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Testing different isolation distances in woodpecker territory mapping in Central Hungary

Csaba Vadász[1,2,3], Gábor Kocsán[1] & Gábor Ónodi[4]*

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Abstract Woodpeckers as cavity excavators are crucial in forest ecosystems, therefore, it is important to study their ecological needs, specifically at the territory scale, using mapping methodologies, of which there are uncertainties considering detection probabilities and the distances of the territory centres in different species and habitats. We studied the effects of the number of visits and isolation distance on detected woodpecker territories in the 1,000 ha forest mosaic of the Peszér forest in Central Hungary. We made territory mapping in 2020 along existing trails and forest roads on the present woodpecker species as Black, Eurasian Green, Great Spotted, Middle Spotted, Lesser Spotted Woodpecker and Eurasian Wryneck. We found a very low detection probability for single territories during one visit, while with the increasing number of visits it is more unlikely to overlook territories. Considering the isolation distances, by lowering the distance, more territories can be registered, which suggests that researchers should take great care choosing the proper distance for a given species whilst avoiding the over- or underestimation of territories.

This paper has an actuality as BirdLife Hungary announced the Eurasian Green Woodpecker as the Bird of the Year in 2022, for drawing attention to this species' habitat preferences and conservation.

Keywords: woodpecker ecology, territory mapping, transect surveys, isolation distances, detection probabilities

Összefoglalás A harkályok, mint odúkészítő fajok meghatározó szerepet töltenek be az erdei ökoszisztémákban, így ökológiai vizsgálataik természetvédelmi szempontból kiemelt jelentőséggel bírnak. Fontos élőhely preferenciájuk, azon belül territórium használatuk tanulmányozása különböző térképezési módszerekkel. Ezek esetében a territóriumok ráfordítás-függő észlelési valószínűsége, illetve a territórium központok távolságának tekintetében a különböző fajoknál és élőhelyeknél az irodalomban tapasztalhatók bizonytalanságok. Az 1000 hektáros Natura 2000-es, közép-magyarországi Peszéri erdő mozaikjában vizsgáltuk a bejárások számának és a territóriumok izolációs távolságának a territóriumok észlelésére gyakorolt hatását. A vizsgált területen 2020 tavaszán a meglévő ösvények és erdei utak mentén végeztünk territórium térképezést az előforduló harkályfajokon, mint a fekete harkály, a zöld küllő, a nagy, közép, kis fakopáncs és a nyaktekercs. A territóriumok észlelésének egy bejárás során nagyon alacsony a valószínűsége, ám a bejárások számát növelve a territóriumok nem észlelésének valószínűsége lecsökken. Az izolációs távolság csökkentésével több terület regisztrálható, ez azt sugallja, hogy a kutatóknak nagy gondot kell fordítani az adott faj megfelelő izolációs távolságának megválasztására, elkerülve a területek túl- vagy alulbecslését.

Ennek a cikknek az aktualitása, hogy a Magyar Madártani és Természetvédelmi Egyesület a zöld küllőt jelölte ki a 2022-es év madarának, rávilágítva annak élőhely használatára és természetvédelmi jelentőségére.

Kulcsszavak: harkályok ökológiája, territórium térképezés, transzekt adatgyűjtések, izolációs távolságok, észlelési valószínűség

[1] *Kiskunság National Park, 6000 Kecskemét, Liszt Ferenc utca 19., Hungary*
[2] *Hungarian University of Agriculture and Life Sciences, 2100 Gödöllő, Páter Károly utca 1., Hungary*
[3] *University of Sopron, Faculty of Forestry, 9400 Sopron, Bajcsy-Zsilinszky utca 4., Hungary*
[4] *National Laboratory for Water Science and Water Security, Balaton Limnological Research Institute, 8237 Tihany, Klebelsberg Kuno utca 3., Hungary*
** corresponding author, e-mail: onodi.gabor@blki.hu*

Introduction

Woodpeckers, as major cavity-excavator species have a crucial role in forest ecosystems (Robles & Pasinelli 2014). These species provide nesting opportunities for numerous cavity-dwelling species (Bai *et al.* 2005). Woodpeckers can be examples of umbrella species since, through their protection, it is possible to support other species (Roberge *et al.* 2008, Edman *et al.* 2011, Lammertink 2014, Robles & Pasinelli 2014). For these conservation purposes, it is important to study their ecological needs, specifically their use of available space at the territory scale.

By definition, the territory is "any defended area" that can be used for years, and can be determined by the positions of individuals, showing territorial behaviour, e.g. territorial calls and drumming in woodpeckers (Tomasevic & Marzluff 2018a). In general, territory mapping is a group of methods, dedicated to scaling large areas in a reasonable time counting the individuals and identifying their geographical positions, measuring their abundance and having a deeper knowledge of the habitat utilization of the focal species. In the process, researchers can cover whole areas of forests in a systematic manner (Weißmair & Pühringer 2015), move on transects (Kumar *et al.* 2014, Gerdzhikov *et al.* 2018), visit only designated plots (Gjerde *et al.* 2005). The number of visits per season can also differ from study to study from only one visit (Gerdzhikov *et al.* 2018) to three (Verschuyl *et al.* 2021) or more (Kopij 2017, Miller *et al.* 2018). With the increasing number of visits, the probability to record all existing territories also increases, as there are studies with eight visits or more (Koivula & Schmiegelow 2007). To increase the chance of finding the maximum number of territories of the focal species, one can use playback recordings in a systematic design, using playback stations at equal distances and recording the presence of territories through the mapping bouts (Gjerde *et al.* 2005, Stachura-Skierczyńska & Kosiński 2014, Figarski 2017, Verschuyl *et al.* 2021). According to Kosiński *et al.* (2004), with the playback method, up to 80% of all territories can be found during one visit. However, playbacks can also make individuals erroneously crowded, and modify their distribution (Bocca *et al.* 2007).

In the planning of territory mapping, one should consider carefully the particular scientific questions, the characteristics of the terrain, the manpower that can be used and the time that can be afforded by the observers.

In territory mapping, researchers on the field register the date and even the number of the given visit in the row and take great care of the direction of movements of the birds, to minimise the chance of double counts. Territories can be delimited by e.g. the minimum convex polygon method, drawing a convex polygon around a cluster of encounters of a particular bird species, made in different mapping bouts, by excluding any other encounters from bouts that have one included point in the cluster (Remeš 2003, Duca *et al.* 2006). In addition, a territory can be regarded as occupied when two independent observations of at least one territorial bird in a limited area were made during the same breeding period (Tjernberg *et al.* 1993, Salvati *et al.* 2001). The size of this limited area as well as the minimum distance between individuals of different territories is still not well-defined in the literature. It would be helpful to use particular isolation distances, and only consider points in the same territory, if their pairwise distance is lesser than the chosen isolation distance.

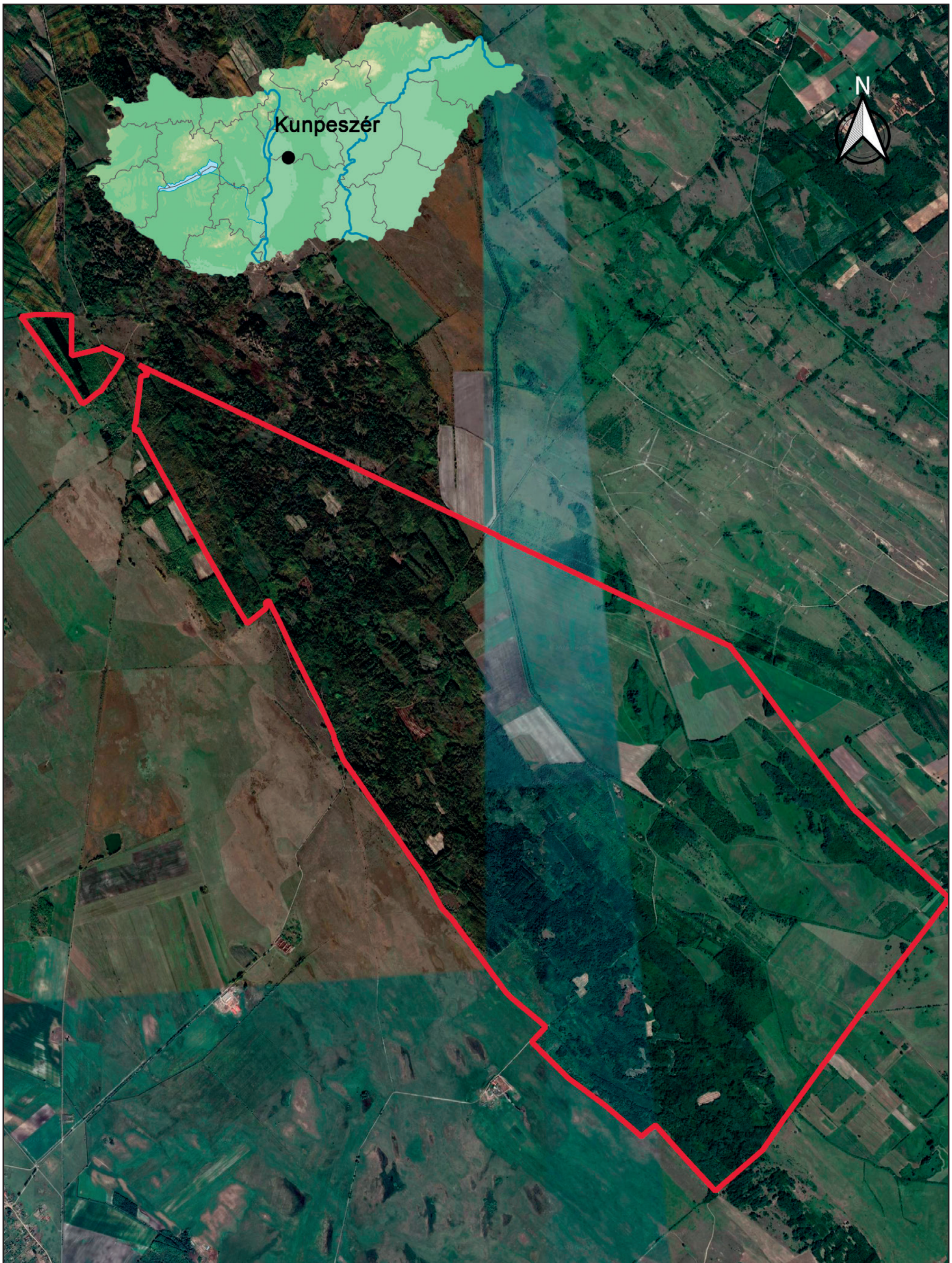

Figure 1. Aerial photograph of the study area with its geographical position in Hungary
1. ábra A vizsgált terület légifotója és földrajzi helyzete Magyarországon

In this paper, we tested how different isolation distances can affect the number of territories in various woodpecker species, with special considerations on the number of visits and detection probabilities. In this way, we aimed to quantify the comparability of the results of surveys with different efforts allocated. Through these efforts, we aimed to share solutions/suggestions on processing/interpreting data on woodpecker territories.

