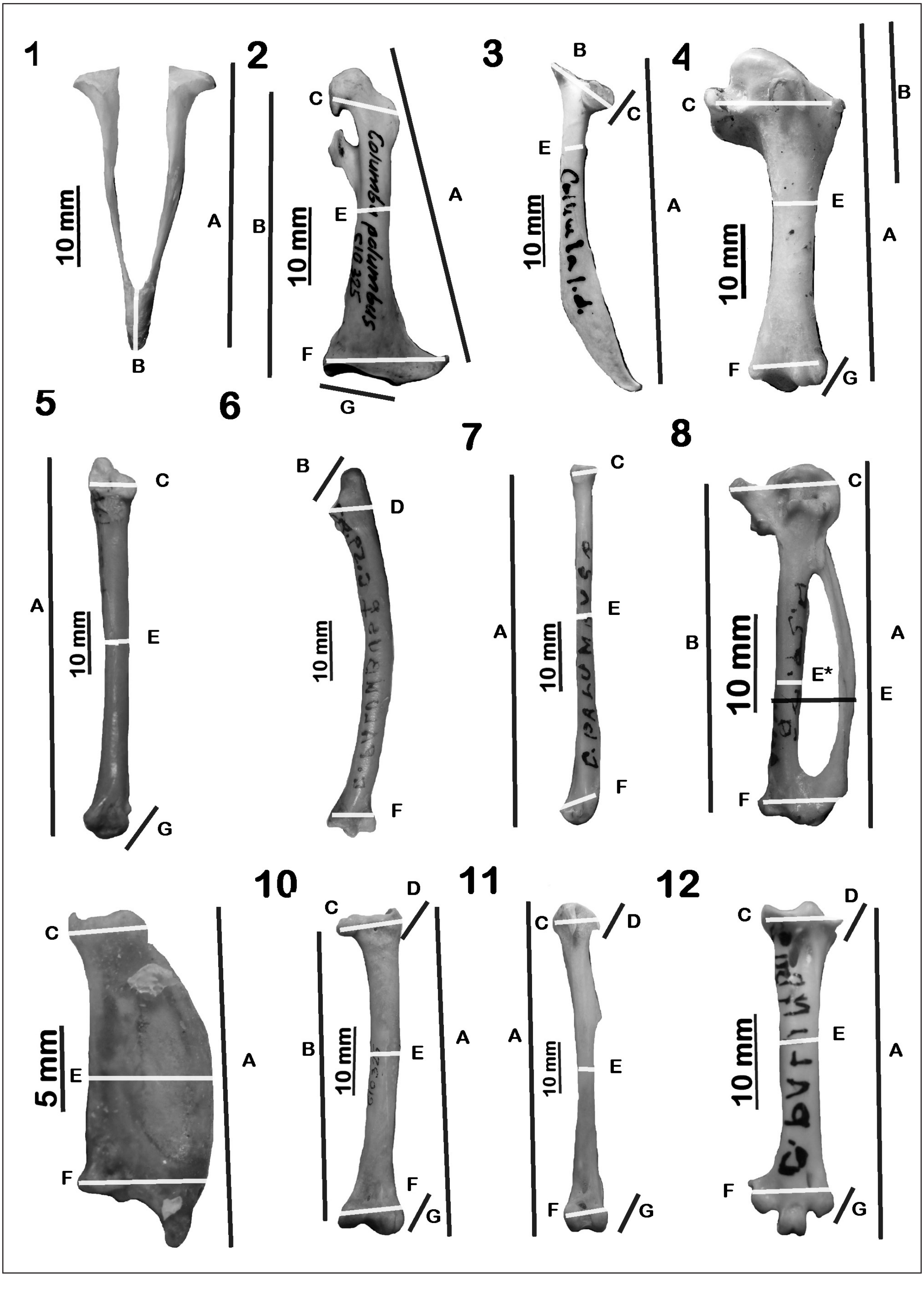
Columba palumbus
G10325
Columba l.d.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Coturnix l.d.
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C. PALUMBUS
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11
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D
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E
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12
C
D
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A
F
G
10 mm

*Figure 2.* Measurements methods of bones:

1. *Mandibula*: A. total length; B. partial length (length of apex);

2. *Coracoideum*: A. total length; B. partial length; C. breadth of the proximal end; E. breadth of the corpus; F. total breadth of the distal end; G. partial breadth of the distal end;

3. *Scapula*: A. total length; C. breadth of the proximal end; E. breadth of the corpus;

4. *Humerus*: A. total length; B. partial length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;

5-6. *Ulna*: A. total length; B. length of the proximal epiphysis; C. breadth of the proximal end; D. thickness of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;

7. *Radius*: A. total length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end;

8. *Carpometacarpus*: A. total length; B. partial length; C. breadth of the proximal end; E. breadth of the corpus; E1: breadth of the *metacarpus majus*; F. breadth of the distal end;

9. Phalanx proximalis digiti majoris: A. total length; C. breadth of the proximal end; E. breadth of the *corpus*; F. breadth of the distal end;

10. *Femur*: A. total length; B. partial length; C. breadth of the proximal end; E. breadth of the *corpus*; F. breadth of the distal end; G. thickness of the distal end;

11. *Tibiotarsus*: A. total length; C. breadth of the proximal end; D. thickness of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;

12. *Tarsometatarsus*: A. total length; C. breadth of the proximal end; D. thickness of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end

*2. ábra* A csontok mérési mintái:

1. Alsó állkapocs: A. teljes hossz; B. a csőr hegy hossza;

2. Hollócsőrcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;

3. Lapockacsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége;

4. Felkarcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;

5-6. Singcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; D. proximális vég átlós szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;

7. Orsócsont: A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége;

8. Kézközépcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; E1: a *metacarpus majus* vastagsága; F. a disztális vég szélessége;

9. Kézujjperc (II. ujj, 1. perc): A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége;

10. Combcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; D. proximális vég vastagsága; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;

11. Lábszárcsont: A. teljes hossz; C. proximális vég szélessége; D. proximális vég vastagsága; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;

12. Csüd: A. teljes hossz; C. proximális vég szélessége; D. proximális vég vastagsága; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága

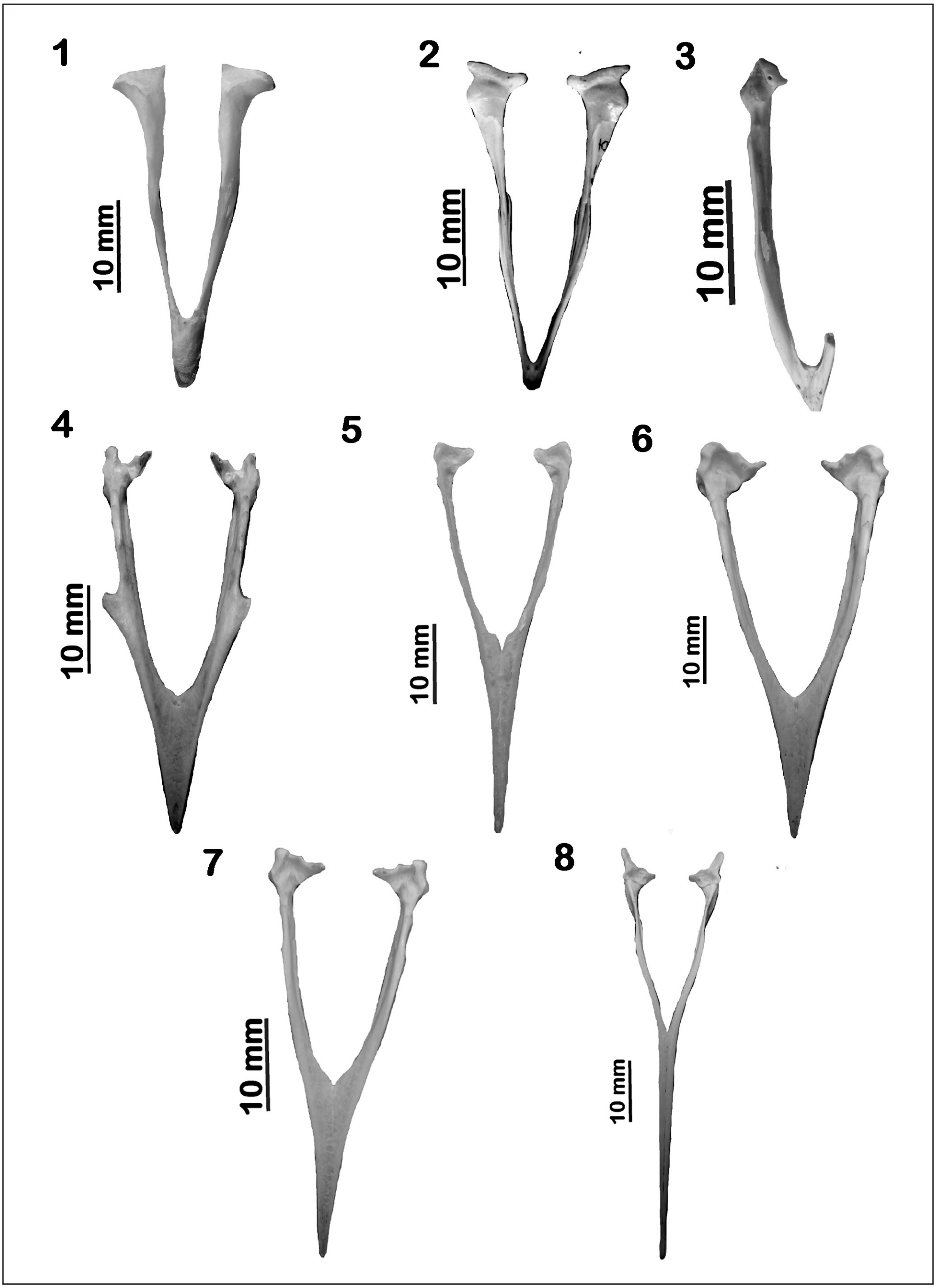

*Figure 3.* Mandibula – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Alcedo atthis;* 6. *Coracias garrulus;* 7. *Merops apiaster;* 8. *Upupa epops*

*3. ábra* Alsó állkapocs – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Alcedo atthis;* 6. *Coracias garrulus;* 7. *Merops apiaster;* 8. *Upupa epops*

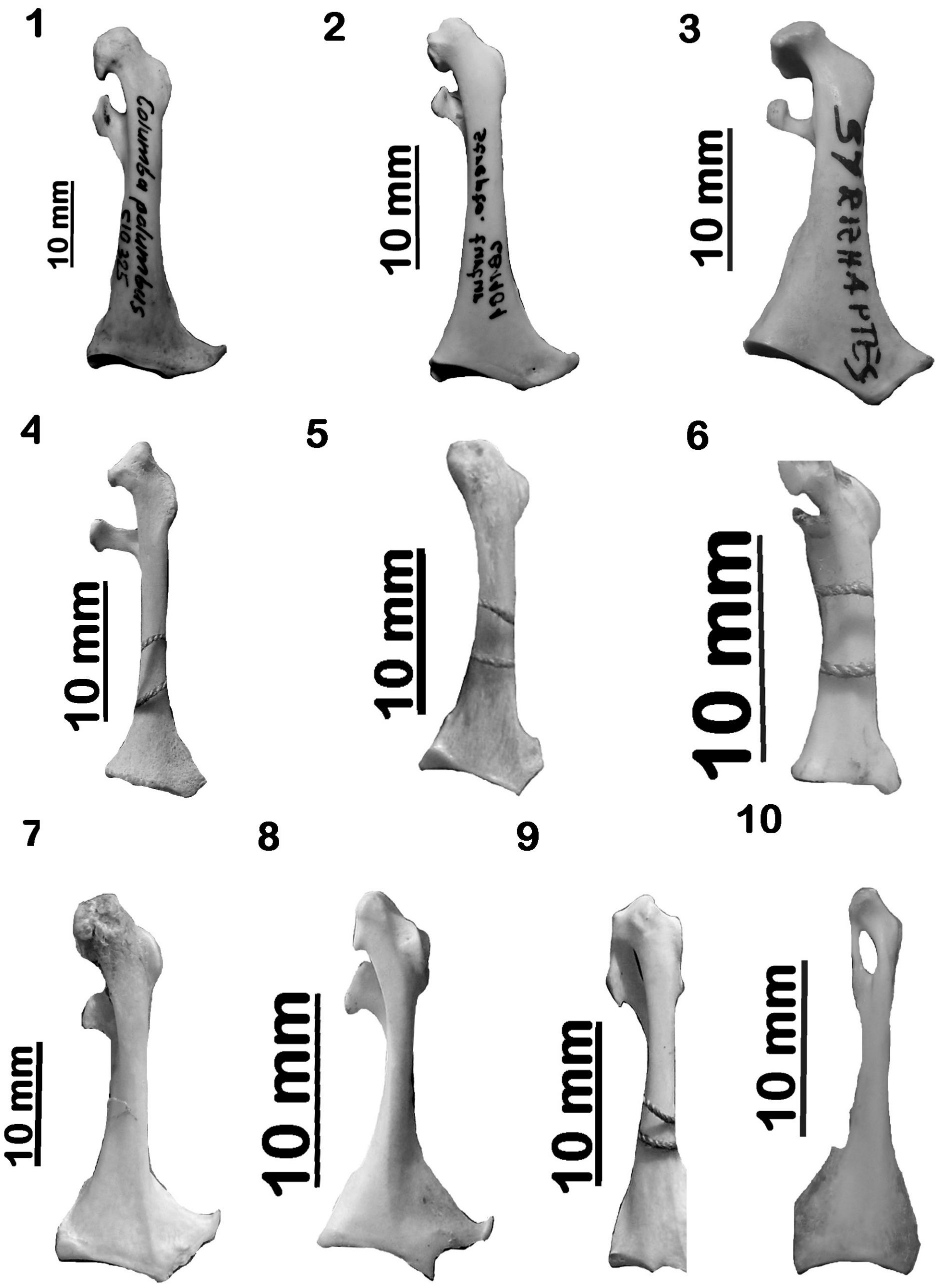

*Figure 4.* Left *coracoideum* (ventral surface) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*4. ábra* Bal oldali hollócsőrcsont (hasi oldal) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

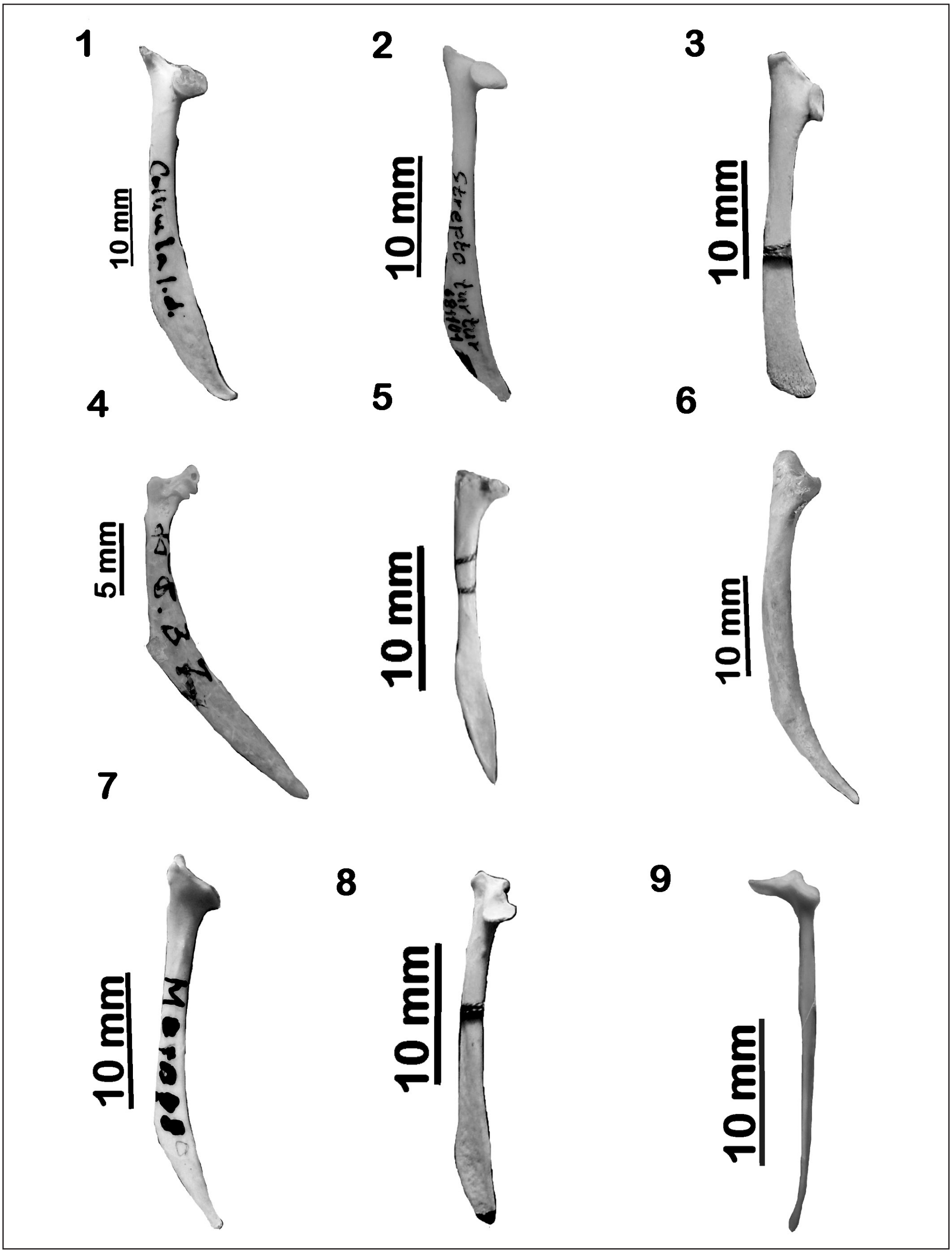

*Figure 5.* Right *scapula* (medial surface) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Cuculus canorus;* 4. *Caprimulgus europaeus;* 5. *Apus apus;* 6. *Coracias garrulus; 7. Merops apiaster;* 8. *Upupa epops;* 9. *Alcedo atthis*

*5. ábra* Jobb oldali lapocka csont (mediális oldal) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Cuculus canorus;* 4. *Caprimulgus europaeus;* 5. *Apus apus;* 6. *Coracias garrulus; 7. Merops apiaster;* 8. *Upupa epops;* 9. *Alcedo atthis*

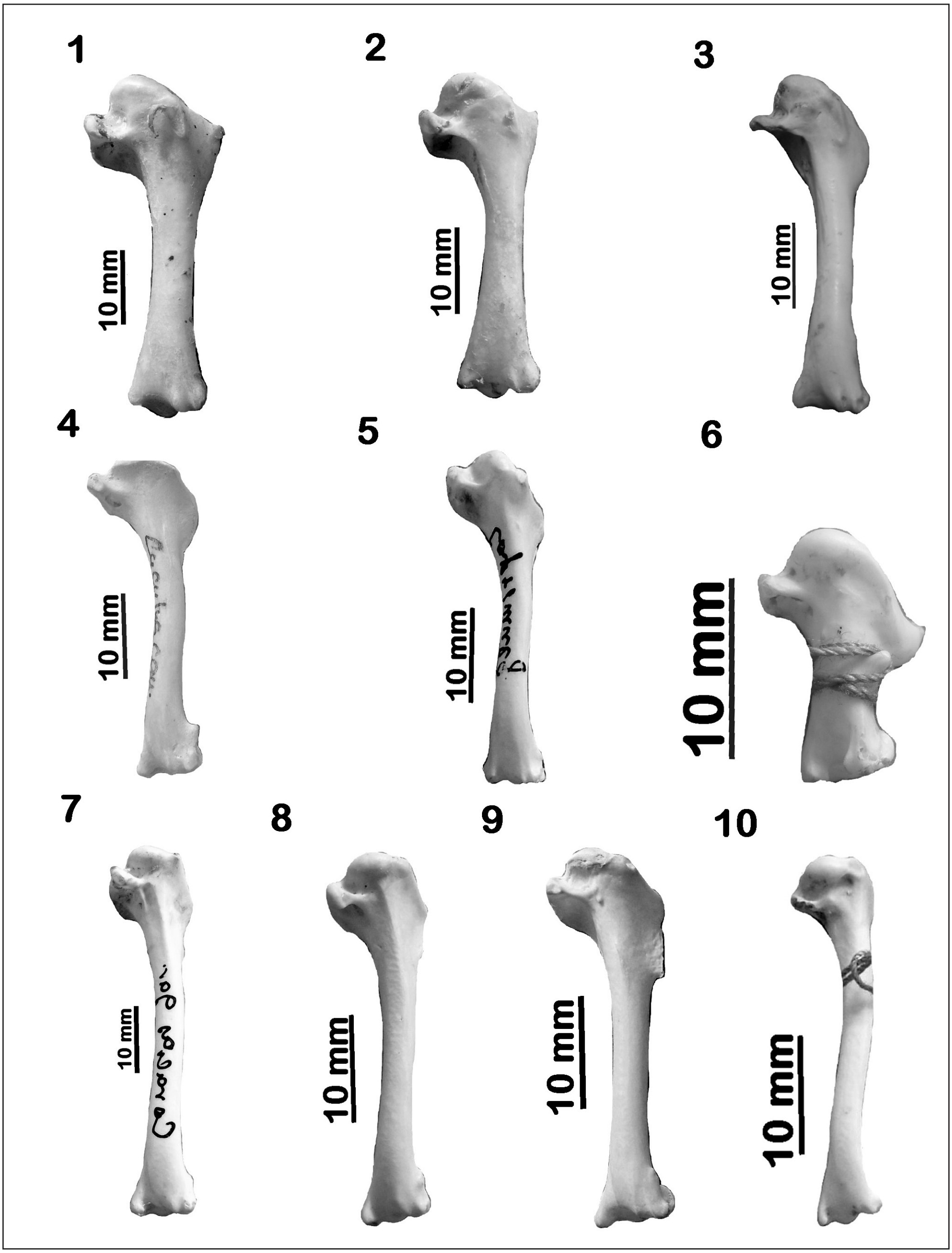

*Figure 6.* Right *humerus* (caudal surface) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*6. ábra* Jobb oldali felkarcsont (palmáris oldal) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