Material and Methods

Study area

The Peszér Forest (HUKN20002), located in Central Hungary, is a part of the Natura 2000 network, covering approximately 1,628 hectares. The total cover of forests is 1,080 hectares, while the rest of the area is covered with high conservation value grasslands. In addition to the forest stands dominated by alien tree species representing low conservation value, the study area hosts some semi-natural forest stands representing unique conservation value. The most typical of the latter is the Euro-Siberian forest steppes dominated by *Quercus robur*, which are found in a mosaic distribution (covering a total of approx. 200 ha), the mixed hardwood forests characterised by the dominant *Fraxinus angustifolia* mixing with *Quercus robur* and *Ulmus minor* (12 hectares) and the Pannonian sand thickets dominated by *Populus alba* and *Juniperus communis* (approx. 85 hectares). Also, approx. 300 hectares of uncharacteristic softwoods dominated by *Populus alba* are present.

Data collection

Data collection was carried out from 10 February to 20 May 2020, for a total of 47 days with favourable weather (rain- and windless periods). Acoustic and visual detection of woodpeckers were applied. The position and behaviour (i.e. drumming, acoustic territory defending behaviour other than drumming, feeding, flying by) of all observed specimens were recorded in ArcPad software running on a handheld device with a built-in GPS receiver.

The census routes covered all the outer forest edges and all the accessible roads and paths inside the forest, summing up to 76.9 kilometres. Due to the overall length of census routes, six census routes were assigned, each being censused at least six times throughout the data collection period (on average 7.9 times). Despite the relatively dense network of inner roads, about 40% of the habitat patches inside the forest were located more than 200 m from the nearest access route. Due to the limits of acoustic detection, it was not possible to survey the territories located there. Accordingly, the number of territories detected/calculated can be considered as a minimum number.

Data analysis

Due to the lack of individual marking (e.g. colour-ringing, attaching radio transmitters), it was not possible to identify individuals performing territorial behaviour. To locate territories and to determine the number of those, the distance between the recorded position of individuals exhibiting territorial behaviour was taken into account. Hereinafter, the distance above which two observations were considered to belong to different territories is referred to as the isolation distance. The number of territories was calculated for isolation distances of 100, 200, 300 and 500 m. Only observations of individuals performing territorial behaviour were included in this analysis.

For calculating the distance between two points, the "Near Analysis" of ArcMap was run. In case more than two points were located close to each other (pairwise closer than the isolation distance), then all these points were considered to belong to the same territory.

Results and Discussion

During the data collection period, 238 woodpecker occurrences were recorded, and 130 of them showed territorial behaviour *(Table 1)*. The average number (± standard deviation) of observations of individuals performing territorial behaviour belonging to the same territory calculated for different isolation distances in the most visited, long transects are shown in *Table 2*. Comparing the average number of observations considering particular woodpecker species and isolation distances with the average number of censuses (7.9) it can be concluded that woodpecker territories can remain undetected during most field visits, as each visit can be regarded as an imperfect registration, where there is a ratio to record a given territory in a single visit (Bibby *et al.* 2000). According to Bibby *et al.* 2000, to confirm a territory, one needs at least two observations for a particular territory in eight or fewer visits, while in nine or more visits, three observations are required in a given area. Although the simultaneous observation of two individuals close to each other can help to find the boundaries between territories, without such encounters, the maximum distance of

Table 1. Number of territories of the different species in different isolation distances

1. táblázat A különböző fajok territóriumai az egyes izolációs távolságokon, a territoriális madarak, illetve az összes észlelés száma. A fajok fentről lefelé: fekete harkály, nagy, közép, kis fakopáncs, zöld küllő, nyaktekercs

Species	**No. of territories calculated for different isolation distances**				**Number of records of specimens performing territorial behaviour**	**Total number of records**
	100 m	200 m	300 m	500 m		
Black Woodpecker	23	20	18	15	29	52
Great Spotted Woodpecker	43	28	22	16	52	87
Middle Spotted Woodpecker	19	16	13	9	19	52
Lesser Spotted Woodpecker	7	7	5	4	7	24
Eurasian Green Woodpecker	12	12	10	9	12	12
Eurasian Wryneck	10	10	8	6	11	11

Table 2. The average number (± standard deviation) of observations of individuals performing territorial behaviour belonging to the same territory was calculated for different isolation distances in the most visited, long transects. In these parts, no Eurasian Wrynecks were found

2. táblázat Az adott territóriumokhoz köthető észlelések átlaga és szórása a különböző izolációs távolságokon, a legtöbbször bejárt, hosszú transzekteken. Ezeken a helyszíneken nyaktekercseket nem figyeltünk meg. A fajok fentről lefelé: fekete harkály, nagy, közép, kis fakopáncs, zöld küllő

Species	**Isolation distances**			
	100 m	200 m	300 m	500 m
Black Woodpecker	1.10 ± 0.32	1.22 ± 0.67	1.38 ± 0.74	1.67 ± 0.82
Great Spotted Woodpecker	1.06 ± 0.24	1.36 ± 0.50	1.44 ± 0.53	1.71 ± 0.76
Middle Spotted Woodpecker	1.00 ± 0.00	1.36 ± 0.92	1.88 ± 1.36	2.80 ± 1.30
Eurasian Green Woodpecker	1.13 ± 0.35	1.14 ± 0.38	1.33 ± 0.52	1.33 ± 0.52

observations from different visits for one single territory is still undefined (Gottschalk & Huettmann 2011). In this regard, Pakkala and coworkers used a 500 m isolation distance to distinguish between Three-toed woodpecker territories (Pakkala *et al.* 2002). Also, due to this low detection probability, it is not likely that we can draw maps with expressed spatial aggregation of observations of territorial individuals which could result in unambiguous separation of territories applying the traditional transect method having been used by us.

With decreasing isolation distance from 500 m to 100 m (the extremes set in our calculations), the calculated number of territories of woodpecker species increased by 53.3%, 168.8%, 111.1%, 75.0%, 33.3% and 66.7% in the case of Black Woodpecker *(Dryocopus martius)*, Great Spotted Woodpecker *(Dendrocopos major)*, Middle Spotted Woodpecker *(Dendrocoptes medius)*, Lesser Spotted Woodpecker *(Dryobates minor)*, Eurasian Green Woodpecker *(Picus viridis)* and Eurasian Wryneck *(Jynx torquilla)*, respectively. Due to a lack of individual marking, it was not possible to directly separate territories, therefore, we were not able to determine the exact number of territories.

The estimated number of territories in our study was 15–23, 16–43, 9–19, 4–7, 9–12 and 6–10 in the case of Black Woodpecker, Great Spotted Woodpecker, Middle Spotted Woodpecker, Lesser Spotted Woodpecker, Eurasian Green Woodpecker and Eurasian Wryneck, respectively. Applying these derived data, the estimated territory density (number of territories per 1,000 ha) was 13.9–21.3, 14.8–39.8, 8.3–17.6, 3.7–6.5, 8.3–11.1 and 5.6–9.3, respectively. The densities of Great Spotted and Lesser Spotted Woodpeckers were nested in the intervals from the literature, while the densities of Black, Eurasian Green Woodpeckers, and Eurasian Wryneck were higher compared to literature intervals, besides, we found lower densities in Middle Spotted Woodpeckers (del Hoyo *et al.* 2002). Given the highly mosaical stand structure of the study site with numerous non-native plantations in the landscape, these experienced intervals can be considered reasonable, as territory size can be influenced by habitat characteristics e.g. stand and landscape structure (Tomasevic & Marzluff 2018b).

Table 3. The average probability of detecting a woodpecker territory during one visit was calculated for different isolation distances in the most visited, long transects. In these parts, no Eurasian Wrynecks were found

3. táblázat Egy territórium detektálási valószínűsége különböző fajoknál és izolációs távolságoknál a legtöbbször bejárt, hosszú transzekteken. Ezeken a helyszíneken nyaktekercseket nem figyeltünk meg. A fajok fentről lefelé: fekete harkály, nagy, közép, kis fakopáncs, zöld küllő

Species	**Isolation distances**			
	100 m	200 m	300 m	500 m
Black Woodpecker	6.88%	7.64%	8.59%	10.42%
Great Spotted Woodpecker	6.62%	8.52%	9.03%	10.71%
Middle Spotted Woodpecker	6.25%	8.52%	11.72%	17.50%
Eurasian Green Woodpecker	7.03%	7.14%	8.33%	8.33%

Alongside the most frequently visited, long transects (in total, 16 visits per transect throughout the whole census period), the average probability of detecting a woodpecker territory during one visit is summed up in *Table 3*.

This low detection probability (ranging between 6.25% and 17.50% across species and isolation distances) can be originated from the characteristics of the transect method. These experienced detection probabilities are way lower than the ones Bibby *et al.* (2000) published. According to them, the chance of registering a particular territory during one visit is between 0.25 and 0.33. Walking with 4 km/h speed and a maximum detection distance hypothesised to be 200 m, the surveyor spends approx. 6 minutes in the vicinity of a woodpecker territory. Other methods (e.g. point transect surveys, playing species-specific sounds) may provide much better detection probabilities. Although, because of the higher amount of time spent in the vicinity of a territory, these methods can be used for mapping territories in smaller areas or larger areas, by using a higher number of observers (Kosiński *et al.* 2004). Considering the low detection probability of woodpecker territories during one visit when applying the transect method, it can lead to serious underestimation of the number of territories with low (2–5) repetition of visits (Bibby *et al.* 2000).

Our results suggest that the number and size of territories can fairly vary in the case of different woodpecker species depending on the number of visits and the isolation distances chosen. With this in mind, researchers should take into consideration choosing parameters with great care.

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The acoustic communication of the Eurasian Green Woodpecker *(Picus viridis)*

Kyle Turner[1*], Gerard Gorman[2] & Danny Alder[3]

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Abstract Woodpeckers, having a fairly well-defined range of acoustic signals, offer a valuable opportunity to link acoustic repertoires to behavioural observations. Instrumental and vocal sounds from more than 70 individual Eurasian Green Woodpeckers were analysed using 305 sound recordings. Eighteen separate acoustic signals are described, together with field observations of associated behaviour. Sixteen are illustrated by clear spectrograms supporting the phonetic descriptions. With one exception, calls consisted of repeated elements, with the first element often containing varying degrees of emphasis. Variation within call types, especially the advertising call, differentiated individuals and their motivation and did not appear to be regionally significant. Instrumental signals, while soft and easily overlooked, constituted an important intimate communication between breeding pairs.

Keywords: woodpeckers, instrumental sounds, vocal sounds, signal characteristics, call types, drumming, tapping

Összefoglalás A harkályfélék jól elkülöníthető akusztikus jelzései lehetővé teszik azok viselkedési megfigyelésekkel való összekötéseit. 70 zöld küllő egyedtől származó, összesen 305 hangfelvételen található dobolási és vokális hangokat elemeztünk. 18 hangtípust írtunk le a terepi vizuális megfigyelésekkel párosítva, melyek közül 16-hoz spektrografikus elemzést is közreadunk. Egy kivételével a hangjelzések ismételt elemekből álltak. Az egyes hangtípusok varianciáját az egyedi eltérések, a belső állapot is meghatározták, de lényeges földrajzi hatás nem mutatható ki. A tanulmány felhívja a figyelmet arra, hogy a külső felületen keltett halkabb hangok a fészkelő párok egymás közötti kommunikációjában lehetnek fontosak.

Kulcsszavak: harkályfélék, külső felületen képzett hangok, vokális hangok, hangjellemzők, hangtípusok, dobolás, kopogás

[1] *Independent Bio-acoustics Researcher, St. Andrews Farm, Woodbridge Lane, Bedchester, Shaftesbury, Dorset, SP7 0BF, United Kingdom*
[2] *Independent Picid Researcher, Hungarian Woodpecker Working Group, MME Központ, 1121, Budapest, Költő utca 21., Hungary*
[3] *Independent Ecologist, 12 Elm Close, Motcombe, Shaftesbury, Dorset, SP7 9HN, United Kingdom*
** corresponding author, e-mail: kyleturner@orange.fr*

Introduction

The global distribution of Eurasian Green Woodpecker *(Picus viridis)* falls entirely within the Old World and mostly within the Western Palearctic region. Around 95% of the total population is considered to be in Europe (BirdLife International 2020). Populations are resident, non-migratory and usually sedentary, although some short-range post-breeding dispersal of juveniles takes place (Glutz von Blotzheim & Bauer 1994, Winkler *et al.* 1995, Gorman 2004, 2020).

The species is polytypic, with three subspecies generally recognised: *viridis* which is found in Britain, southern Scandinavia, continental Europe and western Russia; *karelini* in

Italy, the southern Balkans, the Caucasus and eastwards to Turkmenistan; and *innominatus*, which is occurs solely in the Zagros Mountains in Iran and Iraq (Gorman 2014, 2020). All of the birds which were recorded for this paper were the nominate *viridis* subspecies. Eurasian Green Woodpeckers inhabit a variety of sparsely wooded habitats across this range, which covers three eco-climatic regions: the temperate, Mediterranean and boreal zones. Typical breeding habitats occupied include open forests and woodlands; riparian woods; hedgerows with large trees; parkland; orchards and large gardens. Deciduous trees are habitually utilised, but in some regions mixed deciduous-coniferous woodlands are occupied. Closed forests are avoided. In all areas a home-range requires grasslands adjacent to the breeding territory where birds can forage for terrestrial ants (Alder & Marsden 2010). In Europe, both lowlands and uplands, to around 2,000 m, only occasionally higher, are inhabited (Gorman 2020). Although there have been declines locally, often owing to grassland and/or wooded habitat degradation, the overall trends for this species are positive and it is not considered to be threatened. In the IUCN Red List of Threatened Species, Eurasian Green Woodpecker is classified as Least Concern (BirdLife International 2016).

To date, the most detailed study of the voice of the Eurasian Green Woodpecker was carried out in the 1950s and 1960s and was summarised in a later publication which described six calls and two instrumental signals (Blume 1955, 1961, 1996). This study, together with other historical observations, formed the most comprehensive, contemporary account available (Cramp 1985) in which vocal signals were found to be the same and used equally by both sexes throughout the year, while tapping and drumming were rare. Another account featured eight calls and two instrumental signals and described the ‘laughing’ call as the most familiar and easily identifiable of the species (Glutz von Blotzheim & Bauer 1994).

Instrumental signals

Drumming by woodpeckers consists of a rapid, repetitive series of strikes with the bill on a substrate and is distinct from the mechanical sounds produced during foraging or cavity excavation (Pynnönen 1939). When performed loudly and in series it is a unique method of communicating information about ownership of suitable breeding sites (Winkler & Short 1978) and serves to establish and maintain the breeding pair (Gorman 2004, Tremain *et al.* 2008). As a long-distance signal it transmits this information to territorial neighbours and potential rivals. By contrast, soft drumming is used by some species close to potential nest holes (Florentin *et al.* 2017) and in Middle Spotted Woodpecker *(Dendrocoptes medius)* appears to signal a motivation for breeding (Turner 2020). Tapping, when performed in discrete bursts of more or less equally spaced strikes is termed ‘demonstrative tapping’ (Blume 1996) and acts as a signal, either to advertise a potential nest site or to encourage a change-over during excavation or incubation. It is always slower than drumming and does not form a ‘roll’, exceeding the minimum of 90 milliseconds between strikes which divides the two forms of instrumental communication (Florentin *et al.* 2016, Turner & Gorman 2021). However, according to Glutz von Blotzheim and Bauer (1994) instrumental signals have only negligible importance in communication between Eurasian Green Woodpeckers.

More recently, bioacoustics has become an important tool for biologists and conservationists, improving our understanding of the natural world (Shaw *et al.* 2021). High quality recordings of species coupled with detailed observations are especially valuable in revealing new behaviour (Dalziell & Welbergen 2016) and, with the emergence of digital technology, have increased the opportunities for ornithologists to contribute to science (Vella *et al.* 2021) providing scope to review and revise our understanding of vocalisations and auditory signals for a range of species including woodpeckers (Węgrzyn *et al.* 2021).

When describing the acoustic repertoire of any species an understanding of behavioural contexts can provide functional labels, although calls having more than one function (for example: contact and alarm) are problematic. While the potential for ambiguity inherent in phonetic descriptions limits their usefulness, when combined with clear spectrogram images they enable effective cross-referencing. In particular, a thorough knowledge of the repertoire of any species facilitates the evaluation of similarities in the form of calls and the situations in which they are used (Winkler & Short 1978).

Vocal signals

In common with other members of the Picidae, Eurasian Green Woodpecker vocalisations generally consist of a series of repeated elements and are not learned (Winkler *et al.* 1995). This includes what is sometimes referred to as the 'song' which, while it is largely restricted to the breeding season (Cramp 1985), lacks the complexity of rhythm and modulation more typical of species with learned songs (Catchpole & Slater 2008), and is more suitably described as an 'advertising call'. It is nevertheless more ritualized and idiosyncratic than its other calls, having a slightly more complex and variable structure which should enable individual recognition by partners and young (Glutz von Blotzheim & Bauer 1994). Its distinctive 'laughing' quality makes it one of the best-known and easily recognized bird sounds in Europe and one of the few to have its own colloquial name '*Yaffle'* in English. The individual elements of the advertising call visible on spectrograms are characterized by variables of shape, length, pitch, emphasis, speed of delivery and extent of repetition. In seven examples from Scandinavia, advertising calls were slower, decelerated more and were lower in pitch (Fauré 2018). Interestingly, although they are geographically separated, Eurasian Green Woodpeckers in Britain do not seem to call differently from birds in continental Europe. The only other European species with a similar advertising call is the closely related Iberian Green Woodpecker *(Picus sharpei)* which was formerly regarded as conspecific with *viridis*. In southwest France and northeast Spain, where the two species sometimes interbreed, it is often difficult to separate them in the field by their advertising calls since although *sharpei*'*s* consists of only one dominant frequency, *viridis* also has advertising calls with a single dominant frequency in addition to its more typical double version (Fauré 2013).

Other calls of *viridis* contain short and relatively simple elements which are usually repeated in irregular series (Gorman 2020). A written interpretation of calls ranging from '*Whurdles'* to '*Wickas'* contains detailed measurements of component characteristics but does not employ spectrograms, concentrating instead on comparisons across woodpeckers worldwide (Short 1982).

The aim of this study was to present an up-to-date account of the fullest range of acoustic signals employed by the Eurasian Green Woodpecker based on an extensive collection of high-quality sound recordings. Production of spectrograms from this source has enabled an objective analysis, providing statistical comparison of signal types to augment functional and phonetic descriptions.

Materials and Methods

Despite its relatively common status throughout Europe, the Eurasian Green Woodpecker is a difficult bird to approach. It is very vigilant and alert while foraging and quick to move away when approached, whether on open ground or in woodland. Fieldwork was carried out in the spring to establish areas with potential for nesting, where observations would be possible during recording sessions. Sound recordings were made of instrumental and vocal signals produced by the species in England, France and Hungary, mostly from within thirty metres. No 'play-back' of calls was used. The spectrograms used in this study were selected from 305 recordings of Eurasian Green Woodpecker extracted from the archive of the first author. The majority of recordings were made since 2001 and were obtained during the period from March to July, the most vocal period for this species. Before 2005, recordings were made on a Kenwood DMC-G7R Minidisc @ 44.1kHz/16bit (Atrac 4.5) using a pair of Sennheiser MKH 105 microphones in a 50×13cm parabolic reflector. Subsequently, a pair of DPA 4051 compact microphones were used into a Sound Devices 722 file recorder at 44.1kHz/16bit and since 2018 at 44.8kHz/24bit. Nest recordings were made with a pair of DPA 4060 miniature microphones mounted on an extendable roach pole. Searches were also made of the xeno-canto online bird sound resource (www.xenocanto.org) in order to increase the number of individuals available for analysis of drum-rolls(1) and the autumn call(2). The autumn call was thought to be a variant on the advertising call (Cramp 1985) and thus needed sufficient recorded and dated examples for comparisons to be made.

Following Short (1982), all recordings were analysed focusing on the repeated elements which formed each acoustic signal. Lengths were measured in milliseconds (ms) and pitch (fundamental frequency) in kilohertz (kHz) on Cool Edit Pro II software, processed as 32bit PCM wave files with Blackman Harris 256 resolution. For instrumental signals, we assessed duration, number of strikes, average interval between strikes and changes in tempo. The amplitude of strikes was measured by pulse train analysis using Avisoft SASlab lite. For vocal signals, we assessed the number of elements in a call, the number per second, changes in tempo and the length and pitch of individual elements. Spectrograms were produced using Raven Lite 2.0 (Cornell) with the coloured elements obtained using Gimp 2.10.28 photo editing software by selecting the stronger tones. Exploratory data analysis was carried out using Microsoft Excel 2016. When not sound-recorded, acoustic communications heard outside the breeding season were logged, together with observed behavioural contexts. In our paper, we use 'advertising call' in place of 'song'. Where averages are given, ranges are shown in parenthesis. 'Element' is used to define the individual components of calls. Phonetic descriptions are based on Cramp (1985).

Results

Instrumental signals

Three signal types performed by mechanically striking wood were recorded.