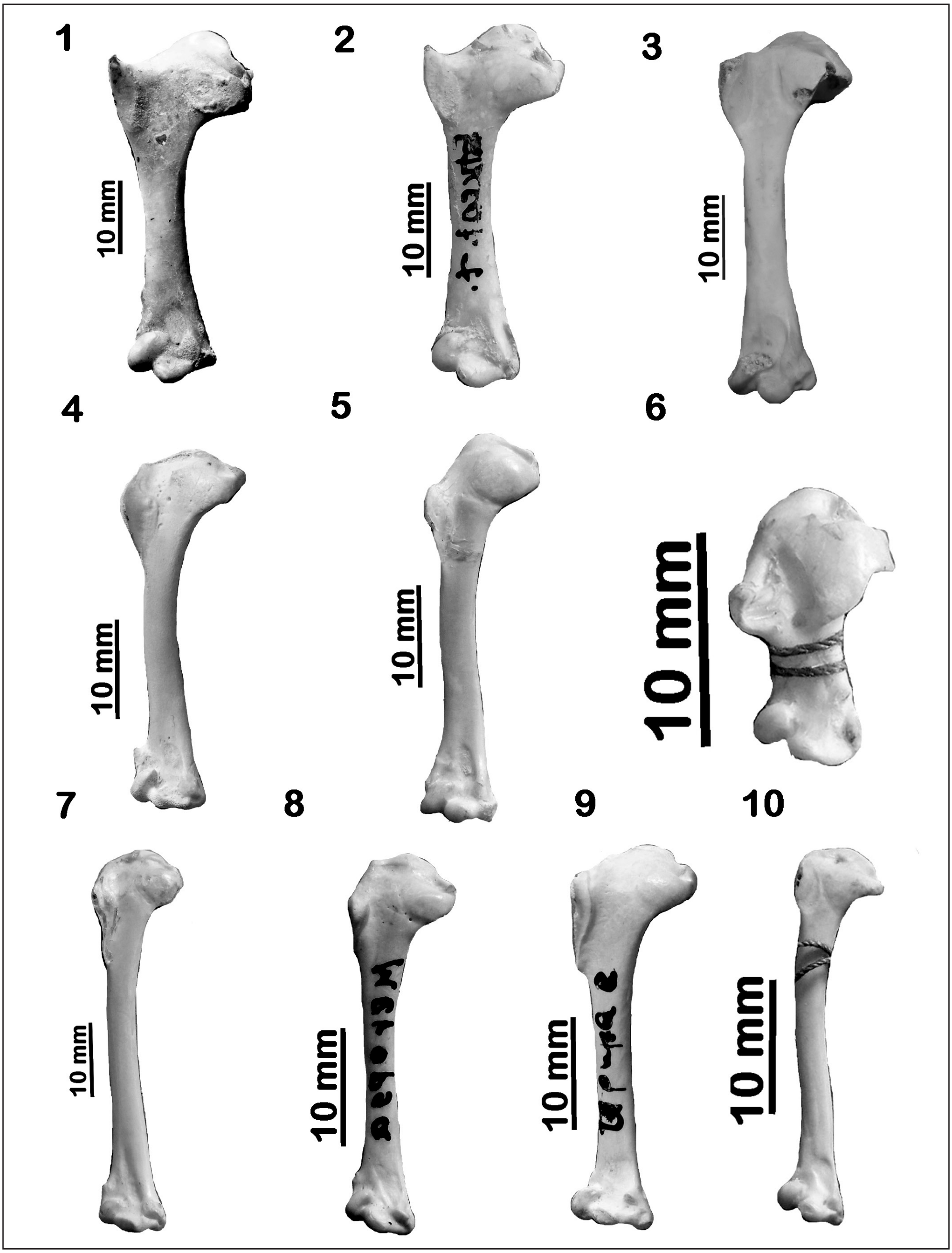

*Figure 7.* Right *humerus* (cranial surface) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*7. ábra* Jobb oldali felkarcsont (dorzális oldal) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

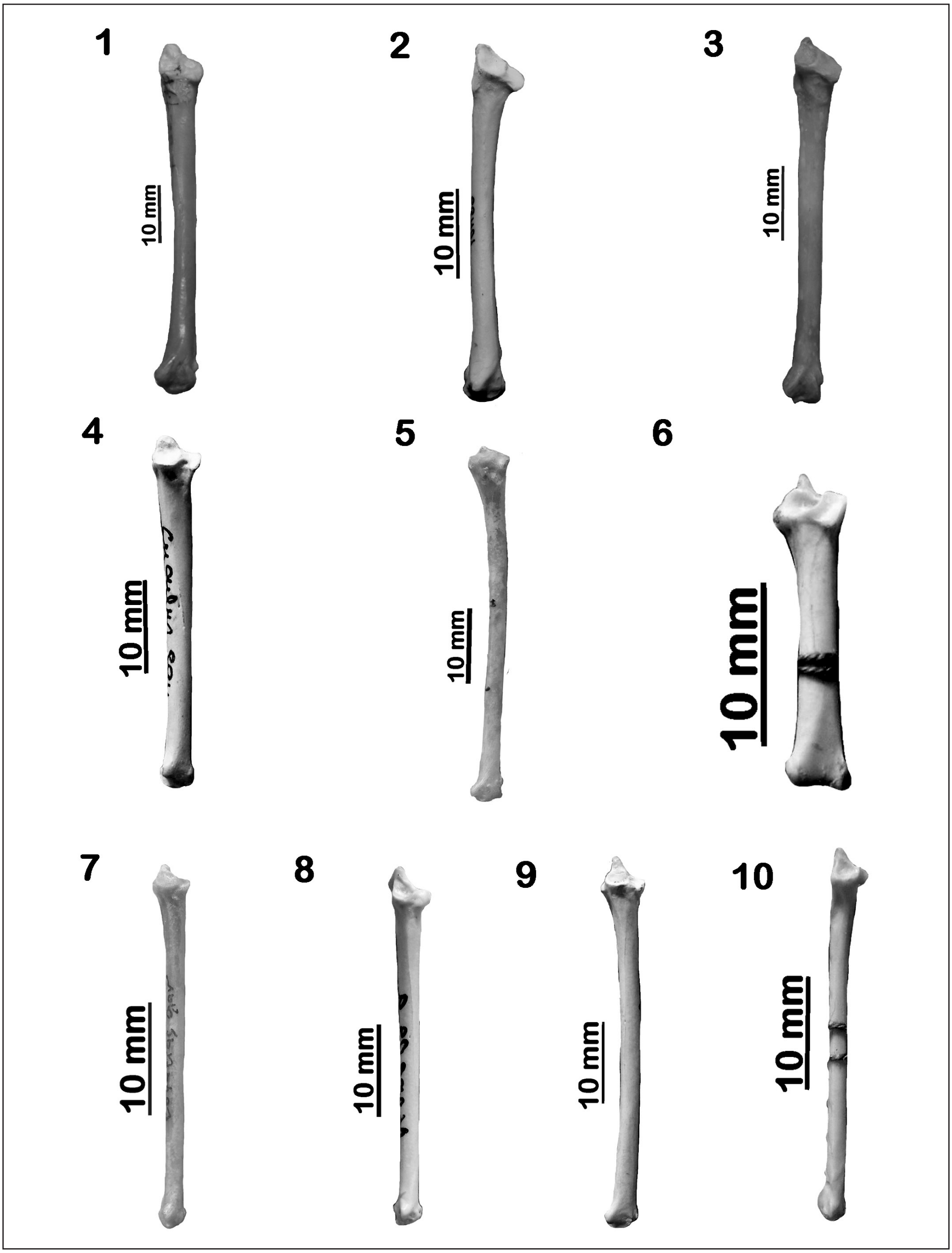

*Figure 8.* Left *ulna* (ventral aspect) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*8. ábra* Bal oldali singcsont (hasi nézet) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

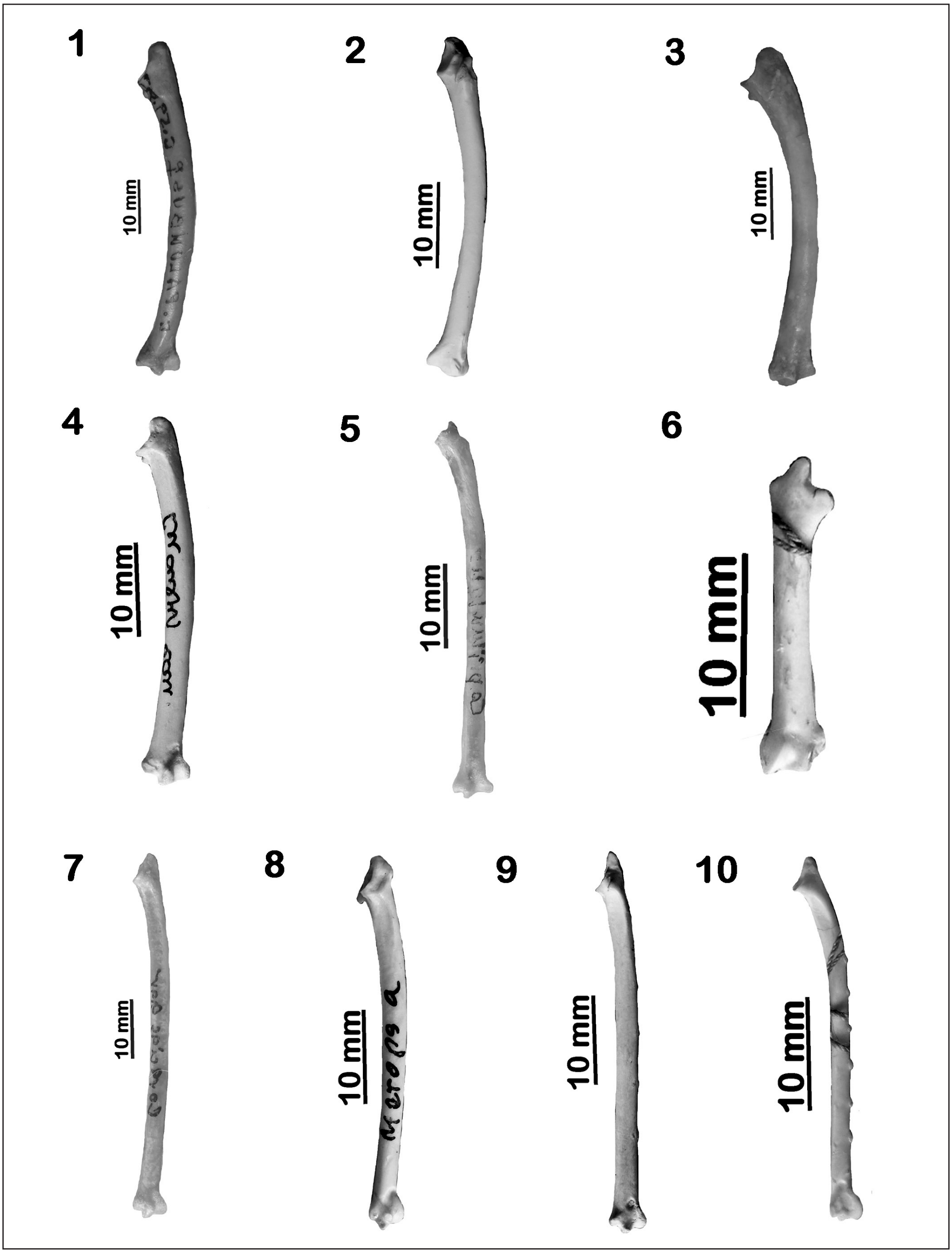

*Figure 9.* Left *ulna* (dorsal aspect) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*9. ábra* Bal oldali singcsont (háti nézet) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

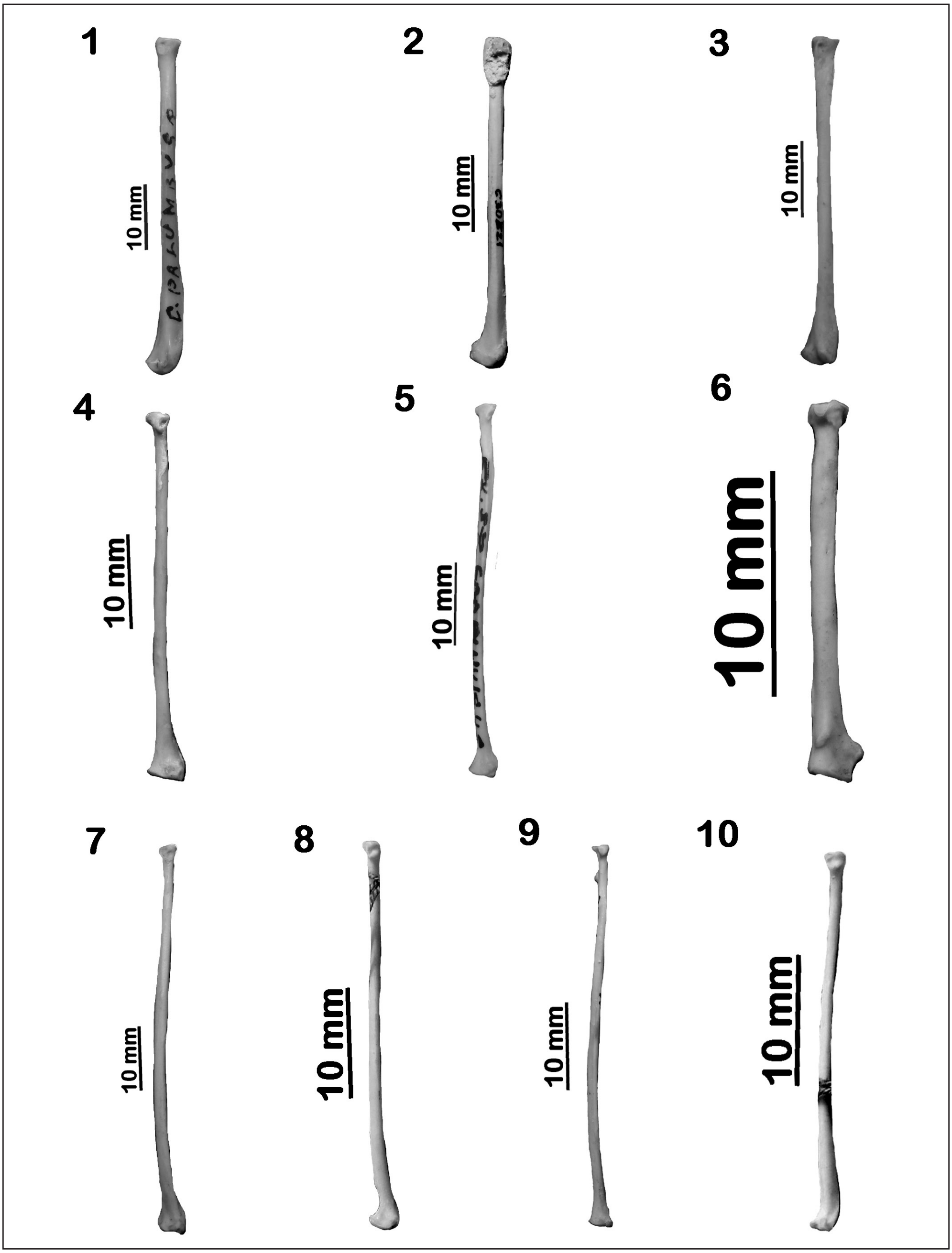

*Figure 10.* Left *radius* (dorsal aspect) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*10. ábra* Bal oldali orsócsont (háti nézet) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

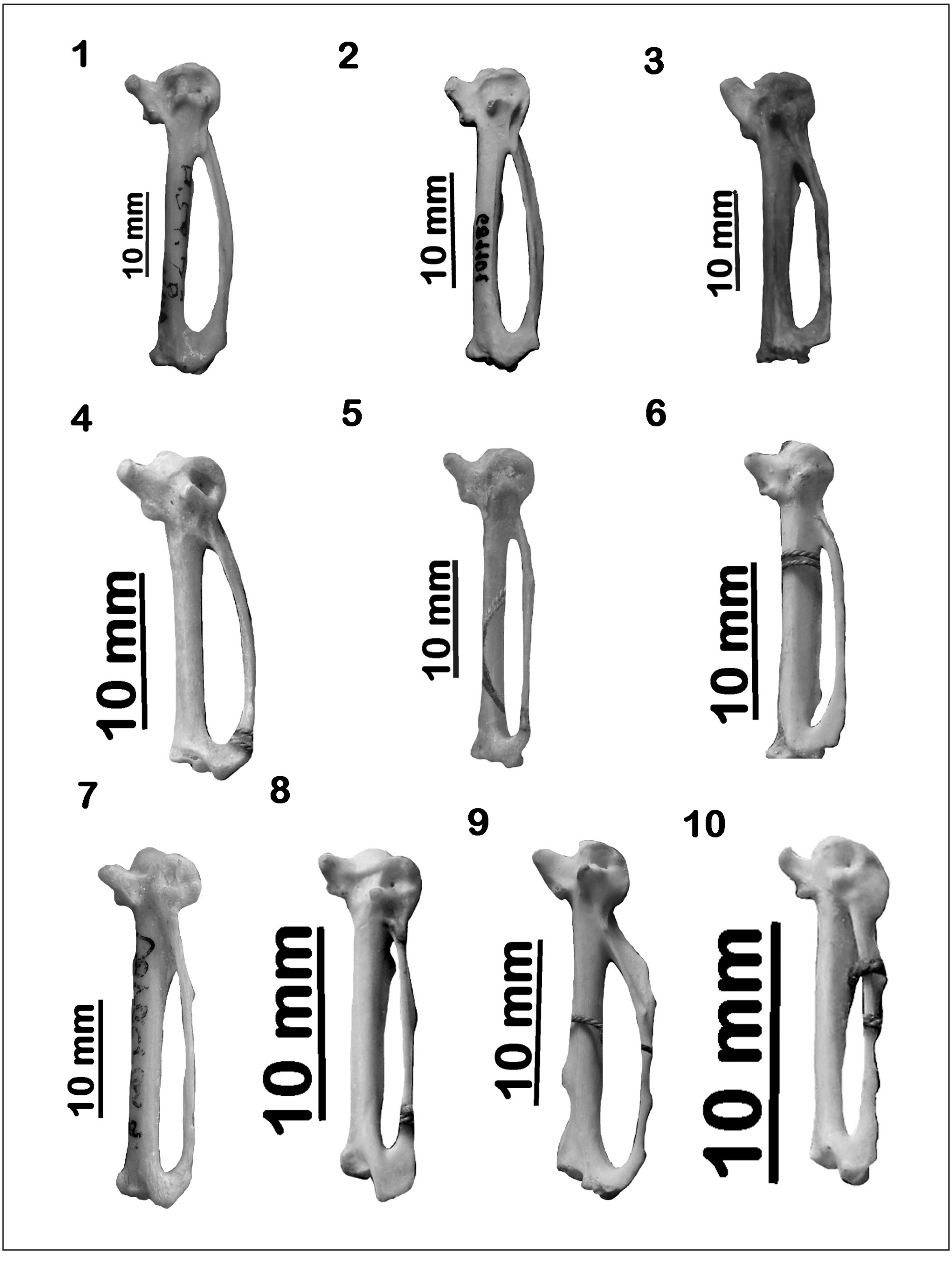

*Figure 11.* Left *carpometacarpus* (ventral aspect) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*11. ábra* Bal oldali kézközépcsont (hasi nézet) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

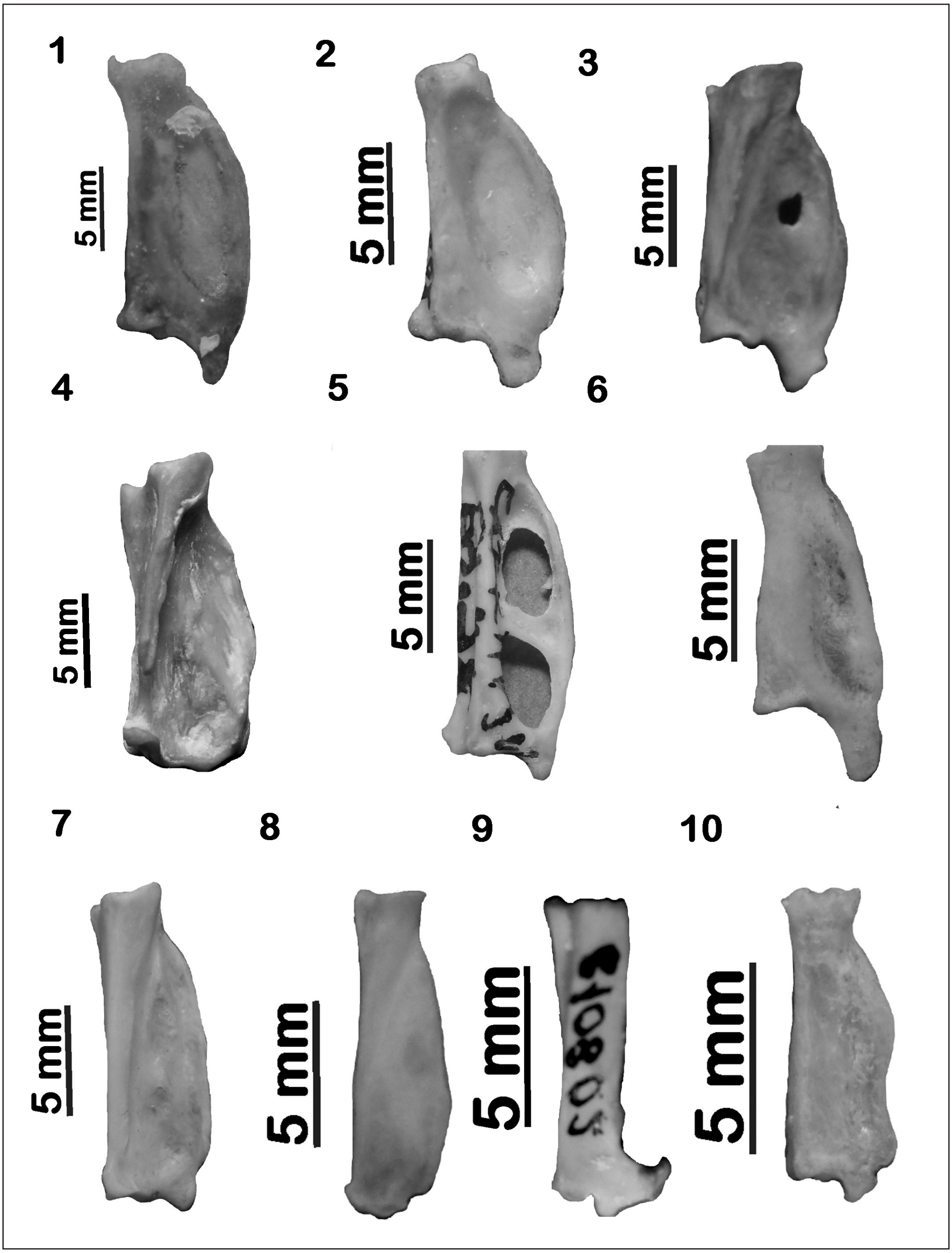

*Figure 12.* Left *phalanx proximalis digiti majoris* (ventral aspect) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*12. ábra* Bal oldali kézujjperc (I. ujjperc, 2. ujj, hasi nézet) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