(a) ***Drumming (n=101)***

In an analysis of drum-rolls from 16 individual birds (4 from the online xeno-canto archive) the average for the duration of rolls was 1220 ms (276–2322), with an average of 24 strikes (5–45) per roll given at 20.7 strikes per second (17.5–26.1). Average intervals between strikes were 51 ms (42–61) with an overall deceleration from 46 ms (34–58) between the first two strikes to 64 ms (47–84) for the last two strikes *(Figure 1)*, excluding four rolls that petered out into tapping. Birds drummed without selecting acoustically resonant substrates and drum-rolls were

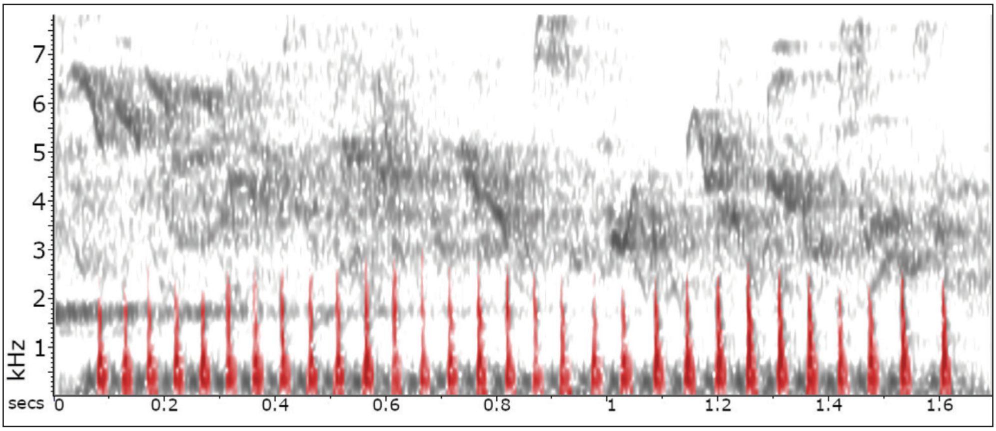

Figure 1. Drum-roll, showing a decelerating strike rate. Lot, France. 16.03.2002.
1. ábra Csökkenő tempójú dobolási sorozat. Lot, Franciaország. 2002.03.16.

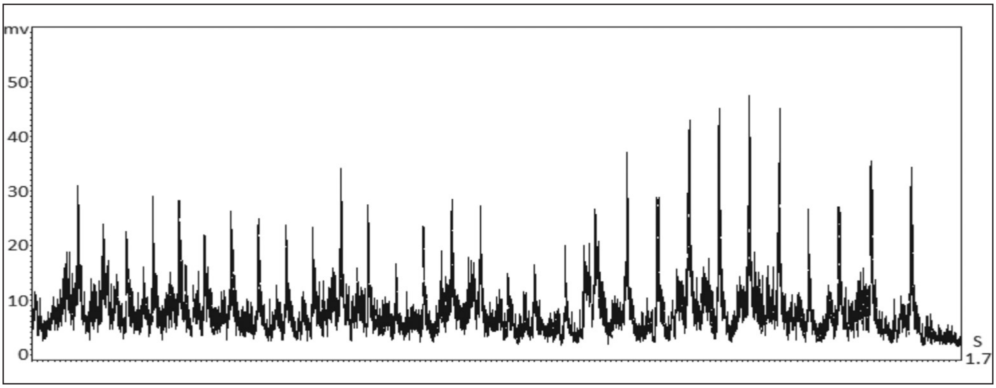

Figure 2. Pulse train analysis – the same drum-roll as *Figure 1*, showing the variable amplitude of strikes (measured in millivolts on the Y axis) throughout the roll
2. ábra Impulzussorozat elemzési ábra, amely az *1. ábra* dobolási sorozatáról készült, és amely mutatja az eltérő amplitúdójú impulzusokat

often barely audible. They were performed close to a potential nest hole and usually involved both birds in a loose duet, serving as an intimate communication for bonding between the pair. No examples of loud drumming, as a means of claiming or defending a territory were heard. All signals aimed at potential rivals were communicated vocally. Soft, isolated drum-rolls were occasionally given during excavation, and one was heard during a series of advertising calls.

Pulse train analyses of relative strike amplitude throughout drum rolls of different individuals (n=12) revealed a lack of any regular pattern in the loudness of the strikes *(Figure 2)*. The rolls ranged from 18 to 36 strikes but despite a predominance of louder strikes in the second half in 9 of the rolls, there was no consistency in the overall rhythm. This is illustrated by the irregular positions of the weakest and strongest strikes within each roll *(Table 1)*.

Table 1. Strikes per roll for 12 different individuals and positions of the weakest and strongest strikes within each roll.

1. táblázat 12 egyed dobolás sorozatának elemzése a leggyengébb és legerősebb ütések sorszámának megadásával

Individuals	Strikes	Weakest	Strongest
1	30	15	24
2	23	6	20
3	18	10	16
4	37	3	29
5	30	27	18
6	30	2	31
7	36	4	31
8	20	3	1
9	35	4	11
10	26	1	9
11	29	7	20
12	29	29	1

In an example of a pair drumming quietly (audible only within ten metres) in a potential nesting tree over a period of 47 minutes, one bird drummed 17 times, with an average of

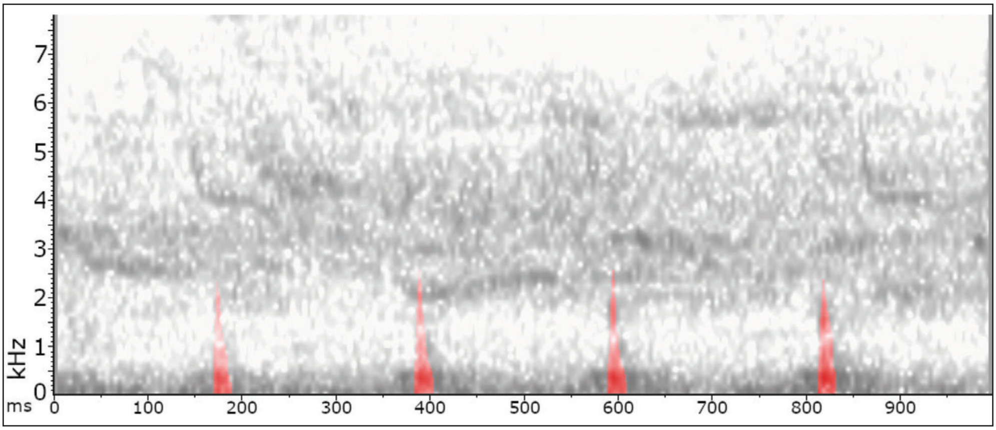

Figure 3. Demonstrative tapping, given during a drumming duet. In this example, the four very soft taps were fairly evenly spaced, with average intervals of 215 ms, while the force of each strike increased slightly. Lot, France. 16.03.2002.

3. ábra Egy dobolási duett közben produkált „tapping" – kopogás. Ebben a példában a négy halk koppanás egyenletesen követi egymást, átlagosan 215 ms idővel, míg a koppanások erőssége enyhén nő. Lot, Franciaország. 2002.03.16.

27.3 strikes per roll (7–39) while the other drummed 25 times with an average of 25.8 strikes per roll (6–36). Eight quiet advertising calls were also given early in the sequence (3 by the first bird and 5 by the second) and one bird gave a series of 14 very soft '*Peeuw*' calls *(Figure 14)* after 9 minutes (Lot, France. 16.03.2002).

(b) ***Tapping (n=22)***

Bursts of demonstrative tapping, containing 4 or more strikes, were heard at three nests, showing average intervals of 186 ms (124–236) at 7.5 per second (4.5–9.7). The maximum number of strikes in a burst was 6. The tapping was performed during the selection and excavation of the nest hole and was usually interspersed with drumming which it matched in quietness *(Figure 3)*. A single burst of 3 strikes was given by a bird emerging from its roost hole (Lot, France. 02.05.2010).

(c) ***Tapping/drumming combinations (n=6)***

In addition to the four drum-rolls that had longer strike intervals at the end, six examples of very soft combinations of tapping and drumming were recorded during courtship drumming duets at one nest site. In each case the taps were slightly louder, and the drum-rolls were shorter than average at 17.7 strikes per roll. Two examples were given within 4 ½ seconds after 6 minutes of drumming and demonstrative tapping. The first started with 4 taps (117,103 and 101 ms apart) leading into a roll of 22 strikes (av. int. 44 ms) *(Figure 4)*. The second started with 2 taps (104 ms apart) leading into a roll of 19 strikes (av. int. 46 ms).

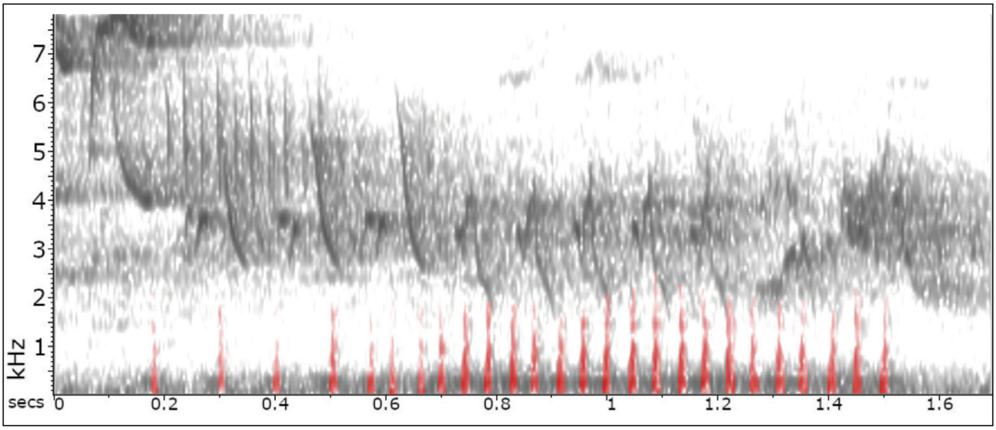

Figure 4. Tapping/drumming combination. Four taps preceding a drum-roll of 22 strikes. Lot, France. 16.03.2002.

4. ábra „Tapping" (kopogás) / „drumming" (dobolás) kombináció. Négy kopogás után 22 elemből álló dobolási sorozat látható. Lot, Franciaország. 2002.03.16.

Vocal signals

Ten distinct vocalisations were heard from adult Eurasian Green Woodpeckers *(Table 2)*, three transitioning calls were heard from nestlings and two from juveniles.

Table 2. Adult call types, functions and phonetic destriptions
2. táblázat Felnőtt egyedektől származó hangtípusok, azok funkciói és fonetikus leírásuk

Call ref.	Call Name	Call Function	Phonetic Description
(a)	Advertising Call, (Song, Yaffle, Laughing Call)	Territorial proclamation, Pair formation, Contact	*Kew, Klu*
(b)	Regular Call	Contact, Arrival, Departure, Alarm	*Tiew, Kew, Teuk*
(c)	'*Kuk*' Call	Contact, Alarm	*Kuk, Kik*
(d)	Flight Call	Movement within home-range	*Kjaek, Kjeuk*
(e)	Flight Alarm Call	Fleeing from predator	*Kju-kju-kjuk*
(f)	Autumn Call	Static (declaration of immature independence?)	*Kjaek, Kjeuk*
(g)	Threat Call	Conflict, Antagonism	*Kjaik*
(h)	'*Peeuw*' Call	Courtship, Presence at nest hole	*Peeuw, Piu, Pweep, Tche-uw, T-we*
(i)	'Wa' Call	Presence at nest hole	*Wa*
(j)	Squeak Call	Frustration, Anxiety	*We-we-we*

(a) ***Advertising Call (Song) (n=50)***

Analysis of advertising calls recorded in 31 different territories showed 80% dropping in pitch while 10% remained flat and 10% rose. There was an overall average reduction of 0.23 kHz between the fundamental frequencies of the first and second elements. Two calls rose and then fell. The average speed, measured in the middle of the calls was 5.9 elements per second (4–7.5). Calls as a whole decelerated from an average interval of 76 ms (43–147) between the first two elements to 94 ms (51–164) between the last two elements. The length of elements reduced through calls by an average of 47 ms from 123 ms (60–176) to 76 ms (23–127). Five calls contained elements of increasing length and two remained constant. With the possible exception of the first example in *Figure 7*, the peak in frequency came after the middle of the element. In general, elements reduced in amplitude throughout the call. The length of calls was greater during the breeding period with an average of 13.8 elements during March, April and May (n=205) compared to 5.2 (n=29) for the rest of the year. Unpaired birds vocalised more frequently. One individual, moving around its territory called once every 30 seconds at its most visited tree, giving 12 calls with an average of 15.6 elements (8–25) in six minutes (Dorset, England. 18.04.2021). In December and January, isolated, short, piping calls were occasionally heard. Insufficient gender-identified advertising calls were obtained that could point to a reliable separation based on differences in characteristics (see Discussion).

Advertising calls consisted of a series of '*Kew*' or *'Klu'* elements showing as inverted 'U's in their purest, single dominant frequency form *(Figure 5)*. Increased motivation, especially during the competitive period of establishing a breeding pair, led to a more frequent repetition and often resulted in sharper elements, producing spikes at the highest frequency in spectrograms *(Figure 6)*. Greater variation was achieved when both shapes occurred in a single call.

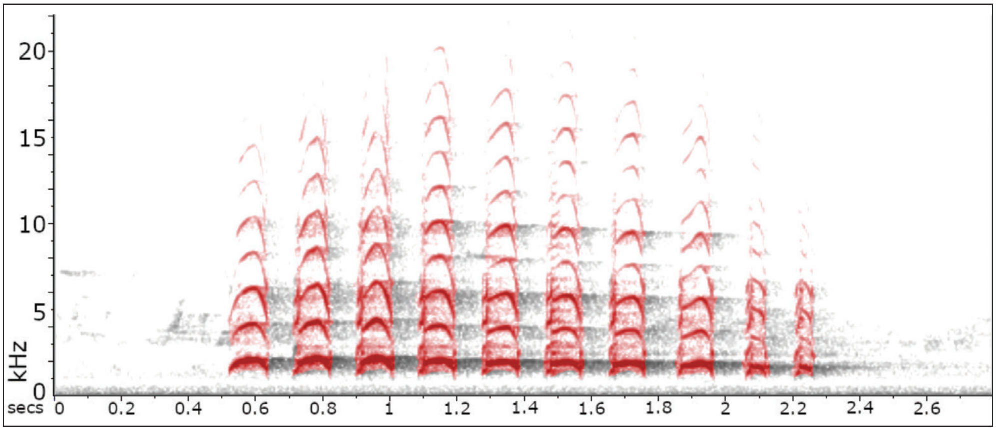

Figure 5. Advertising call, showing simple inverted 'U' elements plus two smaller, quieter and more pointed elements at the end. Dorset, England. 02.02.2007.

5. ábra „Advertising call", nászidőszaki hang, egyszerű, fordított 'U' alakú elemek, a végén két rövidebb elemmel. Dorset, Anglia. 2007.02.02.

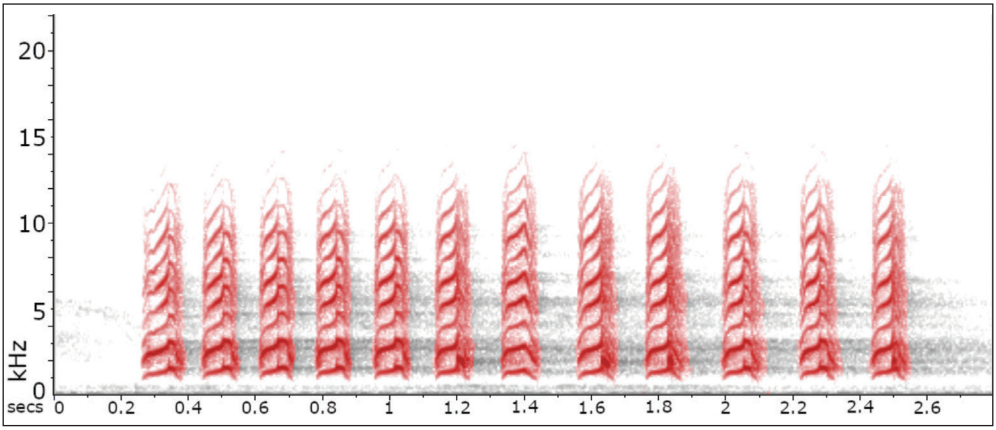

Figure 6. Advertising call, showing sharp elements of fairly consistent length and shape but with a clear deceleration. Lot, France. 19.03.2005.

6. ábra „Advertising call", nászidőszaki hang, éles hangzású, azonos hosszúságú elemekkel, csökkenő tempóban előadva. Lot, Franciaország. 2005.03.19.

Calls were loudest and highest pitched at the start and decelerated towards the end. This pattern, however, was highly variable depending on the individual and its circumstances. By isolating the initial element from eight selected calls, differences of shape, length, pitch and complexity can be clearly illustrated *(Figure 7)*.

Softer and shorter versions of the call were exchanged between pairs and between adults and young near to, or in the nest tree, with an average of 5 elements (2–9, n=37) and calls of between 3 and 5 elements were heard on consecutive days from a pair 200 m apart, each with juveniles in attendance (Dorset, England. 14/15.08.21). Also, short, harsh versions were given by a bird near a nest with young in reaction to a party of Jays *(Garrulus glandarius)* moving past (Lot, France. 25.05.08).

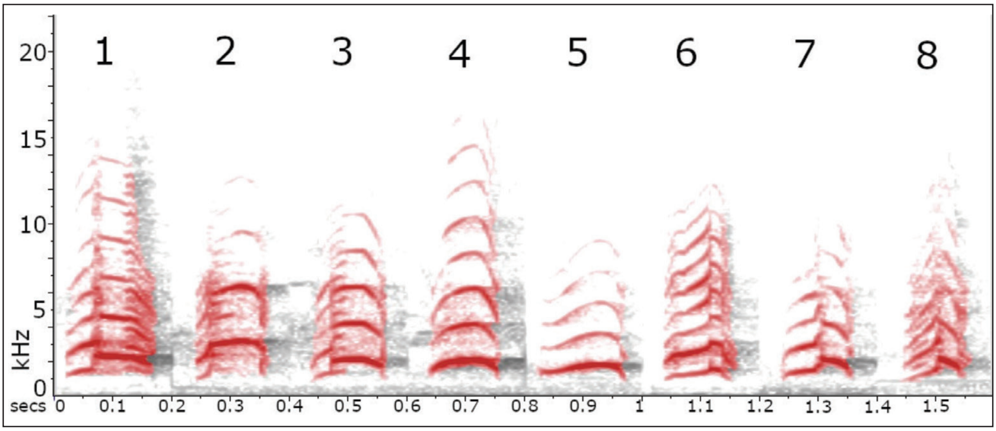

Figure 7. Individual elements (expanded on the x axis) extracted from eight advertising calls given by different birds, showing different fundamental frequencies and some sub-harmonics. (1,2,3,6,8 – Lot, France. 07.04.2013, 01.04.2014, 04.03.2003, 19.03.2005, 26.04.2010, 4 – Dorset, England. 02.02.2007, 5 – Wiltshire, England. 06.05.2008, 7 – Zemplén Hills, Hungary. 14.04.2006)

7. ábra Különböző egyedektől származó vokális hangsorozatok egyes elemei egymás mellé rendezve. (1,2,3,6,8 – Lot, Franciaország. 2013.04.07., 2014.04.01., 2003.03.04., 2005.03.19., 2010.04.26., 4 – Dorset, Anglia. 2007.02.02., 5 – Wiltshire, Anglia. 2008.05.06., 7 – Zempléni-hegység, Magyarország. 2006.04.14.)

(b) ***Regular Call Tiew, Kew, Teuk (n=103)***

The most regularly heard call was always composed of repeated elements decelerating through the call and either dropping slightly in pitch from 2.07 to 1.95 kHz (n=30) or remaining flat. Three element shapes were used, from the simple inverted U to slightly more complex and fragmented forms. Unusually, all three shapes (timbres) were given in a single call by a bird arriving to feed young in the nest *(Figure 8)*. In contrast to the advertising call, the stress was always nearer the start of each element.

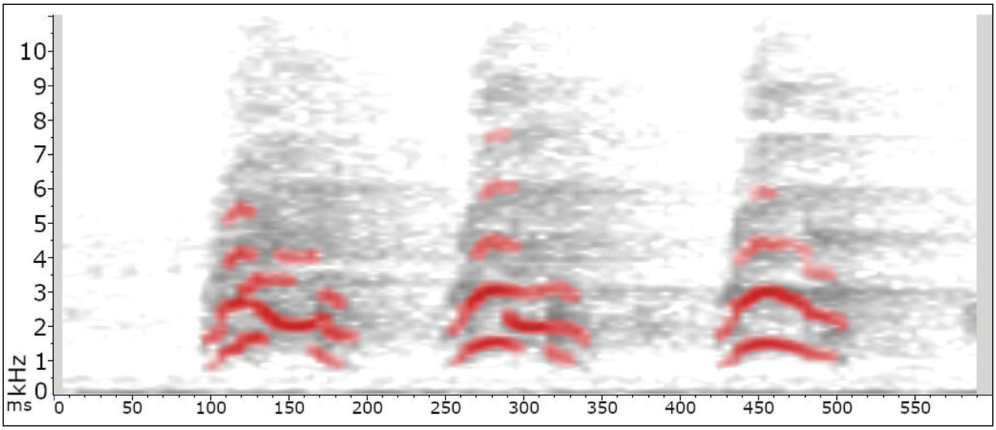

Figure 8. Regular Call *Kew Kew Kew*, three element shapes in a single call. Dorset, England. 12.06.2005.

8. ábra A három elemből álló *„Kew Kew Kew"* hang. Dorset, Anglia. 2005.06.12.