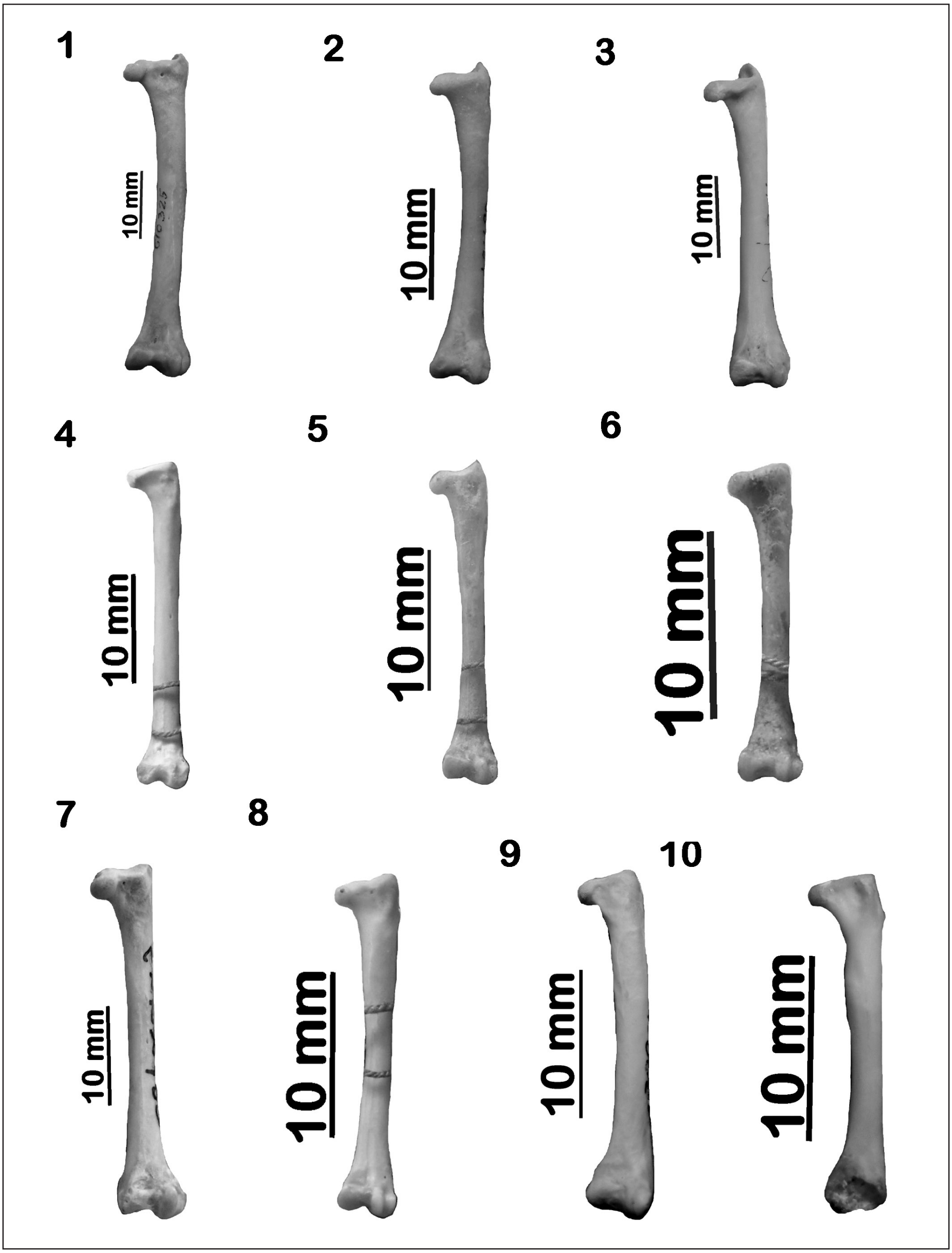

*Figure 13.* Right *femur* (caudal aspect) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*13. ábra* Jobb oldali combcsont (háti nézet) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

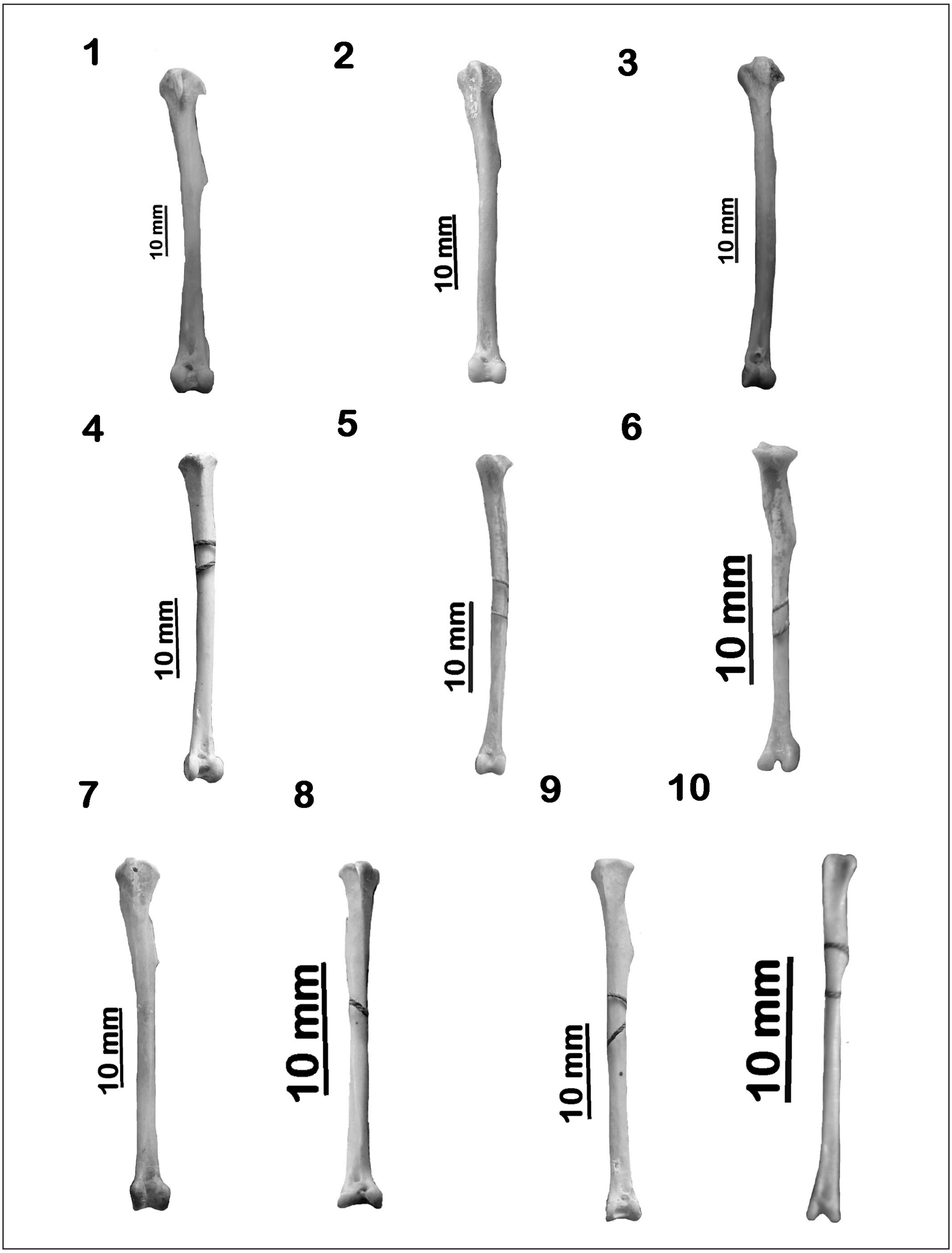

*Figure 14.* Left *tibiotarsus* (cranial aspect) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*14. ábra* Bal oldali lábszárcsont (hasi nézet) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

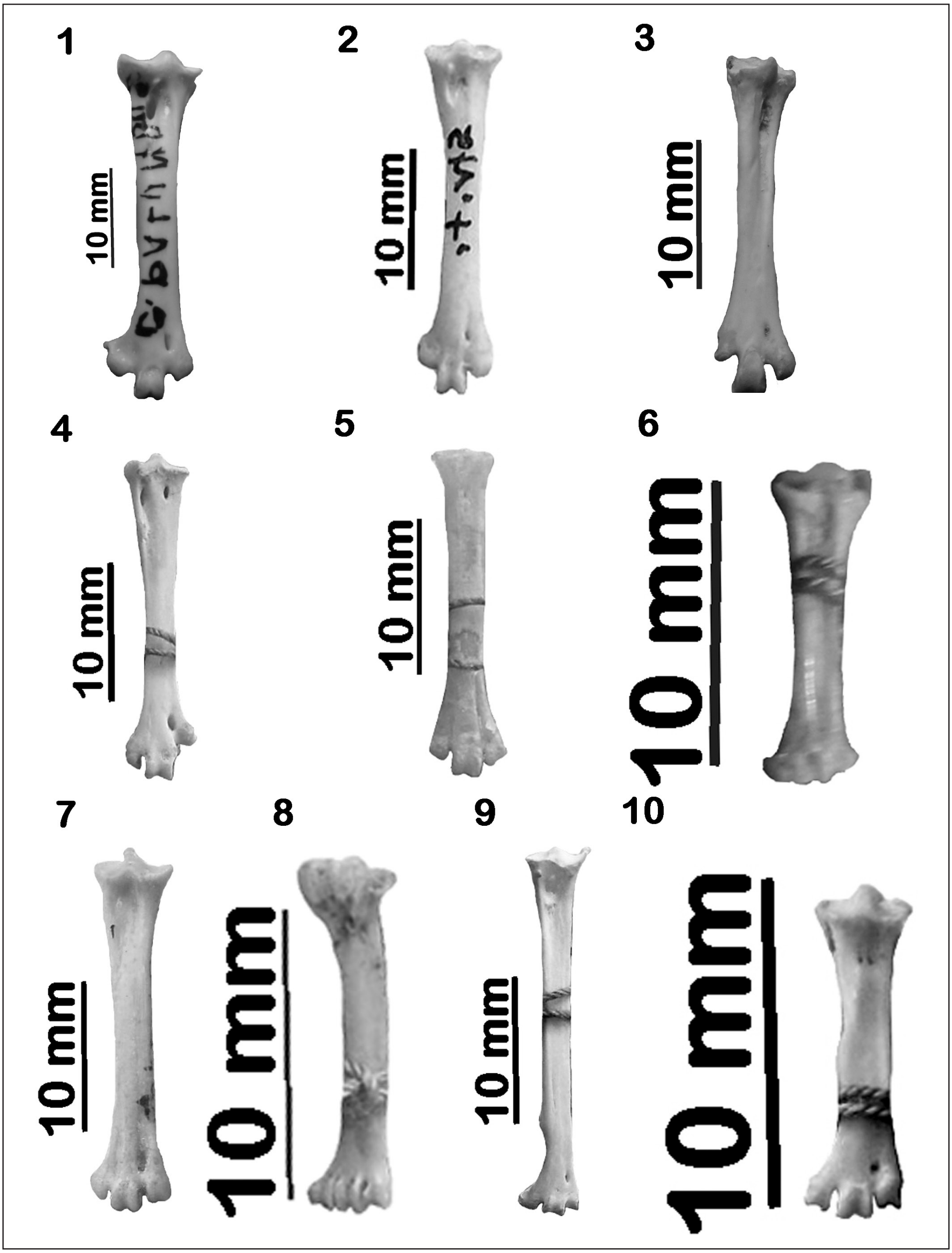

*Figure 15.* Left *tarsometatarsus* (dorsal aspect) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*15. ábra* Bal oldali csüd (háti nézet) – 1. *Columba palumbus;* 2. *Streptopelia turtur;* 3. *Syrrhaptes paradoxus;* 4. *Cuculus canorus;* 5. *Caprimulgus europaeus;* 6. *Apus apus;* 7. *Coracias garrulus;* 8. *Merops apiaster;* 9. *Upupa epops;* 10. *Alcedo atthis*

*Table 1.; 1. táblázat*

| **Bones** | ***Columba palumbus*** | ***Columba livia*** | ***Columba oenas*** | ***Streptopelia turtur*** | ***Streptopelia decaocto*** | ***Syrrhaptes paradoxus*** | ***Cuculus canorus*** | ***Caprimulgus europaeus*** | ***Apus apus*** | ***Coracias garrulus*** | ***Merops apiaster*** | ***Alcedo atthis*** | ***Upupa epops*** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mandibula | | | | | | | | | | | | | |
| A | 44.35 | | | 30.91 | | 28.00 | 41.30 | | | 57.00 | 45.00 | 49.51 | 65.50 |
| B | 9.12 | | | 3.53 | | 4.20 | 19.70 | | | 20.00 | 19.50 | 24.50 | 36.00 |
| Coracoid | | | | | | | | | | | | | |
| A | 43.50 | 36.14-37.30 | 32.86 | 26.00 | 29.50 | 29.47 | 25.30 | 19.60 | 14.30 | 29.90 | 20.90 | 21.30 | 21.80 |
| B | 40.00 | 34.58-35.70 | 30.79 | 25.20 | 28.30 | 26.30 | 23.90 | 18.20 | 13.10 | 27.10 | 19.20 | 21.00 | 21.00 |
| C | 5.00 | 4.07-6.09 | 4.69 | 3.60 | 4.60 | 3.60 | 4.00 | 3.90 | 3.40 | 4.30 | 3.20 | 1.90 | 4.00 |
| D | 6.20 | 6.01-7.60 | 6.14 | 5.00 | 6.90 | 5.25 | 6.50 | 4.60 | 3.80 | 6.10 | 4.50 | 2.40 | 4.50 |
| E | 4.80 | 3.81-4.10 | 3.18 | 2.70 | 3.00 | 3.75 | 1.40 | 2.00 | 1.90 | 2.90 | 1.20 | 1.60 | 1.30 |
| F | 17.00 | 13.65-15,40 | 13.56 | 10.70 | 12.00 | 12.36 | 8.20 | 6.90 | | 12.80 | 9.10 | 5.80 | 7.00 |
| G | 11.00 | 9.76-10,30 | 9.00 | 6.80 | 8.40 | 10.56 | 6.90 | 5.90 | 4.50 | 8.50 | 6.20 | 5.80 | 5.20 |
| Scapula | | | | | | | | | | | | | |
| A | 53.64 | 42.00-46.10 | 37.10 | 31.20 | 37.40 | 43.23 | 26.90 | 25.80 | 24.00 | 38.00 | 26.30 | 23.00 | 26.40 |
| B | 10.90 | 9.60-10.30 | 8.59 | 7.00 | 8.8 | 9.72 | 6.50 | 6.00 | 4.10 | 6.30 | 4.20 | 5.00 | 4.60 |
| C | 5.00 | 4.11-5.20 | 3.78 | 3.50 | 4.10 | 4.07 | 3.20 | 3.00 | 2.40 | 3.00 | 2.20 | 3.50 | 2.60 |
| D | 3.90 | 3.80 | 3.11 | | 3.20 | 3.07 | | | | | | | |
| E | 3.40 | 3.34 | 3.07 | 2.40 | 2.80 | 2.89 | 1.80 | 1.50 | 1.20 | 3.00 | 1.80 | 1.50 | 1.80 |
| Humerus | | | | | | | | | | | | | |
| A | 52.00-53.92 | 48.00 | 42.74 | 36.00 | 37.90 | 43.51 | 37.50 | 35.60 | 12.40 | 53.20 | 31.00 | 25.70 | 34.20 |
| B | 20.00 | 20.00 | 15.34 | 13.60 | 13.60 | 17.01 | 12.60 | 13.60 | 7.90 | 13.20 | 9.50 | 6.10 | 13.60 |
| C | 21.00 | 18.10 | 13.20 | 14.10 | 14.00 | 12.62 | 12.60 | 9.00 | 6.40 | 11.10 | 8.90 | 6.00 | 11.00 |
| E | 6.50 | 5.40 | 5.29 | 4.10 | 4.50 | 4.47 | 3.40 | 3.00 | 3.70 | 3.90 | 2.50 | 2.00 | 3.20 |
| F | 12.20 | 11.00 | 10.12 | 7.60 | 8.90 | 9.44 | 8.40 | 6.70 | 5.00 | 9.60 | 5.80 | 4.80 | 8.00 |
| G | | 4.70 | 6.46 | 3.40 | 3.90 | 6.07 | 3.10 | 2.40 | 2.40 | 3.50 | 2.30 | 2.00 | 2.90 |
| Ulna | | | | | | | | | | | | | |
| A | 61.27 | 54.40-56.10 | 48.67 | 42.70 | 45.00 | 47.52 | 39.00 | 47.50 | 19.30 | 64.30 | 38.70 | 32.00 | 45.90 |
| B | 8.70 | 6.88-7.80 | 6.52 | 6.00 | 6.50 | 6.57 | 4.90 | 3.20 | 3.50 | 6.10 | 4.20 | 3.40 | 5.00 |
| C | 8.00 | 6.84 | 6.37 | 8.00 | 8.30 | 6.13 | 6.20 | 5.00 | 3.70 | 7.30 | 5.10 | 3.40 | 6.00 |
| E | 4.50 | 4.00 | 3.60 | 2.80 | 3.10 | 3.96 | 2.00 | 2.10 | 2.40 | 3.20 | 1.90 | 1.90 | 2.20 |
| F | 8.00 | 7.01-7.80 | 6.41 | 5.80 | 6.00 | 6.84 | 5.20 | 5.00 | 4.10 | 6.20 | 3.80 | 3.00 | 4.50 |

*Table 2.; 2. táblázat*

| **Bones** | ***Columba palumbus*** | ***Columba livia*** | ***Columba oenas*** | ***Streptopelia turtur*** | ***Streptopelia decaocto*** | ***Syrrhaptes paradoxus*** | ***Cuculus canorus*** | ***Caprimulgus europaeus*** | ***Apus apus*** | ***Coracias garrulus*** | ***Merops apiaster*** | ***Alcedo atthis*** | ***Upupa epops*** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| G |  | 5.35-6.50 | 5.46 | 5.10 | 5.20 | 6.07 | 3.80 | 3.80 | 3.70 | 5.00 | 3.10 | 2.10 | 3.10 |
| Radius |  |  |  |  |  |  |  |  |  |  |  |  |  |
| A | 54.17 | 49.44-51.80 | 43.59 | 38.20 | 40.50 | 42.90 | 37.80 | 45.80 | 18.00 | 61.00 | 35.80 | 29.80 | 42.00 |
| C | 4.80 | 4.53-4.90 | 4.10 | 3.70 | 3.70 | 4.21 | 3.00 | 3.00 | 1.90 | 4.00 | 2.40 | 2.00 | 2.50 |
| E | 3.00 | 2.50-2.62 | 2.08 | 1.70 | 1.90 | 2.08 | 1.50 | 1.40 | 1.00 | 2.00 | 1.20 | 0.90 | ,1.20 |
| F | 5.70 | 5.18-5.50 | 4.29 | 4.00 | 4.00 | 4.80 | 3.90 | 3.20 | 2.40 | 4.60 | 2.90 | 4.50 | 2.30 |
| Carpometacarpus |  |  |  |  |  |  |  |  |  |  |  |  |  |
| A | 38.18 | 34.79-35.00 | 30.04 | 26.50 | 27.00 | 28.09 | 21.30 | 26.00 | 21.30 | 29.50 | 18.50 | 13.30 | 21.00 |
| B | 34.50 | 32.53-32.80 | 28.67 | 24.50 | 25.50 | 25.90 | 19.00 | 24.60 | 20.20 | 27.20 | 16.60 | 11.80 | 19.00 |
| C | 11.20 | 9.38-10.00 | 8.47 | 7.50 | 7.50 | 9.14 | 6.80 | 7.20 | 5.90 | 8.70 | 5.40 | 4.00 | 5.60 |
| E | 8.30 | 7.00 | 6.78 | 6.00 | 6.00 | 6.85 | 5.20 | 4.50 | 4.40 | 5.20 | 3.20 | 2.70 | 5.50 |
| E* | 3.40 | 2.79-3.70 | 2.41 | 2.80 | 3.10 | 2.50 | 3.00 | 2.40 | 2.30 | 3.00 | 1.80 | 1.30 | 2.00 |
| F | 7.00 | 6.03-6.20 | 5.77 | 5.00 | 5.40 | 5.46 | 5.00 | 5.00 | 4.00 | 5.40 | 4.10 | 2.70 | 5.50 |
| G |  | 3.93-4.40 | 3.78 | 3.50 | 3.20 | 3.96 | 3.30 | 3.30 | 3.00 | 3.50 | 2.10 | 1.60 | 2.20 |
| Phalanx alae |  |  |  |  |  |  |  |  |  |  |  |  |  |
| A | 20.00 | 21.00 |  | 15.10 | 14.30 | 17.00 | 23.30 | 14.00 | 13.20 | 15.00 | 11.00 | 6.90 | 9.80 |
| C | 3.50 | 4.00 |  | 4.50 | 3.00 | 5.00 | 4.40 | 3.00 | 3.00 | 4.00 | 2.70 | 1.70 | 2.20 |
| E | 7.00 | 7.20 |  | 5.00 | 6.30 | 7.00 | 5.00 | 4.70 | 5.00 | 5.00 | 3.00 | 2.20 | 1.70 |
| F | 8.70 | 7.00 |  | 6.00 | 6.20 | 6.00 | 4.50 | 4.40 | 5.00 | 4.00 | 2.20 | 1.80 | 3.40 |
| Femur |  |  |  |  |  |  |  |  |  |  |  |  |  |
| A | 45.54 | 40.91-43.00 | 35.68 | 29.00 | 32.70 | 39.39 | 28.30 | 22.40 | 16.80 | 31.20 | 19.20 | 21.00 | 24.40 |
| B | 43.20 | 38.42-40.80 | 33.90 | 27.00 | 31.20 | 36.24 | 27.50 | 21.20 | 16.40 | 30.10 | 18.50 | 19.60 | 23.00 |
| C | 9.20 | 8.64-8.90 | 7.59 | 5.40 | 5.40 | 8.28 | 4.80 | 4.00 | 3.50 | 6.00 | 3.60 | 3.00 | 4.80 |
| D |  | 5.90-6.00 | 5.96 |  | 4.80 | 7.34 | 3.70 | 3.10 | 2.40 | 4.80 | 2.70 |  | 3.70 |
| E | 4.10 | 4.00 | 3.14 | 2.30 | 2.80 | 3.44 | 2.10 | 1.40 | 1.40 | 2.40 | 1.50 | 1.70 | 2.20 |
| F | 8.80 | 7.53-8.00 | 6.55 | 5.50 | 5.80 | 7.04 | 4.80 | 3.80 | 3.60 | 5.70 | 3.40 | 3.00 | 4.40 |
| G |  | 6.70 | 5.35 |  | 4.70 | 6.10 | 4.00 | 3.20 | 2.80 | 5.00 | 2.70 |  | 3.80 |
| Tibiotarsus |  |  |  |  |  |  |  |  |  |  |  |  |  |
| A | 65.57 | 57.68-62.20 | 49.60 | 42.30 | 43.40 | 50.27 | 37.70 | 32.40 | 25.30 | 43.50 | 25.30 | 25.80 | 37.10 |
| C | 9.30 | 9.57-10.20 | 7.87 | 5.80 | 6.80 | 8.55 | 5.50 | 4.00 | 3.80 | 5.40 | 3.40 | 2.80 | 4.70 |
| D |  | 6.68-7.00 | 5.54 | 4.80 | 5.00 | 6.27 | 4.00 | 3.80 | 3.20 | 4.70 | 2.90 | 2.50 | 3.40 |

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# New species on the list of species with intraspecific nest parasitism

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**Abstract** Intraspecific nest parasitism has only recently received more attention from ornithologists. In 2001, Yom-Tov published a list of 234 species that had exhibited this behaviour. I have since found literature data on four additional species in which intraspecific nest parasitism has been observed. No such record has so far been published from Hungary. This study presents records on 25 species from Hungary and on one species from Croatia, out of which I have not found any reference for intraspecific nest parasitism in the literature for Cattle Egret *(Bubulcus ibis)*, Eurasian Thick-knee *(Burhinus oedicnemus)*, Black-winged Stilt *(Himantopus himantopus)*, Collared Pratincole *(Glareola pratincola)*, Mediterranean Gull *(Larus melanocephalus)*, Little Tern *(Sternula albifrons)*, Whiskered Tern *(Chlidonias hybrida)*, Eurasian Roller *(Coracias garrulus)* and Eurasian Jackdaw *(Corvus monedula)*. In addition to records from Hungary, for Black-headed Gull *(Larus ridibundus)* and Mediterranean Gull I also present observations from Slovakia, and for Common Shelduck *(Tadorna tadorna)* from Germany.