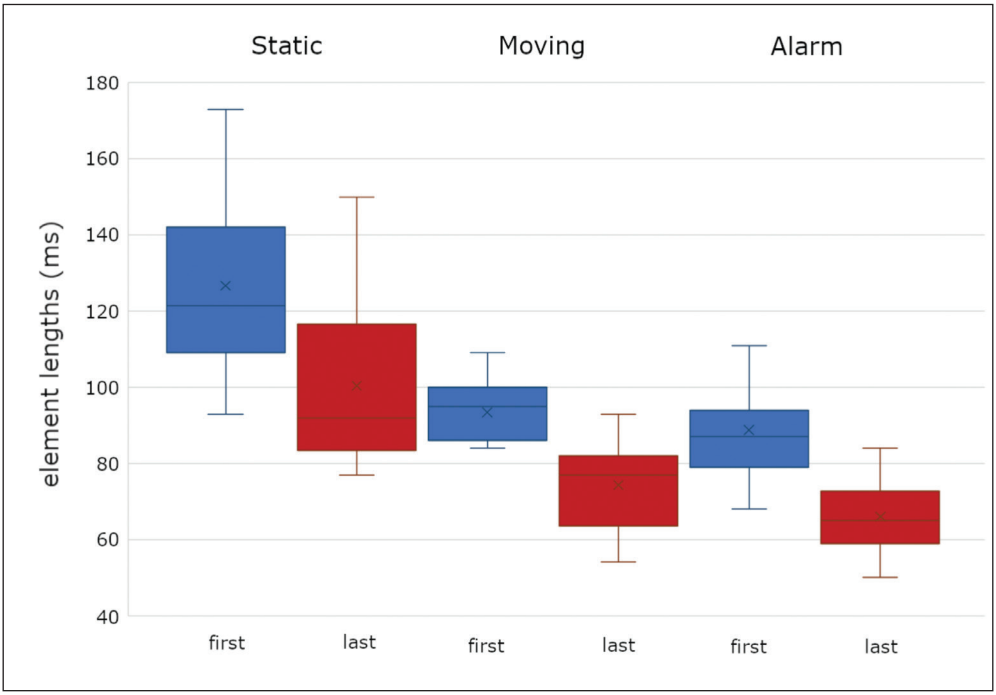

Figure 9. Regular Call: First and last element lengths in milliseconds (blue and red box plots, with median shown as a line and mean shown as X) for the three behavioural contexts

9. ábra „Regular Call": az első és az utolsó elemek hosszának eloszlása három különböző viselkedési helyzetben

The call was associated with three principal behaviours: signalling presence when static, movement (arrival and departure) and alarm near a nest with young. All three element shapes were used in each behavioural context and element lengths consistently reduced through the calls *(Figure 9)*.

Static calls, however, were more frequently composed of longer simple inverted 'U' elements and alarm calls often contained more elements.

(b^1) ***Static Contact Call (n=18)***

The call, given when close to a nest with young or in answer to a mate, was slow, at 4 or 5 elements per second at an average of 3 (2–5) per call and sounded like stretched and tongued '*Tiews*'. The greater range of element lengths and the overlapping of lengths between first and last elements was only heard during the breeding. Occasionally the first element was slurred into a '*Kiaow*', almost twice the average length, sounding more like the typical food begging call of juveniles *(Figure 21)*.

(b^2) ***Movement Call (n=21)***

This call was given by individuals to signal their arrival, following the flight call and also when about to depart. It was faster, delivered at an average of 6 elements per second

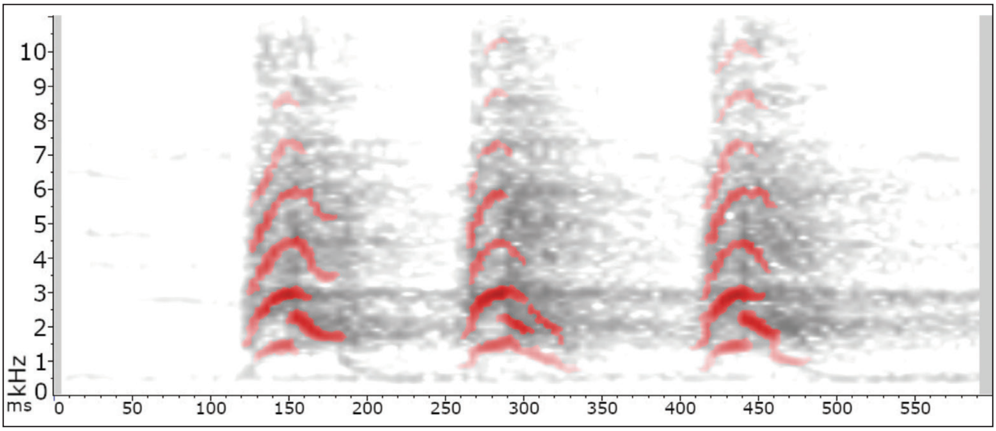

Figure 10. Alarm Call. Dorset, England. 24.06.2001.
10. ábra Három elemből álló „alarm call" (vészhang). Dorset, Anglia. 2001.06.24.

(5–7) and was composed of sharp '*Kews*' or '*Teuks*' at an average of 4.5 (2–7) elements per call *(Figure 8)*. Behaviourally, despite the absence of a potential predator, it may have expressed anxiety when near a nest with young and was structurally close to the alarm call *(Figure 9)*.

(b^3) ***Alarm Call (n=64)***

Calls given in alarm near to the nest tree were rapidly repeated in longer series, with thirty or more calls per minute at 6 elements per second. There was an average of 5 elements per call but with a wider range of from 3 *(Figure 10)* to 18. In one example forty-eight calls, ranging from 3 to 6 elements slowing through the sequence, were given over a seven-minute period by a bird disturbed near a nest.

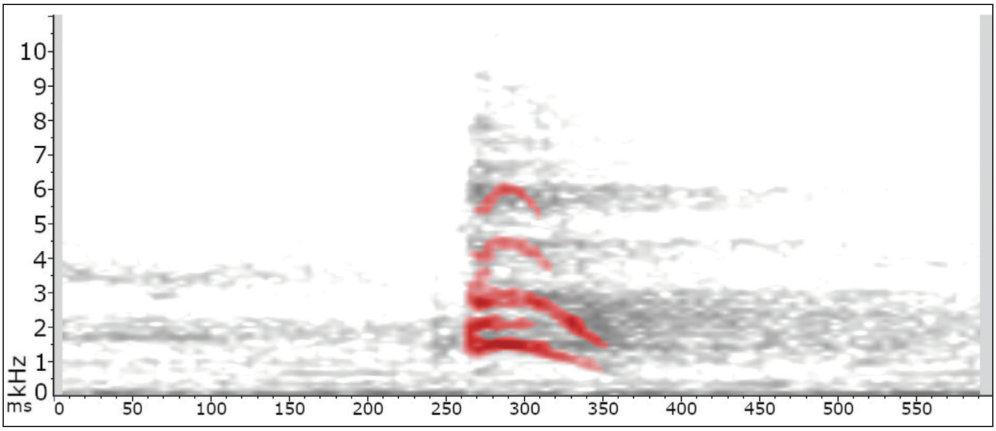

Figure 11. Kuk Call. Bird emerging from roost, responding to its mate's advertising call. Wiltshire, England. 22.01.2006.
11. ábra „Kuk" hang. Az odúból távozás közben, párja hangjára válaszolva. Wiltshire, Anglia. 2006.01.22.

(c) ***Kuk Call (n=3)***

The only single-element call in the Eurasian Green Woodpecker repertoire was the rare '*Kuk'* Call. The best example recorded was short (75 ms) and similar in shape to an element in the *Tiew* call but with a more abrupt start *(Figure 11)* and was lower in pitch (1.48 kHz). No specific functional significance was observed, although in combination with a sharp and higher pitched *'Kik'* element (as in *'Kuk-kik-kuk'*) it was occasionally given by birds when startled in autumn and winter.

(d) ***Flight Call Kjaek, Kjeuk (n=49)***

Flight calls were generally faster than the Regular call, with 7–8 elements per second, slowing on approach to the destination. Calls were higher pitched, dropping from 2.3 to 2.1 kHz through the call when followed at a tangent (n=13). Calls were composed of flat elements, sharp at the start and dropping at the end and were usually short, with an average of 3.2 elements per call (1 to 7). One exceptionally long call of 21 elements was recorded at the start of a sequence. The number of separate calls given in flight varied according to the distance covered, from 1 – between neighbouring trees, to 9 – across a valley (average 3.6, n=14). The call, sounding like repeated *Kjaeks* or *Kjeuks* was given during pair formation and breeding and signalled a change of position within the home-range to the partner or young, especially when approaching the nest when young were about to fledge. It was regularly heard when birds were going to roost and later in the autumn and winter as immature birds were claiming foraging sites. Flight calls associated with disturbance contained changes of pitch between elements *(Figure 12)* and longer, slower, disjointed series (5 elements per second) may have involved more complicated messages.

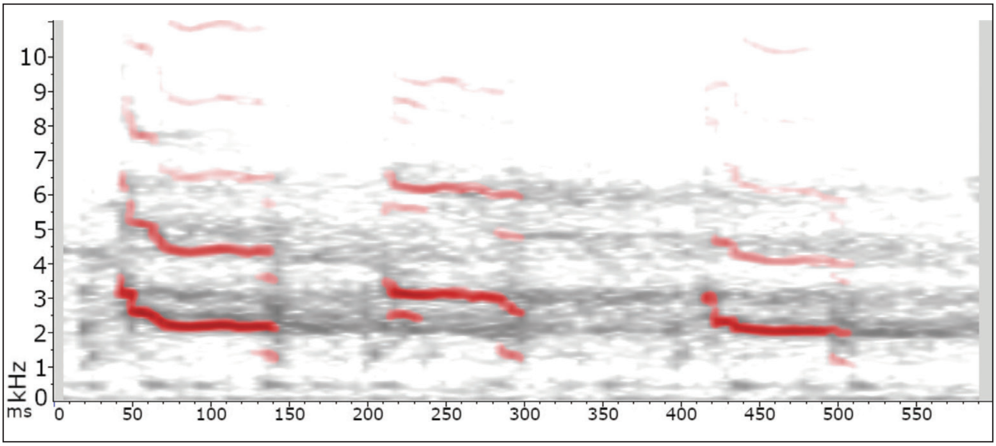

Figure 12. Flight Call, showing a higher pitched second element. The middle of a series of three calls. Lot, France. 29.03.2008.

12. ábra „Flight Call" (repülés közben hallatott hang), melyben a középső elem hangmagassága nagyobb, mint a szélsőké. Hármas hangokból álló hangsorozat egyik közbülső hangja. Lot, Franciaország. 2008.03.29.

(e) ***Alarm Call in Flight (n=1)***

When threatened, usually by an aerial predator, individuals communicated a very real sense of panic, giving loud, modulated *Kju-kju-kjuks* as they fled from danger. In a recording of a bird being chased by a Eurasian Sparrowhawk *(Accipiter nisus)*, a bird gave 18 high-pitched screeches before reverting to a series of fast flight calls (two groups of 5 elements followed by several of 2). The screeched elements, increasing up to 302 ms in length and over 2.8 kHz in pitch, were delivered at 3.5 per second (recorded by K. Barnatt, Lincolnshire, England). The call was most frequently heard in late autumn and may have been given by immature birds being chased out of a home-range. Other threats were observed from Peregrine Falcon *(Falco peregrinus)*, Booted Eagle *(Hieraaetus pennatus)* and Domestic Cat *(Felis catus)*.

(f) ***Autumn Call (n=49)***

This call was heard only for a limited period from approximately four weeks after young had fledged. It was very closely related to the flight call in structure, but given by a bird when static, and contained an average of 9.8 elements per call (4–21), more than twice that of the flight call. Calls were generally sharp and fast, at an average of 7 elements per second (6–9, n=19), decelerating and dropping in pitch from an average of 2.5 to 2.1 kHz (n=12). As with other calls, elements reduced in length as gaps between them increased. From 47 calls (20 from xeno-canto(2)) representing at least 17 individuals, 18 were given in two parts – one call followed by another within 3 seconds, with the first generally longer than the second.

(g) ***Threat Call Kjaik (n=11)***

Threat calls were given during close encounters (often with raised crown feathers): during conflict between rivals; by members of a pair when uncomfortable with a perceived invasive presence; and with juveniles when arriving to feed. They were also occasionally given as

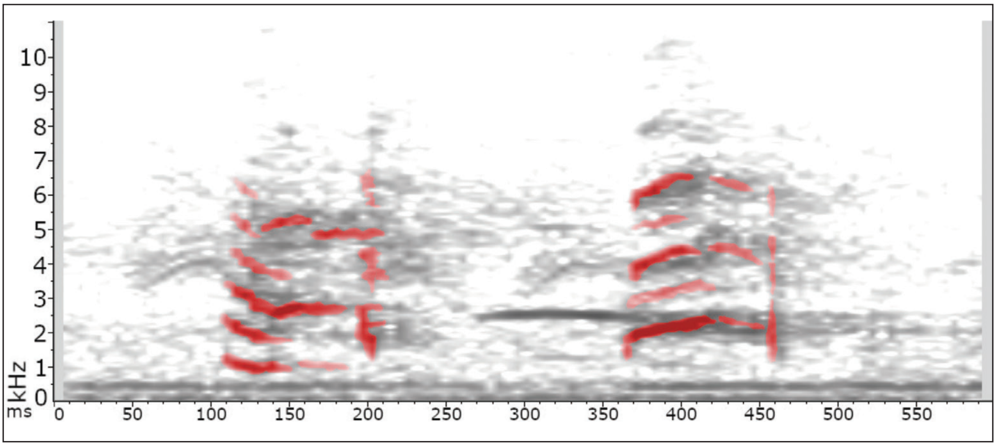

Figure 13. Kjaik Call. First 2 elements from a call containing 34 elements, the first element clearly sharper at the start. Given when in close contact with juveniles. Dorset, England 06.07.2003.
13. ábra „Kjaik” hang. Az első két eleme a 34 elemből álló hangsorozatnak. Fiatalok közelében kiadott hang. Dorset, Anglia. 2003.07.06.

a reaction to the mate's advertising call or during close encounters outside the breeding season. They were not loud and have been aptly described as 'sounding like windows being cleaned with a shammy leather' (Cohen 1946). The call was generally a long repetition of simple, squeaky, *Kjaik* elements (6 to 37) at around 2.5 kHz with the initial element either shorter or irregularly inflected *(Figure 13)*. Element lengths remained consistent throughout the call at about 100 ms and were evenly spaced between 3 to 6 per second over most of the call, although the calls themselves became increasingly widely spaced.

(h) ***Peeuw Call (n=10)***

The *Peeuw (Piu, Pweep)* calls were very soft, thin, intimate signals given during courtship and when a pair met at the nest hole, or a bird arrived to feed young. They were typically delivered in a series of up to 19 long *'Peeuw'* elements from 2 to 3.5 per second and were relatively pure in tone. The average element length was 230 ms (133–355) more than twice that found in any other call (n=53). In the four measurable examples, the average pitch was 2.1 kHz. After a sequence of soft drumming and advertising calls given at dawn, a bird called with 12 regularly spaced elements in response to its mate's soft drum-rolls on arrival in the same tree – recalling the courtship and mating sequences of Grey-headed Woodpecker *(Picus canus)*. '*Peeuw*' calls were also given by pairs in a duet. In one example, the nearer bird gave five calls (14, 19, 5 and 10 elements) which occasionally coincided with the second bird's calls *(Figure 14)*. Only one instance of this call-type was heard outside the breeding season.

Variations of this call included a sharper '*Tche*' at the start of each element and an apparent separation from the '*uw*' at the end, sometimes shortened to a '*T – we*' *(Figure 15a)*. Occasionally these sub-elements or variations on them were given individually.

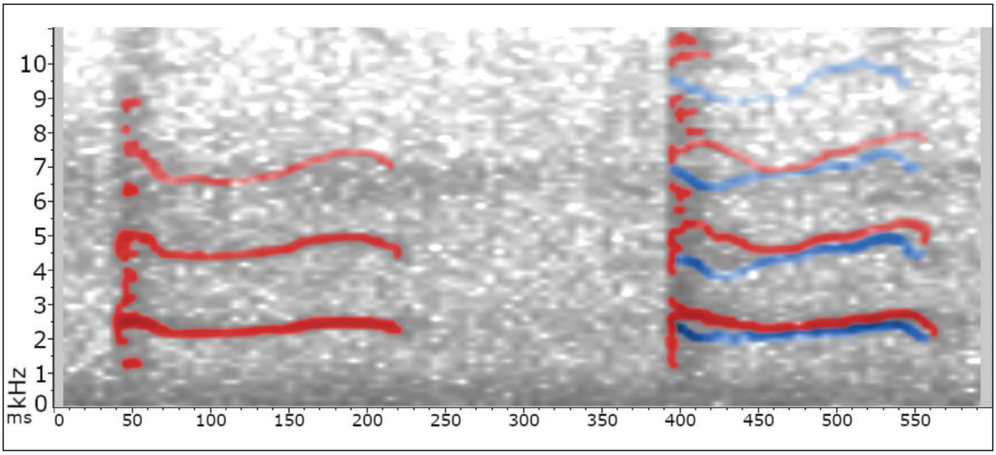

Figure 14. Peeuw call. Pair at the nest hole (containing small nestlings). The second element of the first bird's call (coloured red) is precisely matched by the second bird (coloured blue). Lot, France. 12.05.2008.

14. ábra „Peeuw" hang. Egy pár által a fiókás fészek közelében kiadott hang. Az egyik egyed által kiadott hang (piros) második eleme átfed a másik egyed hangjával (kék). Lot, Franciaország. 2008.05.12.

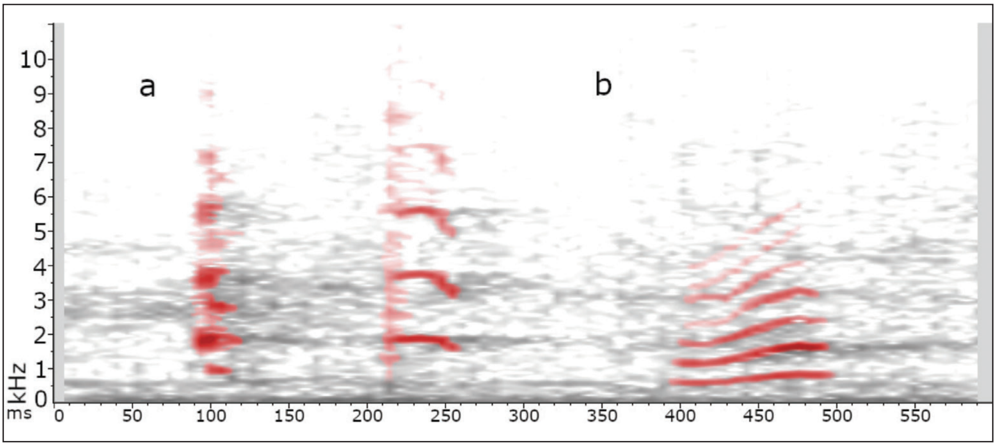

Figure 15. (a) A *'T – we'* variant of the *'Peeuw'* call element and (b) – a separate *'Wa'* given at the nest as the mate came close (300 ms have been cut from between the calls for easier comparison with previous spectrograms). Lot, France. 25.05.2008.

15. ábra A fészek közelében hallatott hangok, (a) „t – we" variánsa a „Peeuw" hangelemnek és (b) „Wa" hang. 300 ms szünet volt kivágva a két hang közül. Lot, Franciaország. 2008.05.25.

(i) *Wa Call (n=1)*

Other extremely faint sounds were made by adults close to nest holes, such as the rising '*Wa*' element (101 ms, ff 0.8 kHz) *(Figure 15b)* which followed a sequence of '*T – we's*.

(j) *Squeak Call (n=1)*

An example of a thin and rapid '*We-we-we*' call, with a sibilant quality similar to *Picus sharpei*, was given by an unmated bird during a series of advertising calls and after a soft drum-roll. Elements shortened from 71 to 42 ms and increased in pitch from 2.47 to 2.64 kHz while the tempo slowed *(Figure 16)*.

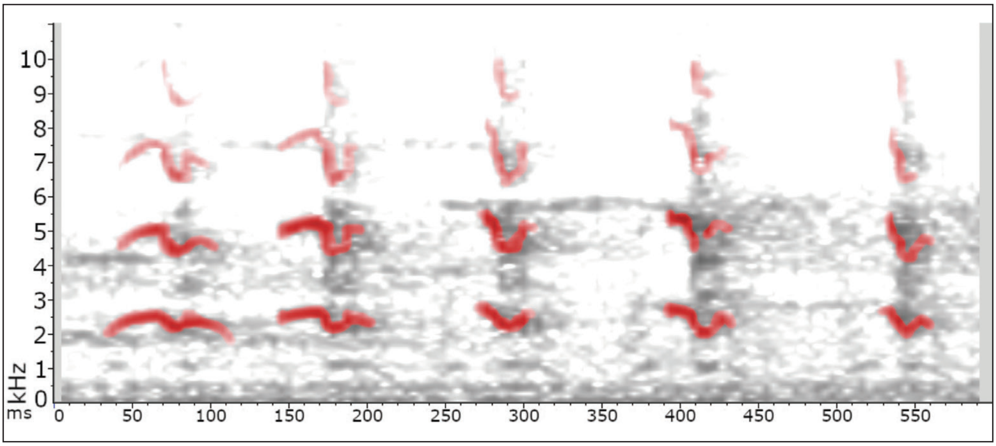

Figure 16. Squeak call. Dorset, England. 02.05.2021.

16. ábra „Squeak" (vinnyogó) hang. Dorset, Anglia. 2021.05.02.

Calls of nestlings and juveniles

During the first week after hatching, nestlings produced long series of continuous, low, rasping noises *(Figure 17)*. These gradually became separated into short, grating elements, sounding like tearing cardboard and were given when an adult was heard near the nest *(Figure 18)*. Before fledging, purer elements were added *(Figure 19)*.