Keywords: intraspecific nest parasitism, new species on the list: Cattle Egrett *(Bubulcus ibis)*, Eurasian Thick-knee *(Burhinus oedicnemus)*, Black-winged Stilt *(Himantopus himantopus)*, Collared Pratincole *(Glareola pratincola)*, Mediterranean Gull *(Larus melanocephalus)*, Little Tern *(Sternula albifrons)*, Whiskered Tern *(Chlidonias hybrida)*, Eurasian Roller *(Coracias garrulus)*, Eurasian Jackdaw *(Corvus monedula)*

**Összefoglalás** A fajon belüli fészekparazitizmus – „összetojás” – (intraspecific nest parasitism) csak a legutóbbi időben keltette fel az ornitológusok figyelmét. Yom-Tov 2001-ben közreadott jegyzékében 234 fajt említ, melyeknél ezt a jelenséget észlelték. Azóta további négy fajnál is felfedezték az összetojást. Magyarországról eddig erre a jelenségre vonatkozóan nem közöltek adatokat. Jelen tanulmányban 25 fajról magyarországi és egy faj esetében horvátországi adatokat közlök, melyek közül a pásztorgém *(Bubulcus ibis)*, ugartyúk *(Burhinus oedicnemus)*, gólyatöcs *(Himantopus himantopus)*, székicsér *(Glareola pratincola)*, szerecsensirály *(Larus melanocephalus)*, kis csér *(Sternula albifrons)*, fattyúszerkő *(Chlidonias hybrida)*, szalakóta *(Coracias garrulus)* és a csóka *(Corvus monedula)* vonatkozásában a szakirodalomban nem találtam utalást arra, hogy ezeknél az összetojást már észlelték volna.

Kulcsszavak: fajon belüli fészekparazitizmus, 25 magyarországi faj, 9 új faj a világlistán

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It has very long been known that certain bird species, in particular some cuckoos, but also representatives of some other bird families, such as the Black-headed Duck *(Heteronetta atricapilla)* or varius whydah species (*Vidua* spp.) do not build a nest but instead lay their eggs in the nests of other species that incubate their eggs and raise their young (Johnsgard 1997, Soler 2017).

A much less explored phenomenon is known as intraspecific nest parasitism, when some females lay some or all of their eggs in the nests of conspecifics. In the majority of cases, this behaviour is difficult or impossible to prove. In species with uniformly coloured eggs, the coloration rarely provides a clue to distinguishing the eggs of two or more females. In species where the eggs typically bear markings, it is still not easier to unambiguously determine the origin of eggs, but the ground colour or the distribution of markings may give a clue in some cases. Unequivocal evidence to the simultaneous presence of eggs from the female occupying the nest and incubating the clutch and from a stranger female can only be obtained from genetic analysis of the chicks. However, this method is obviously not suitable for rapid field work.

This difficulty is certainly the reason why the first list published by Yom-Tov (1980) only mentions 53 species, in which it had been confirmed that two or more females laid eggs in the same nest and only the owner of the nest incubated on them.

The study of the breeding biology of birds has increasingly received more attention in the last 35–40 years. Thanks to this, the updated list of Yom-Tov (2001) twenty years later already contained 234 species. Since then, intraspecific nest parasitism has been observed in some further species: Pied Avocet *(Recurvirostra avosetta)* (Hötker 2000), Northern Flicker *(Colaptes auratus*) (Bower & Ingold 2004), Song Sparrow *(Melospiza melodia)* (Latif *et al.* 2006), Black-headed Gull *(Larus ridibundus)* (Duda & Chectnicki 2012) and Common Redshank *(Tringa totanus)*.

When should a clutch be considered intraspecifically parasited and how to confirm this?

Yom-Tov (1980) laid down the possible basis of evidence in the following eight points:

1. *Direct observation*

   In most cases, this is not possible, but it may sometimes occur. As new ways of individual marking are now available, there will be more opportunity to obtain evidence with this direct method.
2. *Biochemical examination of protein polymorphism of the eggs*
3. *Genetical evidence,* obtained similarly to the former category, by biochemical examination of the eggs or chicks, but in this case the results are compared with similar examination of the parents.
4. *Distinction based on the coloration and markings of the eggs*

   This method may only provide definite evidence to intraspecific nest parasitism in a few species. Such a case is known in e.g. Common Moorhen, which rarely, but regularly lays its eggs in Little Bittern nests (Haraszthy 2018).
5. *Irregular sequence of appearance of eggs*

   By systematically checking one or more clutches on a daily basis, it may occur that the number of eggs in a clutch grows by two or more within 24 hours. In such cases, it is almost certain that the eggs come from more than one female.

6. *Appearance of new eggs after completion of the clutch and start of incubation*
   After the start of incubation on the mean clutch size typical of the species, no more egg is laid in most species. If new egg(s) appear in the clutch some days after the start of incubation, they are certainly from strange females.
7. *Prolonged hatching or two groups of hatchlings*
   A significant part of bird species start incubation only on the complete or near-complete clutch. If the number of eggs increases under a female that has been incubating for days, the new eggs are in all likelihood from strange female(s). Similarly, if hatching occurs in two groups among the chicks, that is an evidence to nest parasitism. The first group of hatchlings belong to the owner of the nest, while several days later and probably not on the same day, but prolonged in the order of egg laying the eggs of the strange female hatch.
8. *Significantly larger clutches than the average*
   The number of eggs in a clutch may be significantly higher than the mean clutch size typical of the species, even twice as large or more. In my opinion, however, large clutches have to be considered with caution, as it may happen that in the same nest or nestbox the parents do not remove the eggs of their failed first clutch and lay the second clutch next to the first. The addled eggs of the first brood may still remain in the nest even after the nestlings of the second brood fledge. I have observed such a case in e.g. Barn Swallow *(Hirundo rustica)* (see photo).

It may also happen that the female dies during or after laying the first clutch, and the male occupies the same nest with his new mate, which lays her eggs next to the ones that remained in the nesthole.

Another situation may be that after fighting for a suitable nestsite, the pair occupies a nesthole where conspecifics have already started to lay eggs or have even completed the clutch. The new pair lay their own eggs in the occupied nesthole or perhaps nest, next to the eggs already lying there, and incubation begins on this oversized clutch. If the new female starts egg laying soon after occupying the nesthole, it may even happen that both clutches hatch, asynchronously, and the new parents raise all of them.

Despite the large number of eggs unambiguously originating from two females, the above cases cannot be considered as intraspecific nest parasitism. However, in those cases where the growth of clutch size is continuous, the additional eggs are certainly the result of intraspecific nest parasitism.

## Among which species is intraspecific nest parasitism more frequent?

13% of all known bird species can be considered as colonial breeders (del Hoyo *et al.* 1992), but out of the 234 species listed by Yom-Tov (2001) 134 (57.3%) breed in colonies.

The proportion of nidifugous species is also high. The reason for this is that clutch size is usually higher among them than in similarly sized nidicolous species (Ar & Yom-Tov 1978). In their case, an unexpected increase in the number of eggs does not necessarily instigate abandonment of the clutch. The latter is a common response to an extra large clutch size, which I have observed in Common Shelduck *(Tadorna tadorna)* in Germany, as well as in Greylag Goose *(Anser anser)* and Red-crested Pochard *(Netta rufina)* in Hungary.

Nidifugous species start incubation after laying the last egg or the one before the last, as it is of utmost importance for them that hatching is synchronous. However, the parents do not protect the eggs before the clutch is complete, so strange female(s) can lay their own eggs among them uninterrupted.

The raising of nidifugous chicks requires significantly less parental effort that does not necessarily increase with the number of chicks, and this augments the success of parasitising females (Sorenson 1992).

## Evaluation of species breeding in Hungary

Among the 234 species listed by Yom-Tov in 2001, 41 are regular, occasional or former (extinct) breeders in Hungary. Based on publications since, I have added Pied Avocet *(Recurvirostra avosetta)* (Hötker 2010) and Black-headed Gull *(Larus ridibundus)* (Duda & Chectnicki 2012) to Yom-Tov's list.

**Pheasants (Phasianidae):** Eurasian Quail *(Coturnix coturnix)*, Common Pheasant *(Phasianus colchicus)*, Grey Partridge *(Perdix perdix)*, Black Grouse *(Tetrao tetrix)*

**Ducks (Anatidae):** Greylag Goose *(Anser anser)*, Common Goldeneye *(Bucephala clangula),* Smew *(Mergellus albellus)*, Goosander *(M. merganser)*, Common Shelduck *(Tadorna tadorna)*, Red-crested Pochard *(Netta rufina)*, Common Pochard *(Aythya ferina)*, Ferruginous Duck *(A. nyroca)*, Tufted Duck *(A. fuligula)*, Garganey *(A. querquedula)*, Gadwall *(A. penelope)*, Mallard *(Anas platyrhynchos)*

**Pigeons (Columbidae):** Wood Pigeon *(Columba palumbus)*, Turtle Dove *(Streptopelia turtur)*

**Grebes (Podicipedidae):** Red-necked Grebe *(Podiceps grisegena)*, Black-necked Grebe *(P. nigricollis)*, Great-Crested Grebe *(P. cristatus)*

**Rails (Rallidae):** Corn Crake *(Crex crex)*, Common Coot *(Fulica atra)*, Common Moorhen *(Gallinula chloropus)*

**Herons (Ardeidae):** Squacco Heron *(Ardeola ralloides)*, Purple Heron *(Ardea purpurea)*

**Avocets (Recurvirostridae):** Pied Avocet *(Recurvirostra avosetta)* (Hötker 2010)

**Plovers (Charadriidae):** Northern Lapwing *(Vanellus vanellus)*

**Snipes (Scolopacidae):** Black-tailed Godwit *(Limosa limosa)*, Eurasian Woodcock *(Scolopax rusticola)*

**Gulls (Laridae):** Black-headed Gull *(Larus ridibundus)* (Duda & Chectnicki 2012), Common Tern *(Sterna hirundo)*

**Falcons (Falconidae):** Lesser Kestrel *(Falco naumanni)*

**Crows (Corvidae):** Eurasian Magpie *(Pica pica)*

**Tits (Paridae):** Willow Tit *(Poecile montanus)*, Great Tit *(Parus major)*

**Swallows and Martins (Hirundinidae):** Barn Swallow *(Hirundo rustica)*, Collared Sand Martin *(Riparia riparia)*

**Starlings (Sturnidae):** Common Starling *(Sturnus vulgaris)*
**Thrushes (Turdidae):** Fieldfare *(Turdus pilaris)*
**Old World Flycatchers (Muscicapidae):** European Pied Flycatcher *(Ficedula hypoleuca)*
**Sparrows (Passeridae):** House Sparrow *(Passer domesticus)*, Tree Sparrow *(P. montanus)*

## Presentation of cases in Hungary

For several decades, I have been studying the breeding biology of bird species breeding in Hungary, and since 2001 I have made a point of searching for, checking and documenting nests on photos. I checked 8,500 nests between 1970 and 2018, and found 64 among them where I considered intraspecific nest parasitism confirmed. Except for one case, I concluded on intraspecific nest parasitism on the basis of a much larger clutch size than that typical of the species, but in some cases, egg markings also indicated this phenomenon.

During this period, I or my colleagues observed intraspecific nest parasitism, or in some other cases they provided photographic evidence to this phenomenon, in the following species.

### Common Pheasant

On 19 April 1981, I found a Common Pheasant nest with 19 eggs in a Black Locust plantation near the Merzse marsh in the outskirts of Budapest. The clearly visible difference in shade of the uniformly coloured eggs and their large number point to their origin from at least two females *(Photo 1)*.

### Greylag Goose

On 25 March 2011, I checked several nests in the Csákvári marsh. One of the nests contained 11 eggs that lay in the unlined nestcup built of reedmace fragments. The external measurements of this nest were 70×90 cm, with a 30 cm diameter nestcup. The external diameter of the nearby six-egg nest was 60 cm, with a 20 cm wide cup, while the external parameters of a third, four-egg nest were 50×60 cm, with a 25 cm diameter nestcup. The eggs were warm in the biggest clutch *(Photo 2)*. On 25 April 2013, there were 9 eggs in an abandoned nest found in the reed belt of the Apaji fishponds *(Photo 3)*. On 8 May 2013, I photographed an abandoned Greylag Goose nest with 14 eggs at the Apaji fishponds. One of the eggs had already broken. *(Photo 4)*. On 7 May 2018, I found a deserted nest with 10 eggs on a small island of the Kis-Balaton marsh, under the trees of a Great Cormorant colony *(Photo 5)*.

In my experience, in those Greylag Goose breeding sites where large water surfaces are only diversified by narrow reed fringes or small reed islands, intraspecific nest parasitism occurs regularly.

### Common Shelduck

In a nest checked on 15 May 2016 near Dunatetétlen, there were 13 eggs. According to Hori (1969), clutches over 12 eggs come from two or more females. If this is true for all clutches, then the 13-egg clutch had to contain egg(s) from a strange female *(Photo 6)*. On 29 May 2016, Bernd Heinze and I visited the Gollwitz area of Insel Poel in northern Germany, where Common Shelducks breed in plastic barrels buried in the ground. Out of six nests examined, four contained eggs from two or more females. These latter nests contained 15, 16, 19 and 31 eggs, respectively. The 31-egg nest had been abandoned, but the female was incubating the clutch of 19 eggs *(Photo 7–10)*.

### Red-crested Pochard

On 6 May 2011, I checked the nests on the islands of the Rétszilasi fishponds. Only one island was suitable for the breeding of Red-crested Pochards, but it was entirely occupied by gulls, and there was hardly any vegetation on it to provide cover for the nests. As I approached the island, only Red-crested Pochards swam away from there. Below the little vegetation, it was literally strewn with duck eggs. They were scattered all over, many singly, some in small groups, loosely together or clustered more like in a nest. I found two clutches in good order, one with 25 eggs, the other with 18. The situation was similar on my 16 May 2017 visit, too. There were eggs scattered all around, stained with faeces. I found two clutches of the species, containing 17 and 29 eggs respectively *(Photo 11–13)*.

### Ferruginous Duck

On 9 June 2011, I found Mallard and Ferruginous Duck nests in several patches of emergent vegetation in a wetland flooded for nature conservation purposes near Somogyfajsz. One of the Ferruginous Duck nests contained 26 eggs, incubated by the female. Thus, in this case, this small duck did not abandon the extremely oversized clutch *(Photo 14)*.

### Tufted Duck

On 12 June 2004, I checked six Tufted Duck nests on a small island of the Soponyai fishponds with László Csihar and István Staudinger, and the number of eggs in the nests were 7, 8, 8, 8, 9 and in one nest, 16. The only safe nesting site out of reach of foxes was this small island, hardly larger than a room *(Photo 15)*.

### Mallard

On 16 May 2011, I checked the duck nests on some smaller islands of the Rétszilasi fishponds. I found four Mallard nests hidden among nettle, containing 12, 13, 15 and in the fourth nest, 19 eggs. Among the latter, three eggs had a distinctly different shade from the rest, visible on the photo, but presumably not only these three came from a strange Mallard *(Photo 16)*.

**Black-necked Grebe**

On 27 June 2006, Levente Viszló and myself discovered a colony that was just being formed on the Zámolyi reservoir, and at that time consisted of only four nests. The number of nests reached 26 on 4 July, and new nests continued to be found until 20 July. During our investigation, we identified three cases of intraspecific nest parasitism. The first nest contained 2 eggs on 4 July, but already 7 eggs on 7 July (this clutch was later abandoned by the birds), in other words the number of eggs increased from 2 to 7 in three days, i.e. more than one egg appeared per day. Another nest was still empty on 4 July, but contained 6 eggs three days later, out of which one disappeared by 11 July (the remaining eggs were not incubated by the birds, and were still in the nest on 3 August, concealed with nesting material). In this case, too, the number of eggs grew by more than one per day. The third nest contained 4 eggs on 4 July and 7 eggs on 7 July. In this last case intraspecific nest parasitism is likely because of the 7 eggs, since according to Prinzinger (1979), clutches of 7 or more eggs come from two or more females *(Photo 17–18)*.

**Common Moorhen**

On 8 May 1977, László Vilmos Szabó found a clutch of 21 eggs in a nest built on a young ash (*Fraxinus* sp.) in the flooded Vajdalaposi forest (Hortobágy). In all likelihood, the clutch had been laid by two or possibly three females *(Photo 19, Szabó L. V.)*.

**Cattle Egret**

On 17 May 2018, I checked the Cattle Egret nests in a woodland heronry at Soponya, in the immadiate vicinity of, and partly on the same tree as the nests of Little Egret *(Egretta garzetta)*, Black-crowned Night-heron *(Nycticorax nycticorax)* and Squacco Heron *(Ardeola ralloides)*. In one of the nests, where we had previously seen the incubating Cattle Egret, I found 9 eggs *(Photo 20)*.

**Purple Heron**

On 16 May 2013, I checked 21 nests of the Purple Heron colony in the reedbeds of Böddi-szék marsh, where clutch sizes were the following: 1×2, 1×3, 3×4, 11×5, 3×6 and in one nest 2 chicks +3 eggs. In addition, I found a nest that contained eight eggs *(Photo 21)*.

**Eurasian Thick-knee**

On 18 May 2007, Attila Szilágyi found four eggs in a nest in an *Artemisio-Festucetum* sward, at Angyal-háza steppe, Hajdúszoboszló. Within the clutch, two couples of eggs can easily be set apart on pattern, indicating their origin from two females *(Photo 22, Szilágyi A.)*.

### Pied Avocet

On 7 June 2007, we checked the breeding colony on a flat island created by the low water level of the Dinnyési Fertő marsh with László Fenyvesi and Antal Széll. In addition to Pied Avocets *(Recurvirostra avosetta)*, Black-winged Stilts *(Himantopus himantopus)*, Common Redshank *(Tringa totanus)*, Little Ringed Plover *(Charadrius dubius)* and Common Tern *(Sterna hirundo)* formed the colony. The Avocet nests contained 2×2, 5×3, 8×4 as well as 1×5, 1×6 and 1×7 eggs, while three of the nests also had 1 or 2 chicks next to the eggs. In two other nests, we found 1 and 4 chicks. The clutches of 5, 6 and 7 eggs were undoubtedly from two females each. We also found two clutches where some further eggs lay next to the clutch but in a separate group. These can be regarded as nest parasitic attempts, in which the strange female did not lay the eggs in the chosen nest, but immediately next to it, hoping that the incubating bird will roll them below itself *(Photo 23–26).*

### Black-winged Stilt

On 7 June 2007, we found five Black-winged Stilt nests at the Dinnyési Fertő marsh with four eggs in each, except for one that had eight eggs in it *(Photo 27)*. On 5 June 2008, László Fenyvesi and I checked the breeding island in the Dinnyési Fertő marsh. Breeding species included Black-winged Stilt, Little Ringed Plover, Pied Avocet, Common Redshank, Black-headed Gull and Common Tern. A total of 48 Black-winged Stilt nests were checked, with the following clutch sizes: 3×1, 7×2, 11×3, 16×4, 6×5, 2×6, 1×7, 2×8. Five-egg (6), 6-egg (2) and 7 as well as 8-egg (2) clutches were the result of intraspecific nest parasitism *(Photo 28–34)*.

### Collared Pratincole

Ádám Kis found a six-egg clutch in the Nagy meadow at Kisújszállás on 14 June 2017, which was certainly laid by two females *(Photo 35, Széll A)*.

### Black-headed Gull

On 5 June 2008, we checked 231 nests with eggs in a Black-headed Gull colony at Dinnyés with László Fenyvesi. Clutch sizes were as follows: 31×1, 88×2, 115×3 and 1×4. The eggs in the biggest clutch could clearly be divided into two pattern types of two eggs each, which certainly came from two females *(Photo 36)*. On 30 April 2017, we counted the nests in a gull colony with Slovak and Hungarian colleagues on an island of the river Danube forming the border between Hungary and Slovakia. 4,200 pairs of Black-headed and 230 pairs of Mediterranean Gulls bred in the colony. I checked 691 Black-headed Gull nests, most of which contained three eggs, while some only had two eggs. However, in two nests the clutch was larger, with five eggs in one, and four eggs in the other. These latter clutches were almost certainly from two females each, based on the number of eggs and the pattern differences within the clutches, which means they were the result of intraspecific nest parasitism *(Photo 37–38)*.

### Mediterranean Gull

On 4 June 1978, while ringing nestlings in a Black-headed Gull colony in the Kelemen-szék sodic lake at Fülöpszállás, I also found a Mediterranean Gull nest with five eggs, which were undoubtedly from two females. This was not the first case when intraspecific nest parasitism was found in Mediterranean Gull in Hungary. In early May 1955, Beretzk (1957) found a 3+1 clutch at Lake Fehér near Szeged, and concluded that the eggs originated from two females. Without providing sample size, Széll and Bakacsi (1996) estimated that 10–20% of Mediterranean Gull clutches contain two eggs, while the majority have three eggs, and less than 5% consist of four eggs. In the latter group, they observed that one egg always differed in pattern from the remaining three, which indicates the clutch had been laid by two females *(Photo 39).*

On 30 April 2017, I found four eggs in a Mediterranean Gull nest on an island of the river Danube forming the border between Hungary and Slovakia. One egg had a distinctly different pattern from the rest and certainly originated from a strange female *(Photo 40).*

### Little Tern (Croatia)

On 20 June 2018, Robert Crnković and I were searching for Little Tern nests at a salt pond in Central Dalmatia (Croatia). We found seven in total, containing 3×3 and 3×2 eggs, while one already abandoned nest had four eggs, which in all likelihood came from two females. The pair that had built the nest probably abandoned it because they did not adopt the strange eggs *(Photo 41).*

### Whiskered Tern

Between 1974 and 2018, I checked more than 300 Whiskered Tern nests with eggs. In 7 of these nests, I found 4 eggs, while the rest contained 1-3 eggs. In Whiskered Tern, four-egg clutches are without any doubt laid by two females. This does not mean that each egg in all three-egg clutches is laid by the female that owns the nest and incubates the eggs. In addition, once I even found a six-egg clutch. On 8 July 2006, Levente Viszló and I checked a Black-necked Grebe colony of 39 nests on the Zámolyi reservoir. Next to the colony, there were 6 Whiskered Tern nests, too. In one of the nests, we found four eggs. *(Photo 42)*. On 3 July 2008, I also found a few nests near Földes, one of which contained 4 eggs. *(Photo 43)*. On 16 May 2013 near Dunatetétlen, in a Whiskered Tern colony established next to a Black-necked Grebe colony (39 nests) also contained a clutch of four eggs *(Photo 44)*. On 18 May 2015, József Berdó, Zoltán Oroszi and myself found a newly formed, mixed colony of Black-necked Grebes, Black-headed Gulls and Whiskered Terns on the same site. Most of the grebe and tern nests were still empty. Five tern nests, however, already had eggs, and two of them contained four eggs each as a result of two females laying in the same nest. The 28 Black-headed Gull nests already had full clutches *(Photo 45–46)*. On 10 June 2016, I searched through a part of the Black-necked Grebe and Whiskered Tern colony on the same spot. The Whiskered Tern nests contained 3×2, 20×3 and 1×4 eggs *(Photo 47).* On 1 July

2016, Gábor Szalai and I checked the Great Crested Grebe *(Podiceps cristatus)* colony established on the Zámolyi reservoir. Approaching the colony was only possible by passing along the scattered, 100-strong Whiskered Tern colony. We checked 31 nests, three of which already had nestlings, while 7 nests had two, 18 nests three, 2 nests four and 1 nest six eggs. In this clutch, which was without any doubt the result of intraspecific nest parasitism, the eggs were already cold, the parents had abandoned the nest *(Photo 48–49)*.

### Eurasian Roller

On 4 July 2014, Tamás Kiss found 8 nestlings during the regular checkup of a nestbox in the vicinity of Kisszállás. Between 2010 and 2014, the breeding of 40 pairs of Eurasian Roller was observed, and in the „better" years of this period, more than 4 nestlings fledged per nest, and one or two pairs even had six nestlings. He observed several times that a helper adult contributed to feeding the nestlings *(Photo 50, Kiss T.)*.

### Common Kestrel

The clutch size in Common Kestrel is normally 5-7 eggs, clutches above this size are certain to contain egg(s) from a strange female. Based on their pattern, the 9-egg clutch I checked had six eggs from one female and three from another. This clutch was in a nestbox near Tiszaeszlár, the photograph was taken on 20 May 2007. *(Photo 51)*.

### Eurasian Jackdaw

Jackdaws regularly occupy nestboxes erected for Common Kestrel or other species, or sometimes specifically for Jackdaws. These pairs form a smaller or larger colony. In such situations, I found clutches from intraspecific nest parasitism on two occasions. On 26 April 2016 at Földes, there were 12 eggs in a nestbox erected on the stable of a farmstead. On the photo, it is clearly visible from the egg pattern that one female laid 7, while the other laid 5 eggs into the same nestbox *(Photo 52)*. On 18 April 2017 at Apajpuszta, three pairs of Jackdaws occupied the nestboxes erected for Rollers on some Black Locust trees. One of the boxes contained 5+5 eggs that were clearly from two females, while I found 4 and 5 eggs in the other two boxes *(Photo 53)*.

### Great Tit

On 22 April 2007, I found a 17-egg clutch in a nestbox at Pilisszentiván. This very high number of eggs indicates intraspecific nest parasitism *(Photo 54)*.

### Barn Swallow

In itself, the large clutch size is not always proof that the eggs were laid by two females. The first clutch of a pair of Barn Swallows in the only occasionally used bathroom of our weekend cottage consisted of four eggs, but they were sterile. The adults did not push out the eggs from the nest, but laid their new clutch next to them and successfully fledged all five juveniles. It cannot be excluded that the female was replaced by another, but this is not underpinned by the rather similarly patterned eggs of the two clutches *(Photo 55)*.

### Common Starling

On 1 May 2018, Gábor Szalai found a clutch of 9 eggs in a nestbox near Vértesboglár. The mean number of nestlings in 173 nests checked between 2009–2015 in the area was 4.4. Eight of these nests had seven nestlings each, which must have been the result of two females laying in each nest, since according to Yom-Tov *et al.* (1974), clutches above six eggs are the result of intraspecific nest parasitism *(Photo 56)*.

### Tree Sparrow

On 8 June 2018, Gábor Szalai found a Tree Sparrow clutch of 10 eggs in a nestbox at Fornapuszta, near Csákvár. It can be clearly seen that they came from two females *(Photo 57)*.

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*Photo 1.* Common Pheasant; *1. fotó* közönséges fácán

*Photo 2.* Greylag Goose; *2. fotó* nyári lúd

*Photo 3.* Greylag Goose; *3. fotó* nyári lúd

*Photo 4.* Greylag Goose; *4. fotó* nyári lúd

*Photo 5.* Greylag Goose; *5. fotó* nyári lúd

*Photo 6.* Common Shelduck; *6. fotó* bütykös ásólúd

*Photo 7*. Common Shelduck; *7. fotó* bütykös ásólúd

*Photo 8*. Common Shelduck; *8. fotó* bütykös ásólúd

*Photo 9.* Common Shelduck; *9. fotó* bütykös ásólúd

*Photo 10.* Common Shelduck; *10. fotó* bütykös ásólúd

*Photo 11*. Red-crested Pochard; *11. fotó* üstökösréce

*Photo 12*. Red-crested Pochard; *12. fotó* üstökösréce

*Photo 13.* Red-crested Pochard; *13. fotó* üstökösréce

*Photo 14.* Ferruginous Duck; *14. fotó* cigányréce

*Photo 15.* Tufted Duck; *15. fotó* kontyos réce

*Photo 16.* Mallard; *16. fotó* tőkés réce

*Photo 17*. Black-necked Grebe; *17. fotó* feketenyakú vöcsök

*Photo 18*. Black-necked Grebe; *18. fotó* feketenyakú vöcsök

*Photo 19.* Common Moorhen; *19. fotó* vízityúk

*Photo 20.* Cattle Egret; *20. fotó* pásztorgém

*Photo 21.* Purple Heron; *21. fotó* vörös gém

*Photo 22.* Eurasian Thick-knee; *22. fotó* ugartyúk

*Photo 23.* Pied Avocet; *23. fotó* gulipán

*Photo 24.* Pied Avocet; *24. fotó* gulipán

*Photo 25.* Pied Avocet; *25. fotó* gulipán

*Photo 26.* Pied Avocet; *26. fotó* gulipán

*Photo 27*. Black-winged Stilt; *27. fotó* gólyatöcs

*Photo 28*. Black-winged Stilt; *28. fotó* gólyatöcs

*Photo 29*. Black-winged Stilt; *29. fotó* gólyatöcs

*Photo 30*. Black-winged Stilt; *30. fotó* gólyatöcs

*Photo 31*. Black-winged Stilt; *31. fotó* gólyatöcs

*Photo 32*. Black-winged Stilt; *32. fotó* gólyatöcs

*Photo 33.* Black-winged Stilt; *33. fotó* gólyatöcs

*Photo 34.* Black-winged Stilt; *34. fotó* gólyatöcs

*Photo 35.* Collared Pratincole; *35. fotó* székicsér

*Photo 36.* Black-headed Gull; *36. fotó* dankasirály

*Photo 37*. Black-headed Gull; *37. fotó* dankasirály

*Photo 38*. Black-headed Gull; *38. fotó* dankasirály

*Photo 39.* Mediterranean Gull; *39. fotó* szerecsensirály

*Photo 40.* Mediterranean Gull; *40. fotó* szerecsensirály

*Photo 41*. Little Tern; *41. fotó* kis csér

*Photo 42*. Whiskered Tern; *42. fotó* fattyúszerkő

*Photo 43.* Whiskered Tern; *43. fotó* fattyúszerkő

*Photo 44.* Whiskered Tern; *44. fotó* fattyúszerkő

*Photo 45.* Whiskered Tern; *45. fotó* fattyúszerkő

*Photo 46.* Whiskered Tern; *46. fotó* fattyúszerkő

*Photo 47*. Whiskered Tern; *47. fotó* fattyúszerkő

*Photo 48*. Whiskered Tern; *48. fotó* fattyúszerkő

*Photo 49*. Whiskered Tern; *49. fotó* fattyúszerkő

*Photo 50*. Eurasian Roller; *50. fotó* szalakóta

*Photo 51.* Common Kestrel; *51. fotó* vörös vércse

*Photo 52.* Eurasian Jackdaw; *52. fotó* csóka

*Photo 53.* Eurasian Jackdaw; *53. fotó* csóka

*Photo 54.* Great Tit; *54. fotó* széncinege

*Photo 55.* Barn Swallow; *55. fotó* füsti fecske

*Photo 56.* Common Starling; *56. fotó* seregély

*Photo 57*. Tree Sparrow; *57. fotó* mezei veréb

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# The effect of urbanization on population densities of forest passerine species in a Central European city

Grzegorz Kopij

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**Abstract** Typical, but less common, passerine forest species were selected for this study, such as *Lullula arborea*, *Anthus trivialis*, *Troglodytes troglodytes*, *Prunella modularis*, *Turdus philomelos*, *Turdus viscivorus*, *Phylloscopus sibilatrix*, *Regulus regulus*, *Regulus ignicapillus*, *Muscicapa striata*, *Ficedula albicollis*, *Ficedula hypoleuca*, *Parus cristatus*, *Parus palustris*, *Parus ater*, *Certhia familiaris*, *Certhia brachydactyla*, *Oriolus oriolus*, *Garrulus glandarius*, and *Corvus corax*. *M. striata* and *T. philomelos* were the most numerous among the 20 investigated species, the former one nested in a density of 6.7 pairs per 100 ha of wooded area, while the later one at 5.1 pairs per 100 ha. Density of most other species was below 3 pairs per 100 ha of wooded area. *A. trivialis, P. cristatus* and *P. modularis* were unexpectedly rare (< 1 pair per 100 ha). Otherwise, relatively numerous were *T. troglodytes* (1.8 p./100 ha), *R. regulus* (1.8 p./100 ha) and *P. palustris* (1.4 p./100 ha). *P. cristatus, L. arborea,* and *T. viscivorus* were the rarest species investigated (below 0.1 p./100 ha). Several bird species nested in wooded areas only in the outer zone of the city. This group included *A. trivialis, R. regulus, P. ater,* and *C. corax.* Population density of *T. troglodytes, T. philomelos* and *O. oriolus* were significantly higher in outer than in inner zone, while the reverse was true in the case of *M. striata* and *F. hypoleuca*.

Keywords: urban ornithology, urban ecology, urban forestry, population densities, Wroclaw

**Összefoglalás** A tanulmányhoz jellemző, de kevésbé gyakori erdei énekesmadár fajokat választottunk ki: *Lullula arborea*, *Anthus trivialis*, *Troglodytes troglodytes*, *Prunella modularis*, *Turdus philomelos*, *Turdus viscivorus*, *Phylloscopus sibilatrix*, *Regulus regulus*, *Regulus ignicapillus*, *Muscicapa striata*, *Ficedula albicollis*, *Ficedula hypoleuca*, *Parus cristatus*, *Parus palustris*, *Parus ater*, *Certhia familiaris*, *Certhia brachydactyla*, *Oriolus oriolus*, *Garrulus glandarius* és *Corvus corax*. A *M. striata* és a *T. philomelos* fajok voltak jelen legnagyobb számban a felsorolt 20 faj közül: előbbi 6,7 pár/100 ha, míg utóbbi 5,1 pár/100 ha denzitással képviseltette magát. A legtöbb faj sűrűsége a 3 pár/100 ha érték alatt maradt. Az *A. trivialis, P. cristatus* és a *P. modularis* meglepően alacsony denzitással volt jelen (< 1 pár/100 ha), a *T. troglodytes* (1,8 pár/100 ha), a *R. regulus* (1,8 pár/100 ha) és a *P. palustris* (1,4 pár/100 ha) viszonylag nagy számban fordult elő. A legritkább fajok a *P. cristatus, L. arborea* és a *T. viscivorus* voltak (kevesebb, mint 0,1 pár/100 ha). Néhány madárfaj kizárólag a városok körüli erdős területeken fészkelt. Ebbe a csoportba tartozik például az *A. trivialis, R. regulus, P. ater* és a *C. corax*. A *T. troglodytes, T. philomelos* és az *O. oriolus* populáció denzitása jelentősen nagyobb volt a városon kívüli, mint a városon belüli területeken, míg ennek fordítottja igaz például a *M. striata* és a *F. hypoleuca* esetében.

Kulcsszavak: urbanizáció, erdőborítottság, populáció denzitás, énekesmadarak, Wroclaw

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## Introduction

The loss of natural areas for cities' development is regarded as ones of the main factors contributing to the decline of many wildlife species. This decline is further accelerated by environmental pollution, high level of human disturbance and predation by cats and dogs in a city environment. A city may, however, also create conducive environment for some species, as for example an abundance of food resources (processed food such as bread, milk products, meat, fruits, etc.), new nesting sites in man-mad structures (crevices and holes in buildings, artificial nest boxes, pipes, poles, etc.), specific microclimate with usually milder winters and springs, and lack of natural predators (Kalcey & Rheinwald 2005, Sanesi *et al.* 2009). We can expect that some species may, therefore, benefit from city development and increase in number, but some other may not cope with the rapid environmental changes, may decrease in numbers and finally withdraw entirely from the city.

Among animals, birds appear to be sensitive to some of those changes, especially species which are strictly associated with forest as breeding and feeding habitats. This is because, forests become fragmented as a result of city expansion; older trees are often removed (lack of nesting sites for hole-nesting species), plant diversity is reduced and undergrowth (feeding place for some bird species) often impoverished (Kalcey & Rheinwald 2005, Witt *et al.* 2005). There is also a high level of human disturbance in such habitats (sport, recreation, noise, management). We may, therefore, expect that typical forest species (those which do not breed in habitats other than forests) are negatively affected by urban development, and often disappear from cities, especially from their inner parts. In this study, I test the effect of the urbanization on selected forest species in one of the biggest Central European city.

## Study area

The city of Wrocław (SW Poland), within its administrative boundaries, has a surface area of 293 km$^2$, and the human population of 632 996 (in 2010). It is situated in the large Odra Valley, where four other smaller rivers (Oława, Ślęża, Bystrzyca and Widawa) join the Odra river. There are large areas of grasslands and tree lines along these rivers.

In 2004, arable land comprised 44.8% of the total surface area, whereas 5.6% were covered with forests and wooded areas, 3.4% water, 9.8% roads, 18.7% built-up areas, 3.7% gardens, 6.1% recreational areas, and 1.3% wastelands (data from the city government). Marshlands and meadows comprised together 6.6%.

There are 13 forests with a total surface area of 2,286 ha in Wrocław. Most of these forests are dominated by *Tilio-Carpinetum* stands, but forests situated in the western part (Mokrzański, Rędziński) are dominated by pines *Pinus sylvestris*. Among the biggest forests are Mokrzański (680 ha), Ratyński (295 ha) and Rędziński (218 ha).

In total, there are also 44 parks in Wroclaw, with a total surface of 781 ha. The biggest parks are: Szczytnicki (120 ha), Tysiąclecia (90 ha), Zachodni (75 ha), Grabiszyński (48 ha) and Wschodni (30 ha). Six other parks range in surface size from 10 to 29 ha, and the remaining are between 2 and 10 ha. Small afforested areas are scattered all over the city, especially in its SE part.

Two zones were distinguished in the city: outer and inner *(Figure 1)*. The zones differed in the proportion of densely built-up, open and afforested areas. In the inner zone of the city, most surface (> 50%) is covered with densely built-up areas, while in the outer zone – mostly (> 50%) with open (not built-up) and afforested areas. In the outer zone of the city afforested areas cover 2,380 ha, in the inner part – 820 ha.

The climate of Wrocław is temperate, slightly warmer than the neighbouring areas. The mean annual temperature is 9.7 °C, with the monthly mean of the coldest month (January) –0.5 °C, and the warmest month (July) 19.9 °C. The mean annual precipitation is 548 mm. The mean annual humidity is 76%. There are on average 158 days with rains per year, and 1,670 hours with sunny weather per year. The snow cover lasts on average 35 days per year (Smolnicki & Szykasiuk 2002, Bryś & Bryś 2010).

## Methods

A simplified version of territory mapping method (Bibby *et al.* 2012) has been employed to plot on maps occupied territories of some less common species associated with forests, parks and other timbered areas as their breeding and feeding habitats. All such habitats within the administrative boundaries of Wrocław *(Figure 1)* were surveyed at least twice in breeding seasons. Different parts of the city were surveyed in different years, but each part was surveyed in one year only. Some of the parts were covered by Kopij (2004, 2005, 2007, 2008, 2010, 2014a, 2014b, 2014c, 2016). The whole area was covered within a period from 2002 to 2010. The timing and the effort of the survey were similar in these two zones *(Figure 1)*.

Typical forest (those which do not occur in habitats other than forest), but not common (<10 pairs per 100 ha wooded area) passerine species were selected for this study, such as Wood Lark *Lullula arborea*, Tree Pipit *Anthus trivialis*, Wren *Troglodytes troglodytes*, Dunnock *Prunella modularis*, Song Thrush *Turdus philomelos*, Mistle Thrush *Turdus viscivorus*, Wood Warbler *Phylloscopus sibilatrix*, Goldcrest *Regulus*

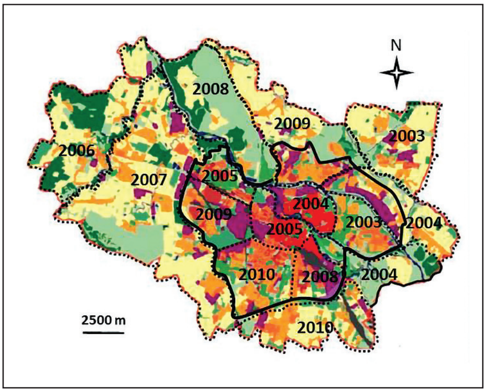


*Figure 1.* The study area (city of Wrocław). Black solid line – a border between the inner and outer zones of the city, black dashed line – borders of particular study plots (a year of survey is given). Black – railway, purple – industry areas, red – densely built-up areas, orange – loosely built-up areas, dark green – urbanized woods, light green – parks, seledin – grassy areas, yellow – arable grounds

*1. ábra* A vizsgált terület (Wrocław). A fekete folytonos vonal a belső és a külső területek közötti határt, a szaggatott vonal az időközönként vizsgált területeket jelöli a vizsgálati évek feltüntetésével. Fekete – vasútvonal, lila – iparterület, vörös – sűrűn beépített terület, narancs – kevésbé beépített terület, sötétzöld – városiasodott fás terület, világos zöld – park, seledin – füves terület, sárga – mezőgazdasági terület *regulus*, Firecrest *Regulus ignicapillus*, Spotted Flycatcher *Muscicapa striata*, Collared Flycatcher *Ficedula albicollis*, Pied Flycacher *Ficedula hypoleuca*, Crested Tit *Parus cristatus*, Marsh Tit *Parus palustris*, Coal Tit *Parus ater*, Eurasian Treecreeper *Certhia familiaris*, Short-toed Treecreeper *Certhia brachydactyla*, Golden Oriole *Oriolus oriolus*, Jay *Garrulus glandarius*, and Raven *Corvus corax*.

Each seen or heard individual was plotted on the map 1:10 000. Special attention was paid to simultaneously singing males and birds performing other territorial and/or breeding behaviour. At least two records of such bird at the same site (in optimal habitat), made in at least three-week-interval, were assumed as representing an occupied territory, i.e. one breeding pair (Sutherland *et al.* 2004, Bibby *et al.* 2012).

Population density was expressed as the number of breeding pairs (= occupied territories) per 100 ha of wooded area. For this calculation, the total number of pairs recorded in all wooded areas in a given zone was taken into account. To test differences in the population density in the outer and inner zones, average population density (pairs per 100 ha of wooded areas) of each species was calculated for all wooded areas (forests, parks and all other timbered areas) in Wrocław. Based on these mean values, expected (proportional) numbers of breeding pairs was calculated separately for afforested areas in the outer and inner zones. These expected values were compared with actual numbers of recorded pairs in those two zones and the difference was tested using $x^2$-test.

Maps were generated to show the distribution of breeding pairs of all species under the study. The distribution is shown on the background of habitats in the city of Wroclaw, so as to elucidate habitat preferences.

## Results

Population densities of 20 forest passerine species were determined and distribution of all breeding pairs recorded for each species are shown in *Figure 2* (1–20). Most of these pairs nested in larger forests, less – in larger parks, and only few in other wooded places. In general, the larger the wooded area, the higher was the number of breeding forest passerine species.

The Spotted Flycatcher and Song Thrush were the most numerous among the 20 investigated species, the former one nested in a density of 6.7 pairs per 100 ha of wooded area, while the later one at 5.1 pairs per 100 ha. Density of most other species was below 3 pairs per 100 ha of wooded area. The Tree Pipit, Crested Tit and Dunnock were unexpectedly rare (< 1 pair per 100 ha), while relatively numerous were the Wren (1.8 p./100 ha), Goldcrest (1.8 p./100 ha) and Marsh Tit (1.4 p./100 ha). The Crested Tit, Woodlark, and Mistle Thrush were the rarest species investigated (below 0.1 p./100 ha).

Among Muscicapidae, the Spotted Flycatcher was by far the most numerous species. Unexpectedly, the Collared Flycatcher was more numerous than the Pied Flycatcher, although the difference was not statistically significant ($x^2 = 2.17$, $p > 0.05$). The population density of the Short-toed Treecreeper was significantly higher than that of the Eurasian Treecreeper ($x^2 = 16.93$, $p < 0.01$). Among *Turdus* species, the Backbird *Turdus merula* was by far more numerous than the Song Thrush. The other member of this genus, the Mistle Thrush, was very rare, with only a single pair recorded. The proportion between *Regulus regulus* and *R. ignicapillus* was 0.83 : 0.17 (N = 71 pairs of both species); *Certhia brachydactyla* and *C. familiaris*: 0.70 : 0.30 (N = 109); *Ficedula albicollis* and *F. hypoleuca*: 0.57 : 0.43 (N = 118).

Several bird species nested in wooded areas only in the outer zone of the city. The group included the Tree Pipit, Coal Tit, and Raven. Population density of the Wren, Song Thrush, and Golden Oriole were significantly higher in outer than in inner zone *(Table 1)*, while the reverse was true in the case of the Spotted Flycatcher and Pied Flycatcher. No statistically significant differences in population densities of the Golden Oriole, Eurasian Treecreeper, Short-toed Treecreeper, Wood Warbler, Collared Flycatcher and Jay were recorded between outer and inner zones *(Table 2)*. Very similar densities in outer and inner zones were recorded for species such as the Jay, Eurasian Treecreeper and Marsh Tit *(Table 2)*.

*Table 1.* Density of selected forest bird species in the outer and inner parts of the city of Wrocław. N – number of breeding pairs in all wooded areas in a given zone, D – density [pairs/100 ha of wooded area]

*1. táblázat* A vizsgált madárfajok területenkénti denzitása Wrocławban. N – költőpárok száma, D – denzitás (pár/100 ha fás területegységre)

| **Species** | **Outer zone [2,380 ha]** | | **Inner zone [820 ha]** | | **Total [3,200 ha]** | |
|---|---|---|---|---|---|---|
| | **N** | **D** | **N** | **D** | **N** | **D** |
| Wood Lark | 2 | 0.08 | 0 | 0.00 | 2 | 0.06 |
| Tree Pipit | 22 | 0.92 | 0 | 0.00 | 22 | 0.69 |
| Wren | 55 | 2.31 | 3 | 0.37 | 58 | 1.81 |
| Dunnock | 10 | 0.42 | 1 | 0.12 | 11 | 0.34 |
| Song Thrush | 132 | 5.55 | 30 | 3.66 | 162 | 5.06 |
| Mistle Thrush | 1 | 0.04 | 0 | 0.00 | 1 | 0.03 |
| Wood Warbler | 71 | 2.98 | 31 | 3.78 | 102 | 3.19 |
| Goldcrest | 38 | 1.59 | 21 | 2.57 | 59 | 1.84 |
| Firecrest | 8 | 0.34 | 4 | 0.49 | 12 | 0.38 |
| Spotted Flycatcher | 120 | 5.04 | 95 | 11.59 | 215 | 6.72 |
| Collared Flycatcher | 43 | 1.81 | 24 | 2.93 | 67 | 2.09 |
| Pied Flycatcher | 18 | 0.76 | 33 | 4.02 | 51 | 1.59 |
| Marsh Tit | 37 | 1.55 | 9 | 1.10 | 46 | 1.44 |
| Crested Tit | 3 | 0.13 | 0 | 0.00 | 3 | 0.09 |
| Coal Tit | 45 | 1.89 | 0 | 0.00 | 45 | 1.41 |
| Eurasian Treecreeper | 26 | 1.09 | 7 | 0.85 | 33 | 1.03 |
| Short-toed Treecreeper | 51 | 2.14 | 25 | 3.05 | 76 | 2.38 |
| Golden Oriole | 54 | 2.27 | 31 | 3.78 | 85 | 2.66 |
| Jay | 47 | 1.97 | 16 | 1.95 | 63 | 1.97 |
| Raven | 8 | 0.34 | 0 | 0.00 | 8 | 0.25 |
| **Total** | **798** | **33.53** | **309** | **37.68** | **1,107** | **34.59** |

*Table 2.* Statistical analysis ($x^2$-test) of differences between population densities of some woodland bird species in inner and outer part of Wrocław city. Tested were only the species, for which expected value (between N and E) was at least five. N – number of pairs recorded, E – expected number of pairs. Level of significance: *: <0.05; **: <0.01

*2. táblázat* A vizsgált fajok populációdenzitás elemzésének eredményei. N – párok száma, E – a párok számának várt értékei. Szignifikancia szint *:<0,05; **:<0,01

| **Species** | **Outer city** | | | **Inner city** | | |
|---|---|---|---|---|---|---|
| | **N** | **E** | **$x^2$** | **N** | **E** | **$x^2$** |
| Wood Lark | 2 | 1.74 | | 0 | 0.00 | |
| Tree Pipit | 22 | 19.18 | 0.83 | 0 | 0.00 | |
| Wren | 55 | 47.95 | 2.07 | 3 | 1.88 | |
| Dunnock | 10 | 8.72 | 0.38 | 1 | 0.63 | |
| Song Thrush | 132 | 115.09 | 4.97* | 30 | 18.84 | 13.21* |
| Mistle Thrush | 1 | 0.87 | | 0 | | |
| Wood Warbler | 71 | 61.90 | 2.67 | 31 | 19.47 | 13.65** |
| Goldcrest | 38 | 43.79 | 0.41 | 21 | 15.09 | 0.90 |
| Firecrest | 8 | 6.98 | 0.30 | 4 | 2.51 | |
| Spotted Flycatcher | 120 | 104.63 | 4.52* | 95 | 59.67 | 41.83** |
| Collared Flycatcher | 43 | 37.49 | 1.62 | 24 | 15.08 | 10.57** |
| Pied Flycatcher | 18 | 15.69 | 0.68 | 33 | 20.73 | 14.53** |
| Marsh Tit | 37 | 32.26 | 1.39 | 9 | 5.65 | 3.96 |
| Crested Tit | 3 | 2.62 | | 0 | | |
| Coal Tit | 45 | 39.23 | 1.69 | 0 | | |
| Eurasian Treecreeper | 26 | 22.67 | 0.98 | 7 | 4.40 | |
| Short-toed Treecreeper | 51 | 44.47 | 1.92 | 25 | 15.70 | 11.01** |
| Golden Oriole | 54 | 47.08 | 2.03 | 31 | 19.47 | 13.65** |
| Jay | 47 | 40.98 | 1.77 | 16 | 10.05 | 7.05* |
| Raven | 8 | 6.98 | 0.30 | 0 | | |

*Table 3.* Population density of forest species in three selected large cities in Poland. N – number of breeding pairs, D – pairs/100 ha of wooded area

*3. táblázat* Erdei fajok populációdenzitás értékei három nagyobb lengyel városban. N – költőpárok száma, D – pár/100 ha fás területen

| **City name** | **Warsaw** | | **Lodz** | | **Wroclaw** | |
|---|---|---|---|---|---|---|
| **Total surface area** | **494 km²** | | **293 km²** | | **293 km²** | |
| **Wooded surface area** | **143.3 km²** | | **28.4 km²** | | **32 km²** | |
| **Study period** | **1986–1990** | | **2001–2008** | | **2002–2010** | |
| **Parameters** | **N** | **D** | **N** | **D** | **N** | **D** |
| Wood Lark | 0 | 0.0 | 30 | 1.1 | 2 | 0.1 |
| Tree Pipit | 200 | 1.4 | 100 | 3.5 | 22 | 0.7 |
| Wren | 500 | 3.5 | 70 | 2.5 | 58 | 1.8 |
| Dunnock | 100 | 0.7 | 65 | 2.3 | 11 | 0.3 |
| Song Thrush | 400 | 2.8 | 80 | 2.8 | 162 | 5.1 |
| Mistle Thrush | 5 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| Wood Warbler | 600 | 4.2 | 200 | 7.0 | 102 | 3.2 |
| Goldcrest | 10 | 0.1 | 30 | 1.1 | 59 | 1.8 |
| Firecrest | 0 | 0.0 | 6 | 0.2 | 12 | 0.4 |
| Spotted Flycatcher | 300 | 2.1 | 250 | 8.8 | 215 | 6.7 |
| Collared Flycatcher | 5 | 0.0 | 2 | 0.1 | 67 | 2.1 |
| Red-breasted Flycatcher | 10 | 0.1 | 16 | 0.6 | 0 | 0.0 |
| Pied Flycatcher | 200 | 1.4 | 100 | 3.5 | 51 | 1.6 |
| Marsh Tit | 40 | 0.3 | 80 | 2.8 | 46 | 1.4 |
| Crested Tit | 40 | 0.3 | 250 | 8.8 | 3 | 0.1 |
| Coal Tit | 30 | 0.2 | 64 | 2.3 | 45 | 1.4 |
| Eurasian Treecreeper | 80 | 0.6 | 40 | 1.4 | 33 | 1.0 |
| Short-toed Treecreeper | 80 | 0.6 | 146 | 5.1 | 76 | 2.4 |
| Golden Oriole | 300 | 2.1 | 280 | 9.9 | 85 | 2.7 |
| Jay | 250 | 1.7 | 260 | 9.2 | 63 | 2.0 |
| Raven | 5 | 0.0 | 8 | 0.3 | 8 | 0.3 |
| Total | 3,155 | 22.0 | 2,077 | 73.1 | 1,107 | 34.6 |
| Sources | Luniak *et al.* 2001 | | Janiszewski *et al.* 2009 | | This study | |

## Discussion

In Wrocław, like in other Polish cities, species such as the Robin *Erithacus rubecula*, Wren, Song Thrush and Dunnock are relatively uncommon. For the contrast, in Western European cities, especially in the United Kingdom, they belong to the most common species in urbanized habitats (Mörtberg 2001, Otto *et al.* 2005). The Dunnock and Wren require dense undergrowth, which are often not available in urban parks. The Robin and Song Thrush forage on the ground among dead leaves and debris, and in Polish urban parks, these are often removed, so that the species are deprived of their main foraging grounds. The situation in urban parks in Western Europe is probably different in that sense.

The Collared Flycatcher is a newcomer to the city. During the years 1978–1987 it was not recorded at all in Wroclaw (Dyrcz *et al.* 1991), but in the years 2002–2010, it was already relatively numerous, even in the inner zone, where it occupied larger parks with old stands of common oaks, *Quercus robur*. Such situation is not known in any other Polish city. This would be, therefore, a first evidence of an urbanization of this species in Poland, and probably in Central Europe.

The first record of nesting Ravens were made in Wrocław in 1986 (Dyrcz *et al.* 1991), but it still occurs only on the periphery of the city, and nest only on trees. Also in other Polish cities, it was recorded only in the city peripheries and nesting on trees only (Luniak *et al.* 2001, Janiszewski *et al.* 2009, Zawadzka & Zawadzki 2014). However, it is known to adopt electricity pylons and other man-made structures in farmlands in some parts of this country (Bednorz 2000, Zawadzka & Zawadzki 2014). It is also well-known as having a wide spectrum of diet, and as being under a low predation pressure. Considering this wide ecological flexibility, weak synurbanization of Raven is a surprise. Other corvids such as the Hooded Crow *Corvus cornix*, Jackdaw *Corvus monedula*, Rook *Corvus frugilegus* and Magpie *Pica pica* have been well-adopted to urban environments for a long time. Probably high overall density of corvids in cities, especially that of the Hooded Crow *Corvus cornix*, is the reason for this weak Raven's synurbanization (Zawadzka & Zawadzki 2014).

The Wood Warbler, a typical forest species, was relatively common in the city of Wrocław. Unexpectedly, it also nested in higher densities in inner than in outer zone. It prefers rather shady and humid places, with dense undergrowth, and this is often removed from most parks. It is virtually absent in West European cities (Mörtberg 2001, Witt *et al.* 2005).

The Golden Oriole nested in relatively high density in inner Wrocław, probably higher than in any other city in Poland and much higher than in West European cities (Witt *et al.* 2005). There is quite a dense net of rivers and canals, with numerous old oaks, poplars and other trees in the inner zone. This setting comprises optimal nesting habitat for the Oriole.

Except for the Great Tit *Parus major* and Blue Tit *Parus caeruleus*, all other species of the family Paridae were recorded as relatively rare in Wrocław, and the Willow Tit *Parus montanus* was not recorded at all. The Crested Tit and Coal Tit were found only in peripheral woods, and only the Marsh Tit was recorded in some urban parks in the inner zone. The Crested Tit, Coal Tit, Marsh Tit, Willow Tit are, however, area-sensitive species. Mörtberg (2001) has shown that they avoid urban forest patches which are smaller than 200–400 ha, and are virtually absent from those which are 10–30 ha in size. All forests are below 200 ha in the inner zone of Wrocław, whereas in the outer zone, there are only four such forests.

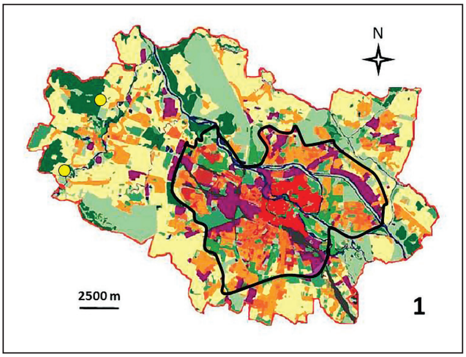
In Wrocław, both tree-creeper species occur often sympatrically at the same park or wood, and even in the same habitats. In such situation they appear to be territorial in relation to each other. The Short-toed Treecreeper is more common and more urbanized that the sibling species, but Wrocław is probably the only city in Poland where such proportions prevail. In all other cities, the proportion is probably reverse.

The Jay is relatively uncommon in Polish urban parks, probably as a result of competition with the Hooded Crow, which nest commonly in urban parks and in their close proximity. Urban parks are also usually devoid of dense young tree stands, which the species prefers as nesting habitat.

In some countries in Western Europe, population densities of most forest passerine species are completely different from those recorded in Wrocław and other big cities in Poland *(Table 3)*. For example, in Sheffield, UK, a city comparable to Wrocław (surface area of 160 km$^2$, and human population of 513 000), densities of the Wren, Robin, and Dunnock were higher than in Wrocław by the order of magnitude. Otherwise, species such as the European Nuthatch, Spotted Flycatcher had lower densities in Western European cities than in Wrocław. The Wood Warbler, Marsh Tit, Eurasian Treecreeper, Fieldfare, Golden Oriole, and Tree Sparrow are common in Wrocław, but were virtually absent in Sheffield (Fuller *et al.* 2009).

Only population size of the Jay and Coal Tit was comparable with that recorded in Wrocław, Warsaw or Łódź *(Table 3)*. Similar large differences in population densities exist if Wrocław is compared to Berlin (Otto & Witt 2002) or Hamburg (Mitschke & Baumung 2001). There is a clear western gradient (an increase of population densities from cities in eastern towards cities in western Europe) for species such as the Dunnock, Wren, Robin, Blackbird, Song Thrush, Mistle Thrush, Chiffchaff, and Greenfinch, and an eastern gradient (an increase of population densities from cities in western towards cities in eastern Europe) for the Golden Oriole, House Sparrow (Witt *et al.* 2005) and probably for the Tree Sparrow, Spotted Flycatcher, Icterine Warbler, Marsh Warbler, Serine and Starling (Kopij 2014b, 2015). In the last two decades the Wood Pigeon, Blue Tit and Blackcap reached population densities typical for west European countries also in Wrocław and other towns and cities in SW Poland (own observ.).

Urban populations may buffer some bird species against regional population declines caused by agriculture intensification, increased predation or loss of suitable breeding habitats. It has been pointed out by many researchers (e.g. Gavareski 1976, Environment Canada 2007, Sanesi *et al.* 2009), that in inner zones of cities the forest patches, called parks, are often structurally less diverse than forests outside the city. As a result, most forest species have decreased population densities in cities than outside. This is due to the removal of undergrowth, ground cover and canopy layers, and old and dead trees (Gavereski 1976, Kopij 2015). However, in Wrocław this situation is not apparent. There are few forest species which have reduced numbers in inner forests, and few species which have increased, and still few others which remain the population density on similar level in forests of the inner and outer zone. In general, hole-nesting forest passerines are not affected. Some species foraging on the ground and shrub layers have indeed reduced densities (Song Thrush, Wren), but other species from this guild have remained similar or even increased densities (Wood Warbler, Marsh Tit). Thus, it is plausible, than factors such as nesting site availability, predation pressure and local microclimate may also play a role in the synurbanization of these wood passerine species in this part of Europe.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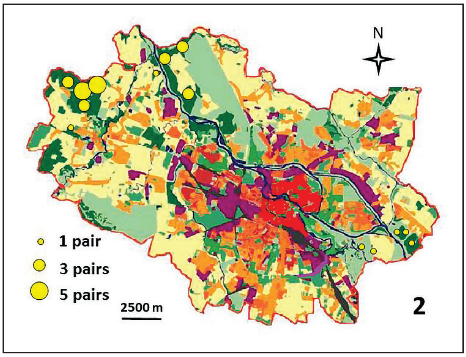
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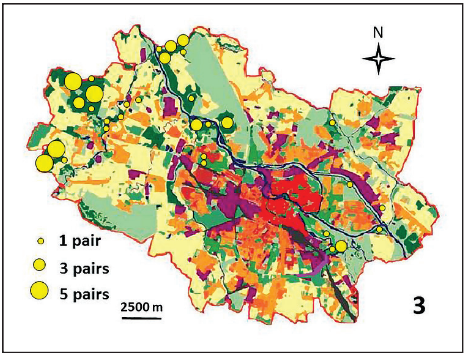
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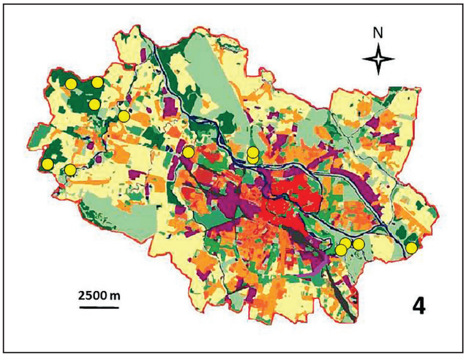
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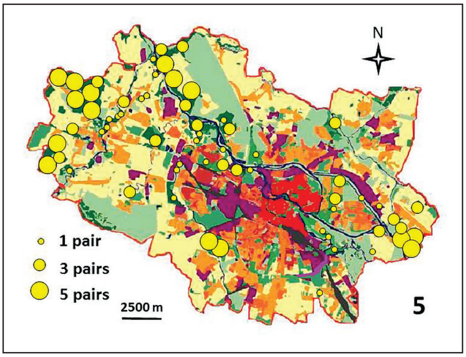
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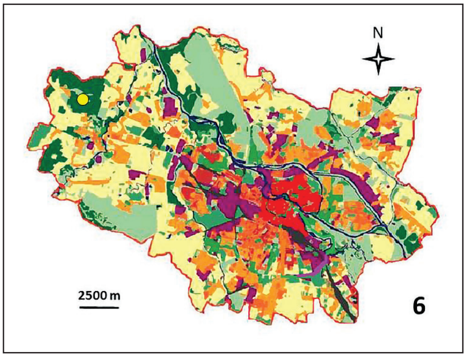
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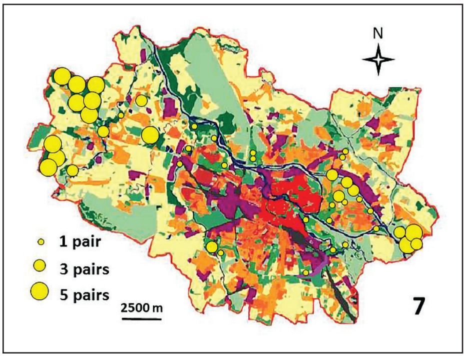
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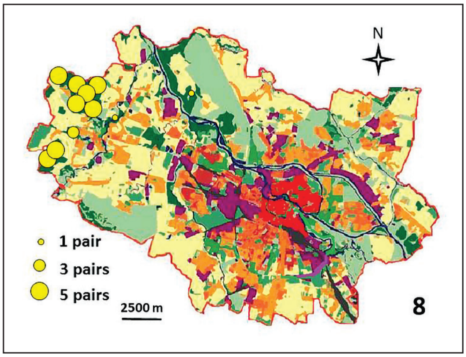
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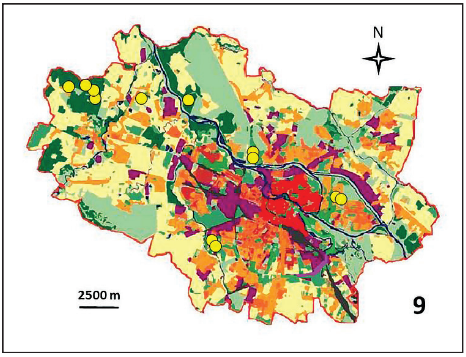
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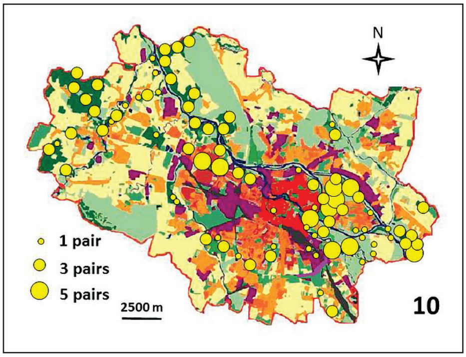
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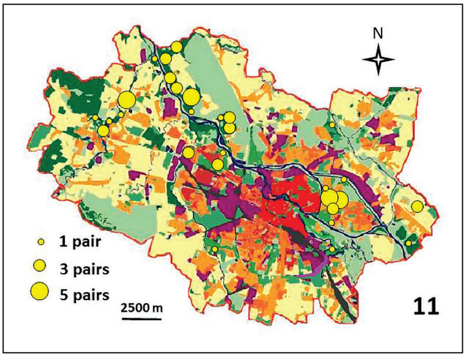
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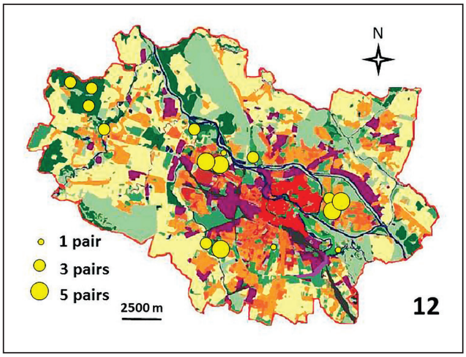
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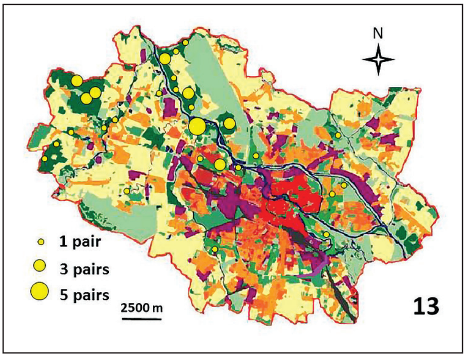
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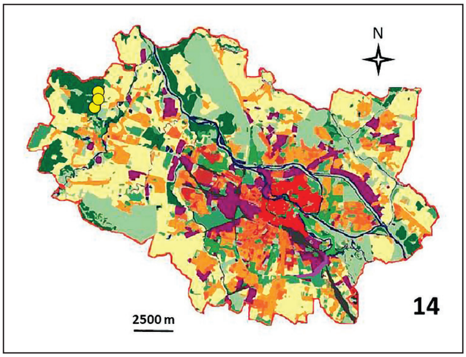
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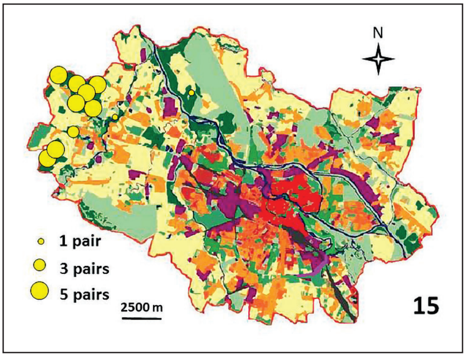
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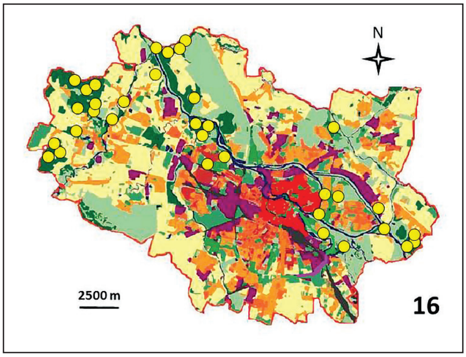
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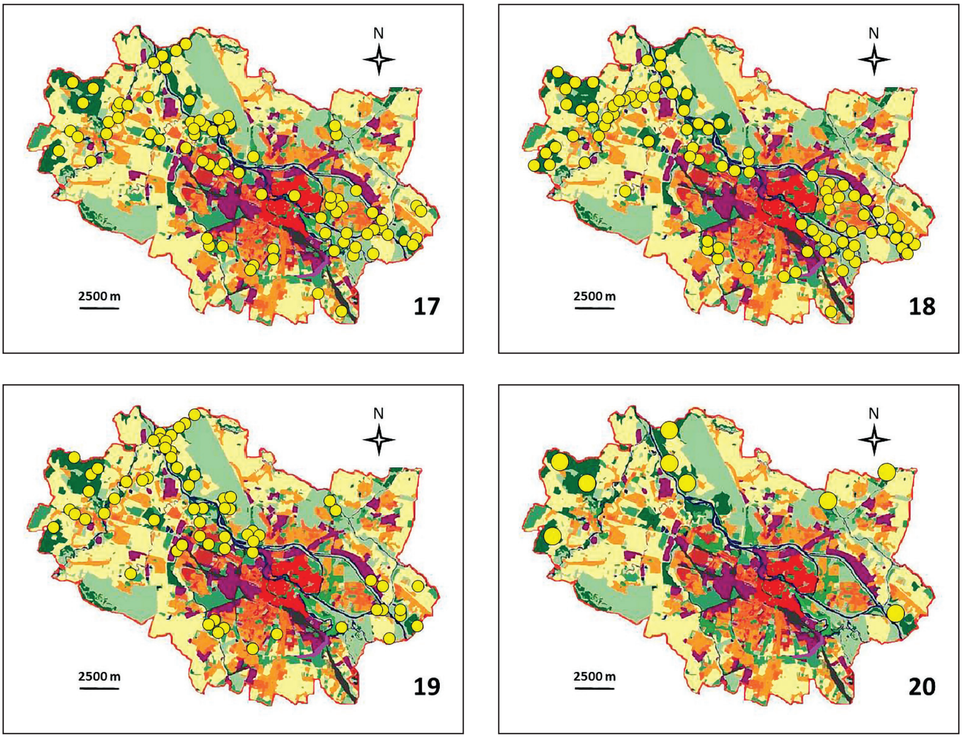

*Figure 2.* Distribution of studied species breeding pairs in the city of Wrocław during the years 2002–2010. The black continuous line indicate the border between inner and outer zone of the city. Black – railway, purple – industry areas, red – densely built-up areas, orange – loosely built-up areas, dark green – urbanized woods, light green – parks, seledin – grassy areas, yellow – arable grounds

1. Woodlark, 2. Tree pipit, 3. Wren, 4. Dunnock, 5. Song Thrush, 6. Mistletoe Thrush, 7. Wood Warbler, 8. Goldcrest, 9. Firecrest, 10. Spotted Flycatcher, 11. Collared Flycatcher, 12. Pied Flycatcher, 13. Marsh Tit, 14. Crested Tit, 15. Coal Tit, 16. Eurasian Treecreeper, 17. Short-toed Treecreeper, 18. Golden Oriole, 19. Jay, 20. Raven

*2. ábra* A vizsgált fajok elterjedése Wroclawban 2002–2010 között. A fekete folytonos vonal a belső és a külső területek közötti határt jelöli. Fekete – vasútvonal, lila – iparterület, vörös – sűrűn beépített terület, narancs – kevésbé beépített terület, sötétzöld – városiasodott fás terület, világos zöld – park, seledin – füves terület, sárga – mezőgazdasági terület

1. erdei pacsirta, 2. erdei pityer, 3. ökörszem, 4. erdei szürkebegy, 5. énekes rigó, 6. léprigó, 7. sisegő füzike, 8. sárgafejű királyka, 9. tüzesfejű királyka, 10. szürke légykapó, 11. örvös légykapó, 12. kormos légykapó, 13. barátcinege, 14. búbos cinege, 15. fenyvescinege, 16. hegyi fakusz, 17. rövidkarmú fakusz, 18. sárgarigó, 19. szajkó, 20. holló

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# Preliminary results on bird collision with overhead power lines in Hungary: a case study around Pusztaszer Landscape Protection Area

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**Abstract** The literature on bird collision with power lines in Hungary is rather limited. We collected published records and carried out research on birds that collided with overhead wires, and we made a list of species, and the number of individuals recorded, around Pusztaszer Landscape Protection Area. The quality of data did not allow us to do robust statistical tests, and a large amount of collected data was not used in this paper, because of uncertainty. Finally, we used the records of 519 individuals of 63 species that got injured or died during collision with overhead wires. We found evidence, that low-, middle- and high-voltage power lines were all responsible for the collision accidents of birds. Birds that use wetlands or both wetlands and farmlands are the most threatened to collide with overhead electric wires. Most victims of collision accidents belong to Gruiformes, Charadriiformes, Pelecaniformes and Anseriformes orders. Our preliminary results suggest that the bigger the rate of weight and wingspan (wing-loading proxy) is, the greater the risk of birds colliding with power lines, probably because of poor manoeuvrability. Birds that move regularly, on a daily basis between their nests/roost sites and foraging areas are at higher risk to collide with electric wires. Our preliminary results do not support the hypothesis that birds which sit on power lines collide more frequently than birds that do not use wires. It seems that foggy weather circumstances increase the probability of collision events particularly in case of Common Cranes. Some large birds were found with burnt feathers after collision with middle-voltage power lines. A sizeable part of collided birds were protected or strictly protected. Bird collision with overhead wires is a serious problem in Hungary. Collision can be stopped on most dangerous part of overhead wires by converting to underground cabling. It is possible to reduce the number of collision events in case of high-voltage power lines by increasing their visibility. We always recommend underground cabling in case of wetlands, if new segments of electric wires would be carried out.

Keywords: birds, collision risk, collision accident, electric overhead power line, habitat use, waterbird

**Összefoglalás** A madarak légvezetékkel történő ütközéséről Magyarországon csak minimális mennyiségű adattal rendelkeztünk. A publikált adatokból és saját felméréseinkből összeállítottunk egy fajlistát, hogy mely fajokat érint a légvezetékkel történő ütközés, és hány egyed pusztult el vagy sérült meg a Pusztaszeri Tájvédelmi Körzetben és környékén. Az adatok minősége miatt megbízható statisztikai elemzéseket nem tudtunk végezni, és az eredetileg összegyűjtött adatok egy részét a bizonytalanságok miatt nem is használtuk fel ebben a tanulmányban. Végül 63 faj 519 egyedével dolgoztunk, melyek vezetékkel való ütközés következtében elpusztultak vagy megsérültek. A kis-, közép- és nagyfeszültségű vezetékeknél egyaránt tapasztaltunk madárpusztulást. A légvezetékkel történő ütközés leginkább olyan madarakat érintett, melyek vizes élőhelyeket, illetve vizes élőhelyeket és mezőgazdasági területeket egyaránt használtak. Az ütközéses balesetekben leginkább a daru-, lile-, gödény- és lúdalkatú madarak érintettek. Előzetes adataink szerint minél nagyobb a testtömeg és a szárnyfesztávolság aránya (nagy a szárnyterhelést helyettesítő érték), annál inkább hajlamosak a madarak az ütközésre, valószínűleg a rossz manőverezőképességük miatt. Azok a madarak, melyek rendszeresen, naponta mozognak a fészkük/pihenőhelyük, és a táplálkozó-területük között, hajlamosabbak voltak arra, hogy légvezetéknek ütközzenek. Előzetes eredményeink nem támasztották alá azt, hogy a légvezetékeket rendszeresen használó madarakból több pusztul el ütközés miatt, mint azokból, amelyek nem használják ezeket. A darvaknál úgy tűnik, hogy a köd fokozta az ütközéses esetek számát. Az ütközés során középfeszültségű légvezetékeknél a nagyobb méretű madarak egy része megégett. Az ütközött madarak nagy része védett vagy fokozottan védett volt. A légvezetékkel ütközés Magyarországon is komoly probléma. A legveszélyesebb vezetékszakaszok földkábelbe helyezése megszünteti az ütközést. A nagyfeszültségű szakaszokon a láthatóság növelésével mérsékelhető a madarak légvezetékkel történő ütközéseinek száma. Javasoljuk, hogy vizes élőhelyeken és vizes élőhelyek között új elektromos vezeték csak földkábeles megoldással létesülhessen.

Kulcsszavak: madarak, ütközési kockázat, ütközéses baleset, elektromos légvezeték, élőhely-használat, vízimadár

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## Introduction

Humans create dozens of infrastructural facilities (e.g. power lines, roads, railways, wind farms, solar power plants), which have serious, and often fatal impacts on birds due to their direct or indirect effects (Trombulak & Frissell 2000, Horváth & Demeter 2010, Smith & Dwyer 2016, Molnár & Andrési 2019). A well-known direct effect of overhead power lines is that the wires and pylons regularly cause bird collision and electrocution of birds (Bevanger 1994, Horváth & Demeter 2010). At the same time, electric cables may dramatically reduce the available habitat of some species, as a negative indirect effect (Lóránt & Vadász 2014). Besides negative impacts, positive effects are also known: 80% of the Hungarian Saker Falcon *(Falco cherrug)* population breeds in artificial nest boxes that are insulated on high-voltage pylons (Bagyura *et al.* 2019).

National park directorates and civil associations regularly carry out surveys in Hungary to look for carcasses of birds that had been electrocuted (Horváth & Demeter 2010, Demeter *et al.* 2018). Monitoring surveys indicated that protected and strictly protected species are often killed by electric shock in Hungary (Horváth & Demeter 2010, Demeter *et al.* 2018). Electrocutions generally happen on middle-voltage power lines and sometimes they occur on low-voltage power lines as well, however, these were never documented on high-voltage power lines (Horváth & Demeter 2010). Collision accidents could occur in all kinds of overhead power lines (low-, middle- and high-voltage), and also on the electric lines of railways (Horváth & Demeter 2010, Vadász & Lóránt 2014).

There could be several factors in the background of bird collisions:

(1) Morphological factors which influence the manoeuvrability of birds are probably one of the most important factors to understand why birds collide with power lines (D'Amico *et al.* 2019). Wing loading is the ratio of weight to wing area, whereas wing aspect ratio is the ratio of wingspan squared to wing area are the most important metrics to estimate manoeuvrability of an avian species (Bevanger 1994, Bernardino *et al.* 2018). Birds with high wing loading and low or average wing aspect ratio (for example in case of Anseriformes,

Podicipediformes, Gruiformes, Charadriiformes) often collide with overhead wires (Quinn *et al.* 2011, Smith & Dwyer 2016, Bernardino *et al.* 2018).

(2) Visual perception is another essential morphological factor that has impact on bird collision. Birds with binocular vision (e.g. raptors, owls) have better chance to locate obstacles and avoid collision, while birds with peripheral vision are less suitable for detection of wires in the air (D'Amico *et al.* 2019).

(3) Several behavioural factors also play key role during collision: birds that tend to fly in flocks are more often found as victims of collision than solitary species (Quinn *et al.* 2011, Bernardino *et al.* 2018). Some species (for example raptors and storks) usually move with soaring flight in higher altitudes than the height of power lines, and this behaviour feature prevent them from collision with power lines (Bernardino *et al.* 2018, D'Amico *et al.* 2019). Birds that migrate during night and also nocturnal birds are in higher risk to collide with power lines, because the wires are less visible during night (Bevanger 1994, Bernardino *et al.* 2018, D'Amico *et al.* 2018, 2019). Birds during their migration usually fly higher above wires and during their flight they are not expected to collide with power lines (Bernardino *et al.* 2018). Collisions generally happen when birds fly in low altitude from one site to another, and they cross power lines during their local, daily movements, often between foraging areas and nest (Bernardino *et al.* 2018). Display flights may also increase the risk of collision (Bevanger 1994, Bernardino *et al.* 2018). Juvenile birds collide more frequently with wires because young birds are less manoeuvrable and they are inexperienced (Bernardino *et al.* 2018).

(4) Visual circumstances are also important. We have already mentioned it as a higher risk for collision with wires during the night (Bevanger 1994, Bernardino *et al.* 2018) or during fog, because the detectability of wires in foggy weather or at night is poor (Molnár & Andrési 2019).

(5) Weather circumstances have influence on flight altitude of birds: fog, rainfall and snowfall also force birds to fly at low altitudes, therefore increase the chance to collide with power lines (Bernardino *et al.* 2018).

(6) Site specific factors also play an important role in these collision incidents. Topographical leading lines are of great importance to migrating birds, and they may contribute to defining migratory flyways, like along rivers and topographical depressions, and electric wires above them would result in frequent collision events (Bevanger 1994, Quinn *et al.* 2011, Bernardino *et al.* 2018). Birds generally fly at lower altitudes above open areas, which means a higher risk for collision, while they tend to fly at higher altitude above forests, which may reduce collision risk (Bernardino *et al.* 2018). Electric wires above wetlands are assumed to be the most hazardous, because huge number of waterbirds can be found there during breeding season, or during their migration and wintering as well (Bevanger 1994, Quinn *et al.* 2011, Bernardino *et al.* 2018).

(7) The features of power lines are also important: there is a general agreement that the higher the structure is, the greater risk it becomes for birds (Bernardino *et al.* 2018).

(8) Anthropogenic disturbance (e.g. hunting) is also known as factor which increases the risk of collision (Bernardino *et al.* 2018).

While the mortality of birds caused by electrocution is more or less monitored in Hungary, the collision events of birds with overhead lines are less so. The goal of this paper is to draw attention to the serious problem of birds' collision with overhead power lines in Hungary.

## Material and methods

### Data collection

Data used for this paper were collected by rangers and officers of Kiskunság National Park Directorate and also by amateur ornithologists. Data were collected from the Great Hungarian Plain, from Csongrád County, mainly from Pusztaszer Landscape Protection Area and the vicinity of this site. The collected data were geographically located between the area called "Homokhátság" and River Tisza *(Figure 1)*. Data were collected without a strict protocol between 1982 and 2019, but the available dataset contains large gaps within this time period, with no surveys. This area has a rich avifauna, with huge number of wildfowls, herons, spoonbills, cranes, shorebirds and gulls (Máté & Nagy 2015, Végvári 2015, Pigniczki 2016).

Data were collected from electric wires, which were located in fishpond systems (Lake Csaj, Fertő at Szeged) or between two fishpond systems (namely Lake Fehér and Fertő at Szeged), and some was located above meadows or agricultural fields. Generally, all of the electric wires were on open areas, and their distance from wetlands (fishponds, soda pans, marshes) was less than 1.5 kilometres. That is the reason why they have a direct impact on birds during their foraging trips, or when they move from a pond to another one, within a fishpond system. The low-voltage power lines were 8–10 m high, the middle-voltage were 10–14 m tall (A. Gerhardt pers. com.). The maximal height of pylons of high-voltage power lines were 50 m in the study area (Gy. Bíró pers. com.).

We collected information on the species; the number of individuals (if it was possible); type of power lines that caused collision accidents; the date (if it was possible) and the location of accidents. We noted if a bird had burnt feathers due to electrocution during the collision accident, and also noted, if a bird survived the collision with other injuries.

Unfortunately, no exact date, number and notes belonged to some of the data: however, we used some of those records with missing dates as well, especially, when relatively rare birds [for example Sanderling *(Calidris alba)* or Whimbrel *(Numenius phaeopus)*] were described. If relatively common birds [for example Grey Herons *(Ardea cinerea)*, Great White Egrets *(Ardea alba)*, Black-headed Gulls *(Larus ridibundus)*, etc.] were mentioned with no exact background information, the record were excluded from the present study to avoid risk of double use of the same record. Therefore, the given number in case of most species means minimum number and can be even much larger in reality.

We used the data of published surveys of Hegedűs (1984) and Mészáros (1989) as well; both authors collected data about high-voltage power lines located between two fishpond system, namely between Fehér-tó and Fertő (the closest settlements are Szeged and Sándorfalva) during 1982–1983 and 1985–1986. We also used published data about accidents of a Kentish Plover *(Charadrius alexandrinus)* (Pigniczki 2006) and Common Cranes *(Grus grus)* (Bakacsi & Puskás 2019).

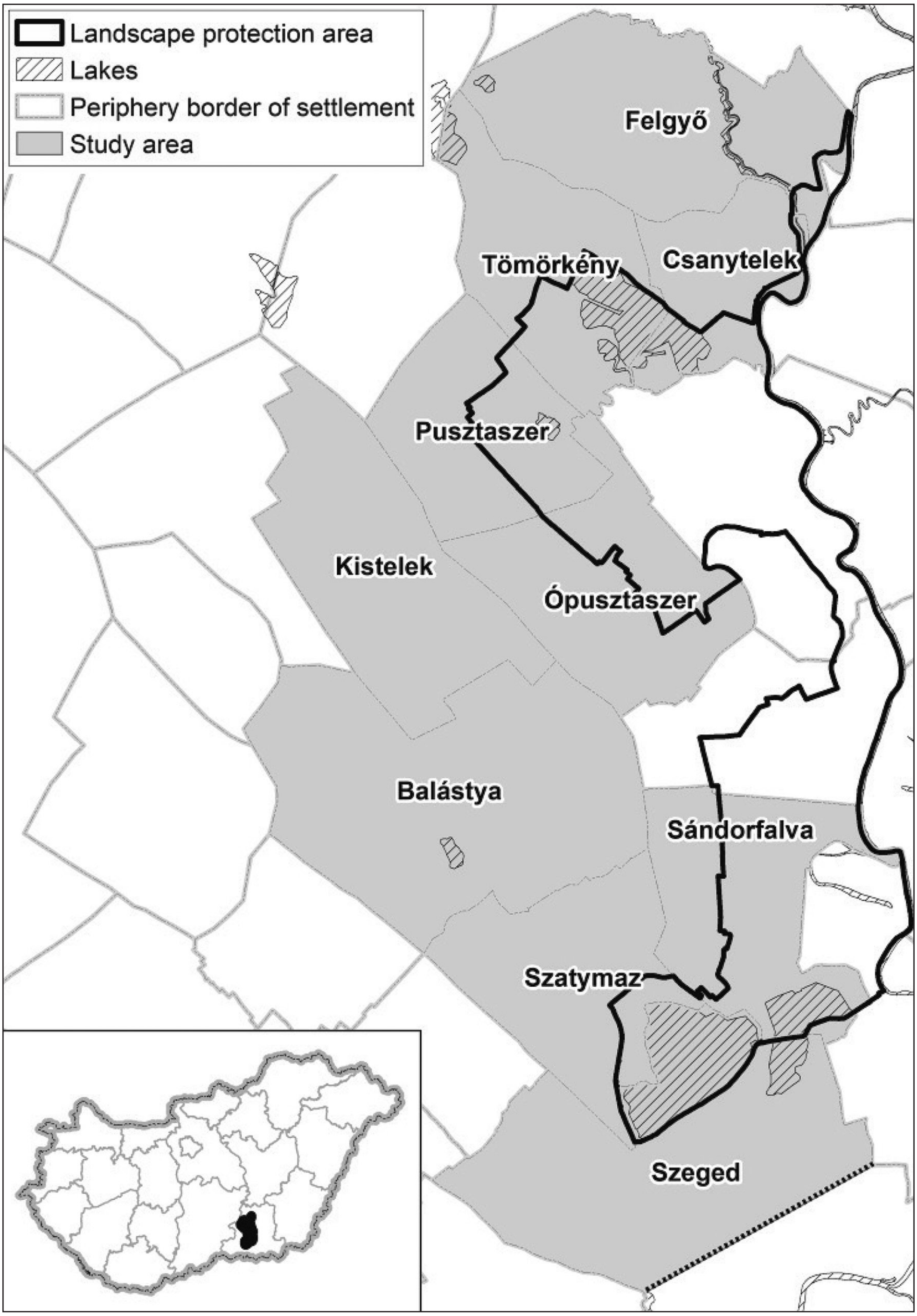

*Figure 1.* Map of study area

*1. ábra* A vizsgálati terület. Jelmagyarázat: landscape protection area: tájvédelmi körzet; lakes: tavak; periphery border of settlement: település külterület határa; study area: vizsgálati terület

## Data analysis

We created a list of species, with detailed information on mortality and injuries as a result of collision with power lines following the taxonomy available on the webpage of Handbook of Birds of the World (www.hbw.com). We collected wingspan, body length and body weight data (www.hbw.com and www.mme.hu/magyarorszagmadarai) for all the species that had collision accidents, to calculate wing-loading proxy, and to find measures for burning events during collision accidents. Wing area data were not available in case of most species to calculate wing-loading value (mass of the bird species divided by its wing area), thus, we used the ratio of weight of a given species (in gram) to its wingspan (in centimetre), and the result was called wing-loading proxy (D'Amico *et al.* 2019). If the value of wing-loading, or wing-loading proxy was high for a species, that meant poor manoeuvrability in flight and high risk of collision (Bernardino *et al.* 2018, D'Amico *et al.* 2019).

We determined the number of individuals and the number of species under the different type of power lines (high-, middle- and low-voltage), and compared them.

We compared the habitat use of species and the risk of collision during their flights. We used the following habitat types: wetlands (including rivers, lakes, fishponds, marshes, reedbeds, wet meadows), farmlands (including agricultural fields, dry grass-areas) and woodlands (including forests and bush-areas). We assigned one or two habitat types to each species. For example, if a species generally breeds or roosts in lakes or fishponds, but regularly forages on corn-fields, we assigned both wetland and farmland habitat types to that species [e.g. Common Crane, Mallard *(Anas platyrhynchos),* etc.)]. We compared the number of species and individuals with regard to the use of different habitat types.

We analysed which taxonomic orders and which species have high risk to collide with wires. We used the number of individuals collided to wires in both cases, and we used the number of species that belongs to a given taxonomic order to measure the impact of collision risk for different taxa.

We estimated the effect of power lines on birds that tend to have regular daily trips between foraging areas and their nests or roosting sites. We created two groups to compare: one of the groups contained species that had no regular, large-distance daily trips between areas, while the other group contained species that did have regular, long-distance daily trips between sites at least during a part of their annual cycle.

D'Amico *et al.* (2019) treated birds with higher collision risk if they bred on pylons, or hunt from wires/pylons. Other authors suggested that the use of power lines increases the chance of electrocutions significantly, but had no significant effect on collision risk (Bernardino *et al.* 2018, D'Amico *et al.* 2018). That is why we also estimated the collision risk, whether a species tend to use power lines to sit there, or not.

We created four interquartile range-groups based on the value of wing-loading proxy: the first group contains species between minimum and lower quartile values, the second group contains species between lower quartile and median value, species that fall between median and upper quartile are in the third group, and finally, the fourth group contains species, which fall between upper quartile and maximum values. We compared the number of individuals in case of the four groups.

We described the chance of collision accidents, whether bird species tend to cover large distances regularly during its daily routine or not. These movements were generally foraging trips between breeding colonies and foraging areas [e.g. herons, spoonbills, ibises, gulls etc.], or between roosting areas and foraging sites [e.g. geese, Mallards, cranes, several species of shorebirds, like Lapwings *(Vanellus vanellus)*, Eurasian Curlews *(Numenius arquata)*, Whimbrels, gulls, Starling *(Sturnus vulgaris),* etc.]. Other bird species rarely move from one location to another, and they spend their time in a relatively small area (e.g. grebes, *Aythya* ducks, several species of shorebirds: *Tringa* species, *Calidris* species, small songbirds, etc.).

Four groups of conservation status were used in this study. We used the most recent conservation status in case of all species to determine, whether the species was a game species, protected species, strictly protected species, or not protected species (www.mme.hu/magyarorszagmadarai).

Rangers of Kiskunság National Park Directorate surveyed dead and injured cranes during foggy weather condition, but at the same time it was not monitored if any accident has happened in better weather conditions.

Occasionally, it was possible to note the cause of death or injury because of how visible they were: for example broken wings or broken neck. However, most of the events it was not possible to determine the cause of death or injury in the field. There were several occasions when birds that had been burnt during a collision were reported. These are only examples and probably not all broken-bone or burnt events were reported, therefore, the given number suggests a minimum number of this phenomenon in the current paper.

We used only descriptive statistical approaches because there was no standard survey in most cases, therefore, the result of statistical tests would be biased.

## Results

519 specimens of 63 species were found dead or injured under overhead wires in the study area. This includes 3 individuals where species identification was not possible. In case of a further 7 specimens it was possible to reduce the possibilities to two or three species but their exact identity remained questionable.

### Type of electric cables and collisions of birds

It was possible to clearly determine the type of electric wires, which caused the accidents in 517 cases: 79.7% of individuals were collected from under high-voltage power lines (N = 412), 19.9% of birds died or got injured because of collision with middle-voltage cables (N = 103) with only 0.4% of the carcasses were found under low-voltage power lines (N = 2).

48 species collided with high-voltage power lines (76.2%), 31 species had accidents with middle-voltage power lines (49.2%), while only two species were documented to have collisions with low-voltage power lines (3.2%) out of 63 species.

## General habitat use of birds and collisions with power lines

Our results indicate that collision accidents with overhead lines have the largest impact on wetland species, together with those species which use both wetlands and farmlands *(Table 1)*.

## Taxonomy of collided birds

Most individuals found after collision accidents taxonomically belonged to Gruiformes (39.5%), Charadriiformes (31.4%), Pelecaniformes (10.5%) and Anseriformes (10.3%) order (Table 2).

Most species that collided with electric wires belonged to Charadriiformes (28.6%), Passeriformes (17.5%), Pelecaniformes (14.3%), Anseriformes (12.7%) and Gruiformes (9.5%) *(Table 2)*.

*Table 1.* Number and percentage of collision events of species and individuals regarded to habitat use

*1. táblázat* Az ütközéses esetek száma és százalékos aránya az élőhely-használati kategóriák alapján fajokra és egyedekre lebontva

| Habitat use | Number of species | Percentage of species (%) | Number of individuals | Percentage of individuals (%) |
|---|---|---|---|---|
| Wetland | 39 | 61.9 | 115 | 22.3 |
| Wetland & farmland | 11 | 15.9 | 375 | 72.7 |
| Farmland | 8 | 12.7 | 13 | 2.5 |
| Farmland & forest | 2 | 3.2 | 10 | 1.9 |
| Forest | 3 | 4.8 | 3 | 0.6 |

*Table 2.* Number and percentage of collided species and individuals regarding to taxonomic orders

*2. táblázat* Az ütközéssel érintett madárfajok, illetve az ütközött egyedek száma és százalékos aránya madárrendenként

| Order | Number of species | Percentage of species (%) | Number of individuals | Percentage of individuals (%) |
|---|---|---|---|---|
| Galliformes | 1 | 1.6 | 2 | 0.4 |
| Anseriformes | 8 | 12.7 | 53 | 10.3 |
| Podicipediformes | 3 | 4.8 | 7 | 1.4 |
| Columbiformes | 3 | 4.8 | 4 | 0.8 |
| Gruiformes | 6 | 9.5 | 204 | 39.5 |
| Pelecaniformes | 9 | 14.3 | 54 | 10.5 |
| Suliformes | 2 | 3.2 | 3 | 0.6 |
| Charadriiformes | 18 | 28.6 | 162 | 31.4 |
| Strigiformes | 1 | 1.6 | 1 | 0.2 |
| Accipitriformes | 1 | 1.6 | 1 | 0.2 |
| Passeriformes | 11 | 17.5 | 25 | 4.8 |

The most common victims of collision accidents were Common Cranes (N = 190; 37.3%), Black-headed Gulls (N = 114; 22.4%), Mallards (N = 38; 7.5%), Lapwings (N = 18; 3.5%), Grey Herons (N = 15; 2.9%) and Great White Egrets (N = 11; 2.2%) *(Appendix 1)*. These calculations are based on exactly identified individuals (N = 509; 100%).

## Wing-loading proxy and collided birds

The calculated wing-loading proxy values of the victim-species ranged between 0.5545 [Sand Martin *(Riparia riparia)*] and 49.0909 [Mute Swan *(Cygnus olor)*], with variation regarding to species. The median of wing loading proxy in case of collided species is 4.4211, and the upper quartile value is 7.9491, while the lower quartile value is 2.2909. One species of Galliformes, six species of Anseriformes, one species of Podicipediformes, two species of Gruiformes, three species of Pelecaniformes, two species of Suliformes and one species of Charadriiformes have higher wing-loading proxy value than upper quartile, with 276 individuals that had an accident. However, six species of Charadriiformes and ten species of Passeriformes have smaller wing-loading proxy value than lower quartile with 30 individuals that had an accident *(Table 3, Appendix 1)*.

*Table 3.* Interquartile ranges of wing-loading proxies and the number of collided species and individuals belong to each range

*3. táblázat* A szárnyterhelést helyettesítő érték interkvartilis értékei és az ezekhez tartozó, ütközéssel érintett faj- és egyedszámok

| | **Interquartile range of wing-loading proxies** | **Number of species** | **Number of individuals** |
|---|---|---|---|
| Group 1 | 0.5545 – 2.0270 | 16 | 30 |
| Group 2 | 2.5547 – 4.3059 | 15 | 158 |
| Group 3 | 4.4211 – 7.7692 | 16 | 45 |
| Group 4 | 8.1290 – 49.0909 | 16 | 276 |

## Regular movement between foraging areas and roosting or nesting sites and collision accidents

Our results suggest that birds with regular, large distance movement have larger risk to die or get injured during a collision accident: among the victims 447 individuals (86.6%) of 26 species tend to move between different areas during their daily routine, while 69 specimens (13.4%) of 37 species belong to the group with no regular, large distance movements. Common Cranes have regular movements on a daily basis in the study area, and they had the most accidents on species level. Our data indicate that species belonging to Charadriiformes (145 individuals, 8 species), Pelecaniformes (50 specimens, 9 species) and Anseriformes (40 individuals, 2 species) orders also have higher risk of collision *(Appendix 1)*.

### Collision risk and use of power lines by different species

26 specimens (5.0%) of eleven species, which regularly use power lines and pylons to sit on, died or got injured due to collision, while 490 individuals (95.0%) of 52 species did not use wires and pylons *(Appendix 1)*.

### Fog during collisions

It was reported that 188 out of the190 individuals (98.9%) of Common Cranes were found to be the victims of collision with power lines during, or shortly after foggy weather conditions between 2009–2017, while they were moving to or leaving their roosting sites at Lake Fehér, near Szeged and Sándorfalva, or Büdös-szék, near Pusztaszer.

### Injuries of birds during collisions

It was documented several times (but not always) during surveys if the birds had visible and obvious injuries: broken wings were documented in case of Grey Heron (1 individual), Eurasian Spoonbill *(Platalea leucorodia)* (3 individuals), Common Cranes (2 individuals) while broken neck were noted in case of Eurasian Spoonbill (1 individual) and Black-headed Gull (1 individual).

Birds that collided with middle-voltage power lines might have suffered electrocution as well, if their body size were large (body length: ≥ 93.5 cm; wingspan: ≥ 155 cm). This phenomenon was documented in case of Mute Swan (1 individual), Great White Egret (1 individual), Grey Heron (2 individuals) and Common Cranes (4 individuals).

Birds may have survived their collision accidents but they could have broken their wings or suffered a concussion. As far as we know, two Spoonbills, 18 Common Cranes, one Lapwing, one Ruff *(Calidris pugnax)* and one Wood Sandpiper *(Tringa glareola)* were found alive. Eleven Common Cranes were set free from Szeged Zoo after they recovered from a collision accident with power lines. At the same time, two young Spoonbills had serious injuries such as broken wing bones and it was not possible to set them free.

### Conservation status of collided birds

23 strictly protected species (36.5%), 34 protected species (54.0%), one not protected species (1.6%) and five game species (7.9%) were found under electric cables due to collision accidents *(Appendix 1)*.

60 specimens of strictly protected species (11.7%), 406 individuals of protected species (78.8%), two individuals of not protected species (0.4%) and 47 specimens of game species (9.1%) were reported from under electric cables as victims of collision accidents.

## Discussion

Our results shed new light on the problem of birds' collision with overhead power lines in Hungary. We collected data on 519 individuals of 63 species, which indicates that collision with power lines have serious impact on bird populations in Hungary.

We demonstrated that the vast majority of birds that collide with wires are protected or strictly protected. These accidents with overhead electric and railway cables are documented in case of some strictly protected species in Hungary, for example in case of Black Stork *(Ciconia nigra)* (B. Kalocsa pers. comm.), Great Bustard *(Otis tarda)* (Vadász & Lóránt 2014), Eastern Imperial Eagle *(Aquila heliaca)* (Horváth *et al.* 2011), Short-toed Snake-eagle *(Circaetus gallicus)* (Molnár & Andrési 2019) and Saker Falcon (Bagyura *et al.* 2018) as well. Several studies showed that the mortality during collision with power lines may had a significant impact on population level (Bernardino *et al.* 2018, D'Amico *et al.* 2018), which is important for conservation efforts to mitigate the effect of overhead wires on protected and strictly protected species.

We demonstrated that waterbirds suffered remarkable losses due to collision with electric cables in our study area, including species with unfavourable conservation status and declining trends worldwide [e.g. Black-tailed Godwits *(Limosa limosa)*, Eurasian Curlews *(Numenius arquata)*] (www.iucnredlist.org), and species with dramatic decline in Hungary (e.g. Kentish Plover) (Pigniczki 2006). Waterbirds are one of the most affected species-group worldwide especially when these collision accidents are considered. These birds are regularly found at wetlands in large numbers, and wires overhanging these wetlands have a serious impact on their populations (Bevanger 1994, Quinn *et al.* 2011, Smith & Dwyer 2016).

There are several reasons why birds are more susceptible to these accidents, for example, bad visual conditions, morphological and behavioural characteristics of species (Quinn *et al.* 2011, Smith & Dwyer 2016, D'Amico *et al.* 2019, Molnár & Andrési 2019). Our preliminary results support that wing-loading proxy has large effect on the probability of collision accidents, and the most affected species are birds with high wing-loading proxy-values: species with heavy weight and relatively small wings (e.g. swans, geese, ducks) or birds with broad wings (e.g. herons, spoonbills, cranes); both biometrical characteristics result poor manoeuvrability, and higher risk for collision accidents (Quinn *et al.* 2011, Bernardino *et al.* 2018, D'Amico *et al.* 2019). Based on our preliminary results, it seems that species, which cover large distances during their everyday-movements between their foraging areas and breeding/roosting sites have a larger chance to collide with overhead lines, especially, if the sites are close to each other and birds fly between those areas in low altitude (Bernardino *et al.* 2018). Our preliminary results do not support the hypothesis that birds using pylons as nesting sites or sitting sites during their hunt may have a higher risk of collision. Generally, authors treat these kinds of behavioural characteristics as high risk factor for electrocution, rather than risk of collision (Bernardino *et al.* 2018, D'Amico *et al.* 2018).

We found evidence, that low-, middle- and high-voltage power lines are all responsible for the collision accidents of birds. We detected the most collision accidents of birds around high-voltage power lines. Most surveys were conducted around high-voltage power lines, however, it is important to note that those involved in the study did not carry out the same amount of searches around low-voltage power lines.

The number of birds that had a collision accident in our study area could be much larger than we have published in this paper. However, data collection was not done regularly and there were no exact notes on carcasses in many times, that is why we may have missed a huge amount of information on the number of individuals and species as well. Results are also influenced by detectability: a large number of individuals would be never detected, if they fall into water or reedbed, and small species are also difficult to find (Borner *et al.* 2017). Furthermore, many injured or dead birds could be collected by predators, in which case carcasses can never be found and never reported (Molnár & Andrési 2019).

It would be possible for the risk of collision to be stopped with underground cabling used instead of overhead wires (Bevanger 1994, Bernardino *et al.* 2018); this method should be applied especially in wetland habitats, because of the high number of victims and high number of protected and strictly protected species. We always recommend underground cabling in case of wetlands, if authorities give permission to carry out new line segments of electric wires. It is possible to mitigate the effect of overhead wires on birds using visual markers (Bevanger 1994, Bernardino *et al.* 2018), especially in case of high-voltage lines.

It is crucial to have a conflict map about birds' possible collision risk (Horváth & Demeter 2010, D'Amico *et al.* 2019). To create this conflict map, it is essential to collect data and information about distribution, morphological and behavioural characteristics of bird species, and about the conservation status of these species as well. This would enable scientists to create a priority rank of species (Horváth & Demeter 2010, D'Amico *et al.* 2019). We suggest adopting the formula of D'Amico *et al.* (2019) to create the priority rank of the species, but with some modifications: we think that the use of power lines by birds do not mean a larger risk for collision accidents (Bernardino *et al.* 2018, D'Amico *et al.* 2018), therefore, we recommend to exclude this from the ranking formula. Species that cover large distances regularly during their daily movements are at high risk (Bernardino *et al.* 2018), which makes it crucial that this behavioural characteristic is used in the ranking formula.

Our results show that a wide range of species could be found under electric wires. It is essential to understand which habitat characteristics and which type of wires have a large impact on collision accidents. It is also important to have good quality data on when collision accidents happen and to have information on the exact number of different species affected by collisions. The only way to have this data is to run a well-designed monitoring program. Tracking flight altitude of birds with GPS-technologies makes also possible to understand better the collision risk of birds with overhead wires. Research into this option is currently running including Spoonbills in Kiskunság National Park (Cs. Pigniczki unpublished data).

We believe that this paper will motivate professional and amateur ornithologists to scout for dangerous lines in Hungary and help the staff of national park directorates and electric companies to solve this problem, or to provide alternative solutions to mitigate the number of collision accidents of birds with overhead power lines.

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# Appendix

*Appendix 1.* List of collided species with overhead power lines; their conservation status in Hungary; the number of individuals found under different types of electric wires; the habitat preferency of species; wingspan (WS) measured in centimetres; weight (W) in grams; wing-loading proxy (WLP); information on regular, large distance movements of species (T) (0 – no regular large distance movement, 1 – regular, large distance movement); information on use of electric cables (U) (0 – no use, 1– use)

*1. függelék* Légvezetéknek ütközött fajok listája, természetvédelmi helyzete Magyarországon (not protected: nem védett; game species: vadászható faj; protected: védett; strictly protected: fokozottan védett), az egyes vezetéktípusok alatt megtalált egyedek száma, a fajok jellemző élőhelye, szárnyfesztávolsága (WS) centiméterben, tömege (W) grammban, szárnyterhelést helyettesítő értéke (WLP), a fajok rendszeres, nagy távolságú mozgására vonatkozó információ (T) (0 – nincs ilyen mozgás, 1 – van ilyen mozgás), vezetékhasználatra vonatkozó információ (U) (0 – nem használja a vezetéket, 1 – használja a vezetéket)

| Order/Species | Conservation status in Hungary | Type of power line | | | | Habitat | WS | W | WLP | T | U |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | High-v. | Middle-v. | Low-v. | Unknown | | | | | | |
| Unknown/ Ismeretlen | – | 3 | 0 | 0 | 0 | – | – | – | – | – | – |
| Galliformes | | | | | | | | | | | |
| *Phasianus colhicus* | game species | 2 | 0 | 0 | 0 | farmland | 80 | 1189.5 | 14.8688 | 0 | 0 |
| Anseriformes | | | | | | | | | | | |
| *Cygnus olor* | protected | 0 | 3 | 0 | 0 | wetland | 220 | 10800 | 49.0909 | 0 | 0 |
| *Anser albifrons* | game species | 0 | 1 | 0 | 0 | wetland-farmland | 147.5 | 2587.5 | 17.5424 | 1 | 0 |
| *Anser* sp. | game species | 1 | 0 | 0 | 0 | wetland-farmland | – | – | – | 1 | 0 |
| *Aythya ferina* | protected | 2 | 1 | 0 | 0 | wetland | 77 | 845.5 | 10.9805 | 0 | 0 |
| *Aythya nyroca* | strictly protected | 2 | 0 | 0 | 0 | wetland | 65 | 597.75 | 9.1962 | 0 | 0 |
| *Spatula querquedula* | strictly protected | 2 | 0 | 0 | 0 | wetland | 63.5 | 401.25 | 6.3189 | 0 | 0 |
| *Spatula clypeata* | protected | 1 | 0 | 0 | 0 | wetland | 77.5 | 630 | 8.1290 | 0 | 0 |
| *Anas platyrhynchos* | game species | 33 | 5 | 0 | 0 | wetland-farmland | 87.5 | 1181.25 | 13.5000 | 1 | 0 |
| *Anas crecca* | protected | 2 | 0 | 0 | 0 | wetland | 61 | 325 | 5.3279 | 0 | 0 |
| Podicipediformes | | | | | | | | | | | |
| *Tachybaptus ruficollis* | protected | 1 | 1 | 0 | 0 | wetland | 42.5 | 183 | 4.3059 | 0 | 0 |
| *Podiceps cristatus* | protected | 2 | 2 | 0 | 0 | wetland | 87.5 | 1043 | 11.9200 | 0 | 0 |
| *Podiceps nigricollis* | strictly protected | 0 | 1 | 0 | 0 | wetland | 50.5 | 357.5 | 7.0792 | 0 | 0 |

| **Order/Species** | **Conservation status in Hungary** | **Type of power line** | | | | **Habitat** | **WS** | **W** | **WLP** | **T** | **U** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **High-v.** | **Middle-v.** | **Low-v.** | **Unknown** | | | | | | |
| Columbiformes | | | | | | | | | | | |
| *Columba livia f. domestica* | not protected | 0 | 2 | 0 | 0 | farmland | 69.5 | 300 | 4.3165 | 0 | 1 |
| *Streptopelia turtur* | protected | 0 | 1 | 0 | 0 | woodland-farmland | 50 | 134.5 | 2.6900 | 0 | 1 |
| *Streptopelia decaocto* | game species | 1 | 0 | 0 | 0 | farmland | 51 | 179.5 | 3.5196 | 0 | 1 |
| Gruiformes | | | | | | | | | | | |
| *Rallus aquaticus* | protected | 1 | 1 | 1 | 0 | wetland | 41.5 | 122.5 | 2.9518 | 0 | 0 |
| *Crex crex* | strictly protected | 1 | 0 | 0 | 0 | wetland | 47.5 | 158.75 | 3.3421 | 0 | 0 |
| *Porzana porzana* | protected | 2 | 0 | 0 | 0 | wetland | 39.5 | 102 | 2.5823 | 0 | 0 |
| *Gallinula chloropus* | protected | 3 | 1 | 0 | 0 | wetland | 52.5 | 319.25 | 6.0810 | 0 | 0 |
| *Fulica atra* | game species | 4 | 0 | 0 | 0 | wetland | 75 | 892.5 | 11.9000 | 0 | 0 |
| *Grus grus* | protected | 159 | 31 | 0 | 0 | wetland-farmland | 232.5 | 5400 | 23.2258 | 1 | 0 |
| Pelecaniformes | | | | | | | | | | | |
| *Platalea leucorodia* | strictly protected | 3 | 4 | 0 | 0 | wetland | 125 | 1545 | 12.3600 | 1 | 0 |
| *Plegadis falcinellus* | strictly protected | 0 | 1 | 0 | 0 | wetland | 87.5 | 595 | 6.8000 | 1 | 0 |
| *Botaurus stellaris* | strictly protected | 0 | 1 | 0 | 0 | wetland | 130 | 1152.5 | 8.8654 | 1 | 0 |
| *Nycticorax nycticorax* | strictly protected | 1 | 0 | 0 | 0 | wetland | 108.5 | 689 | 6.3502 | 1 | 0 |
| *Ardeola ralloides* | strictly prtotected | 4 | 3 | 0 | 0 | wetland | 86 | 300 | 3.4884 | 1 | 0 |
| *Ardea cinerea* | protected | 4 | 10 | 0 | 1 | wetland | 185 | 1546.5 | 8.3595 | 1 | 0 |
| *Ardea purpurea* | strictly protected | 4 | 0 | 0 | 0 | wetland | 135 | 873.75 | 6.4722 | 1 | 0 |
| *Ardea cinerea/ purpurea* | – | 1 | 0 | 0 | 0 | wetland | – | – | – | 1 | 0 |
| *Ardea alba* | strictly protected | 5 | 6 | 0 | 0 | wetland | 155 | 1200 | 7.7419 | 1 | 0 |
| *Egretta garzetta* | strictly protected | 5 | 1 | 0 | 0 | wetland | 95 | 495 | 5.2105 | 1 | 0 |
| Suliformes | | | | | | | | | | | |
| *Microcarbo pygmaeus* | strictly protected | 0 | 1 | 0 | 0 | wetland | 85 | 717.5 | 8.4412 | 1 | 0 |

| Order/Species | Conservation status in Hungary | Type of power line | | | | Habitat | WS | W | WLP | T | U |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | High-v. | Middle-v. | Low-v. | Unknown | | | | | | |
| *Phalacrocorax carbo* | protected | 2 | 0 | 0 | 0 | wetland | 145 | 2310 | 15.9310 | 1 | 0 |
| Charadriiformes | | | | | | | | | | | |
| *Recurvirostra avosetta* | strictly protected | 0 | 1 | 0 | 0 | wetland | 73.5 | 296 | 4.0272 | 0 | 0 |
| *Charadrius alexandrinus* | strictly protected | 0 | 0 | 0 | 1 | wetland | 43.5 | 44 | 1.0115 | 0 | 0 |
| *Vanellus vanellus* | protected | 17 | 1 | 0 | 0 | wetland-farmland | 84.5 | 229 | 2.7101 | 1 | 0 |
| *Numenius phaeopus* | protected | 1 | 0 | 0 | 0 | wetland-farmland | 82.5 | 433.25 | 5.2515 | 1 | 0 |
| *Numenius arquata* | strictly protected | 2 | 0 | 0 | 0 | wetland-farmland | 90 | 813.75 | 9.0417 | 1 | 0 |
| *Limosa limosa* | strictly protected | 2 | 1 | 0 | 0 | wetland | 76 | 336 | 4.4211 | 0 | 0 |
| *Calidris pugnax* | protected | 1 | 0 | 0 | 0 | wetland | 53 | 156 | 2.9434 | 0 | 0 |
| *Calidris alba* | protected | 0 | 1 | 0 | 0 | wetland | 37 | 75 | 2.0270 | 0 | 0 |
| *Gallinago gallinago* | strictly protected | 3 | 0 | 0 | 0 | wetland | 45.5 | 126.5 | 2.7802 | 0 | 0 |
| *Tringa erythropus* | protected | 0 | 1 | 0 | 0 | wetland | 64 | 163.5 | 2.5547 | 0 | 0 |
| *Tringa totanus* | strictly protected | 1 | 0 | 0 | 0 | wetland | 62.5 | 120 | 1.9200 | 0 | 0 |
| *Tringa glareola* | protected | 4 | 0 | 0 | 0 | wetland | 55.5 | 66 | 1.1892 | 0 | 0 |
| *Larus ridibundus* | protected | 104 | 10 | 0 | 0 | wetland-farmland | 100.5 | 260 | 2.5871 | 1 | 0 |
| *Larus michahellis* | protected | 0 | 1 | 0 | 0 | wetland-farmland | 130 | 1010 | 7.7692 | 1 | 0 |
| *Larus cachinnans* | protected | 1 | 1 | 0 | 0 | wetland-farmland | 141 | 1090 | 7.7305 | 1 | 0 |
| *Larus michahellis/cachinnans* | protected | 5 | 0 | 0 | 0 | wetland-farmland | – | – | – | 1 | 0 |
| *Hydroprogne caspia* | protected | 1 | 0 | 0 | 0 | wetland | 134.5 | 678 | 5.0409 | 0 | 0 |
| *Chlidonias hybrida* | strictly protected | 0 | 1 | 0 | 0 | wetland | 67 | 80.5 | 1.2015 | 1 | 0 |
| *Chlidonias niger* | strictly protected | 1 | 0 | 0 | 0 | wetland | 61 | 73 | 1.1967 | 1 | 0 |
| Strigiformes | | | | | | | | | | | |
| *Tyto alba* | strictly protected | 1 | 0 | 0 | 0 | farmland | 89 | 321 | 3.6067 | 0 | 1 |

| Order/Species | Conservation status in Hungary | Type of power line | | | | Habitat | WS | W | WLP | T | U |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | High-v. | Middle-v. | Low-v. | Unknown | | | | | | |
| Accipitriformes | | | | | | | | | | | |
| *Circus aeruginosus* | protected | 1 | 0 | 0 | 0 | wetland-farmland | 130 | 658.75 | 5.0673 | 0 | 0 |
| Passeriformes | | | | | | | | | | | |
| *Corvus frugilegus* | protected | 3 | 1 | 0 | 0 | farmland | 90 | 448 | 4.9778 | 1 | 1 |
| *Alauda arvensis* | protected | 1 | 0 | 0 | 0 | farmland | 33 | 37.75 | 1.1439 | 0 | 0 |
| *Galerida cristata* | protected | 1 | 0 | 0 | 0 | farmland | 33.5 | 42.5 | 1.2687 | 0 | 0 |
| *Acrocephalus schoenobaenus* | protected | 4 | 0 | 0 | 0 | wetland | 19 | 13 | 0.6842 | 0 | 1 |
| *Acrocephalus scirpaceus* | protected | 1 | 0 | 0 | 0 | wetland | 19 | 13.85 | 0.7289 | 0 | 1 |
| *Hirundo rustica* | protected | 1 | 0 | 0 | 0 | farmland | 33 | 20 | 0.6061 | 1 | 1 |
| *Riparia riparia* | protected | 1 | 0 | 0 | 0 | wetland-farmland | 27.5 | 15.25 | 0.5545 | 1 | 1 |
| *Sturnus vulgaris* | protected | 3 | 6 | 0 | 0 | farmland-woodland | 39.5 | 77.5 | 1.9620 | 1 | 1 |
| *Muscicapa striata* | protected | 1 | 0 | 0 | 0 | woodland | 24.5 | 16.55 | 0.6755 | 0 | 1 |
| *Erithacus rubecula* | protected | 1 | 0 | 0 | 0 | woodland | 21 | 19.5 | 0.9286 | 0 | 0 |
| *Luscinia luscinia* | strictly protected | 0 | 0 | 1 | 0 | woodland | 25 | 25.5 | 1.0200 | 0 | 0 |