The combination of harsh, grating calls and purer, more '*Kew'*-like elements gave way to sharp, squeakier sounds repeated in long series at the point of fledging. They were mostly given singly at, on average, one every three seconds, accelerating as an adult arrived, but were also repeated in groups of up to six elements at 5 per second and at 2.86 kHz (n=17). The sharpest element was usually at the start *(Figure 20)*. At about 80 ms in length, they were shorter than the

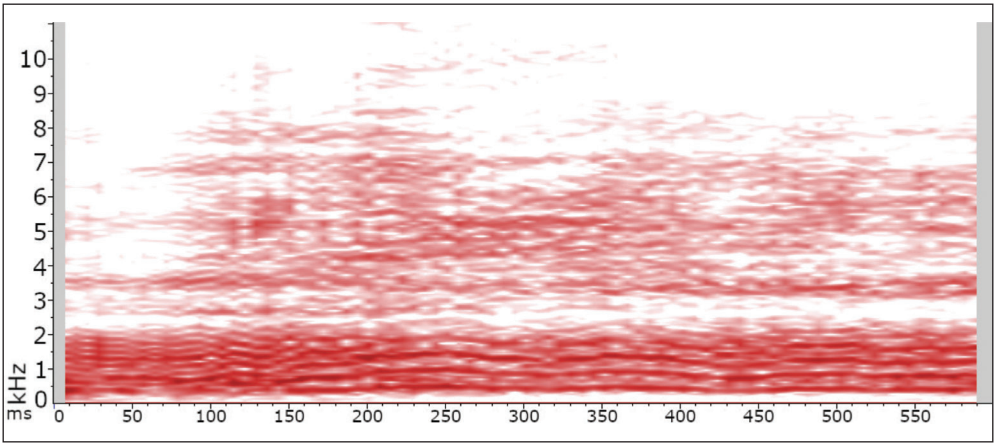

Figure 17. Calls of nestling during the first week after hatching. Lot, France. 13.05.2011.
17. ábra Fiókák hangja a tojásból kibújás utáni első héten. Lot, Franciaország. 2011.05.13.

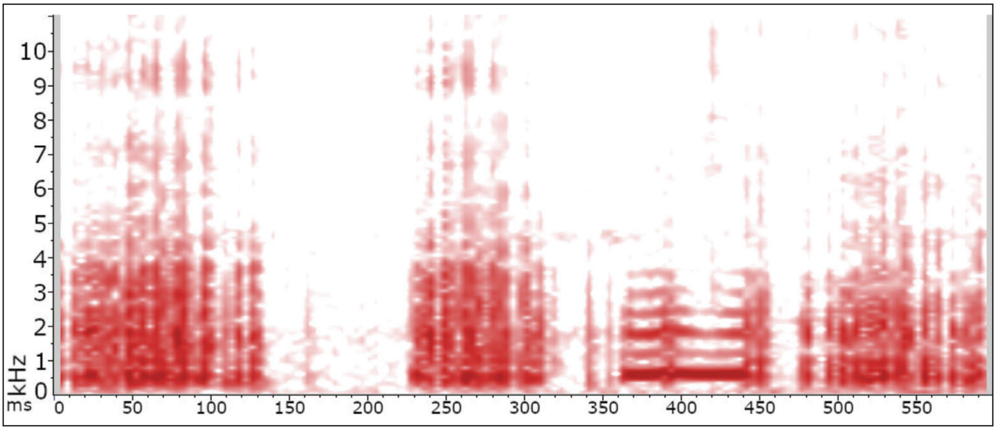

Figure 18. Nestlings making a ripping, tearing sound in very short (8 to 12 ms) staccato elements, with an occasional soft note (at 360 ms). Lot, France. 13.05.2011.
18. ábra Fiókák különböző zörejszerű hangjai és egy lágy, szabályosabb zönge jellegű hangja (360 ms-nál). Lot, Franciaország. 2011.05.13.

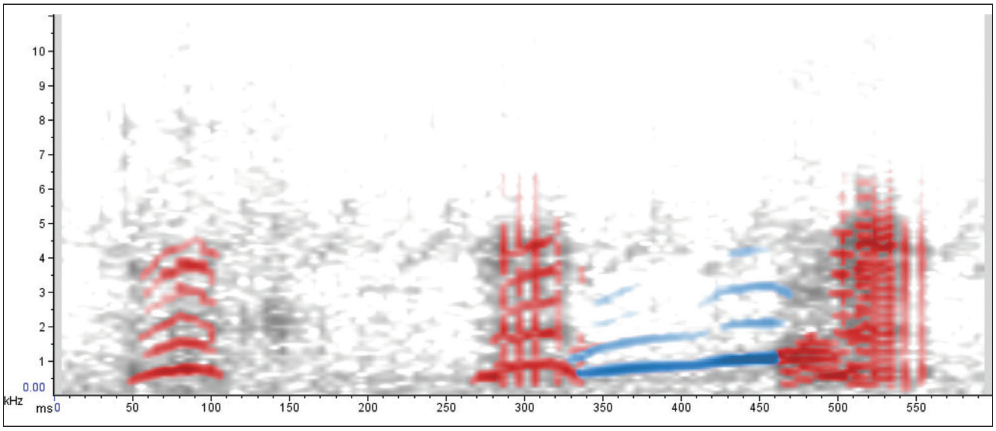

Figure 19. Nestling at approximately 2 ½ weeks, showing a similar shape to an adult call in the first element but sounding more like a squeaky rubber duck, plus two grating transitional elements. A second nestling gives a purer, rising note (coloured blue). Lot, France. 21.05.2011.

19. ábra Fiókák hangja két és fél hetesen. A felnőttekére jobban hasonlító átmeneti jellegű hangok az egyik egyedtől (piros). Egy tisztább, emelkedő hang egy másik fiókától (kék). Lot, Franciaország. 2011.05.21.

lower pitched food calls which soon replaced them. In these calls, which typically consisted of two or three elements (1–7, n=33), the first element was slightly longer (120 ms), higher pitched and more emphasised, with subsequent elements usually descending in pitch *(Figure 21)*. Both calls typically had a longer interval between the first and second elements. A quieter, non-vocal variant (presumably produced by the tongue but sometimes ending in a squeak) sounded more like *'T-lew'*. Juveniles approaching independence often retained a longer, slightly modulated element at the start of an otherwise typical adult's '*Kew Kew Kew*' call.

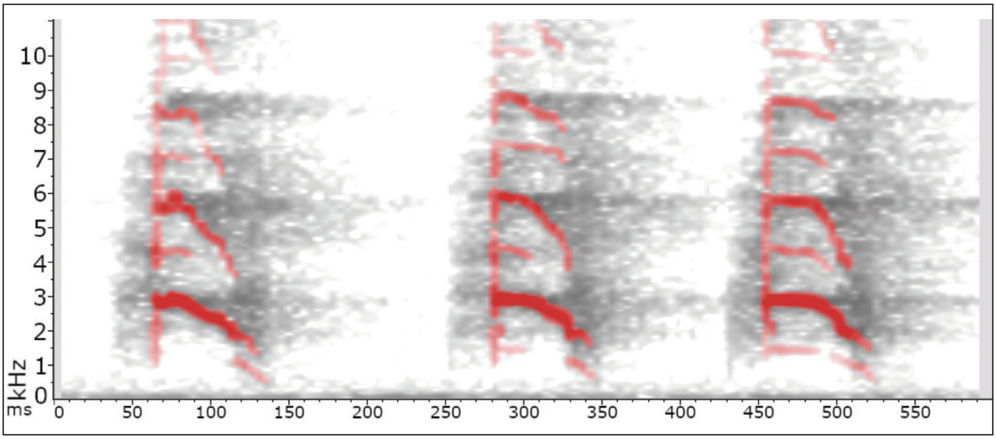

Figure 20. Juvenile giving a sharp, high-pitched call immediately on leaving the nest. Dorset, England. 19.06.2005.

20. ábra Egy fiataltól származó éles, magas hang a fészekelhagyás közben. Dorset, Anglia. 2005.06.19.

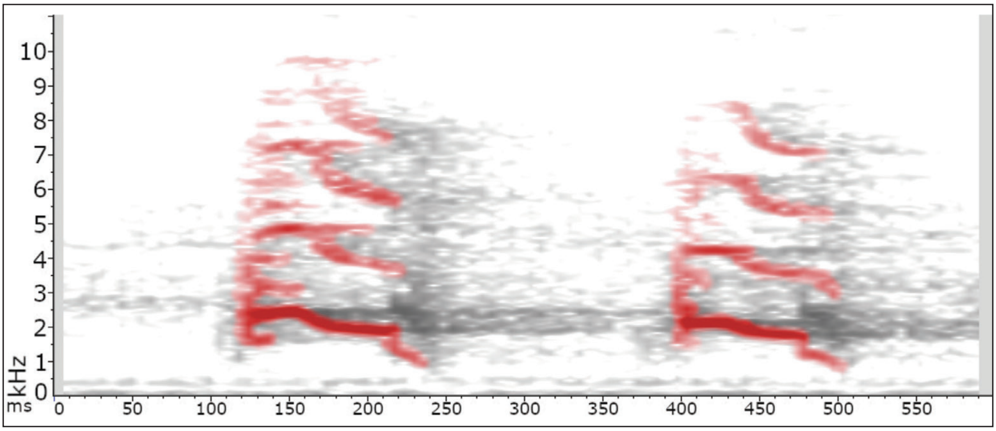

Figure 21. Food call of a juvenile a few days after fledging, showing a longer and more emphasised first element and a drop in pitch to the second of 0.4 kHz. Lot, France. 30.05.2019.

21. ábra Fiatal madár táplálékkéregető hangja néhány nappal a kirepülés után. Hosszabb és erősebb első hang. Lot, Franciaország. 2019.05.30.

Discussion

The absence of loud, rhythmically stable drumming in the Eurasian Green Woodpecker constitutes a behavioural separation from most other European Picinae (Turner 2020). Typical woodpeckers drum on acoustically resonant branches or trunks around a potential nesting site, maintaining regular, species-specific patterns which are either largely uniform or accelerate through the roll (Zabka 1980, Florentin *et al.* 2016). This produces a very effective, far-carrying, advertisement of suitability to a prospective mate while also discouraging rivals (Winkler & Short 1978). The Eurasian Green Woodpecker, however, has evolved to forage terrestrially, in open woodland/grassland habitats, and thus its loud advertising calls, given from isolated trees or clumps, serve better to bring breeding pairs together. In our study, we found that all examples of drumming were extremely weak and irregular *(Figure 2)*, lacking any repeatable structure in the amplitude of the strikes throughout a roll *(Table 1)*. This, together with its predominant use when pairs were close, suggests that it has become a component of courtship once a potential nesting site has been identified. Isolated rolls heard during excavation, or a series of advertising calls appeared to be instinctive reactions to the breeding urge, since they could not have been audible to a second bird. A similar result was found with the rarely heard tap/drumming of Middle Spotted Woodpecker which was thought to have adapted its loud advertising call as a result of the competition of drumming from other, stronger-billed, woodpeckers sharing the same habitats (Turner 2020). A rare example of louder drumming was heard from a Eurasian Green Woodpecker drumming on metal plates surrounding the entrance holes of at least two nest-boxes. Drumming was amplified and could be heard over a hundred metres away (Kramer 2009). The patterns of drumming and tapping described in that account, however, were matched by the extremely soft versions recorded during the present study and none of the authors, in many hours of observations, has encountered such far-carrying examples.

As with the sexual differences apparent amongst woodpeckers that drum territorially (Blume & Tiefenbach 1997), an advertising call used also for pair bonding would only be effective if males and females were able to identify each other (Węgrzyn *et al.* 2021). There are, indeed, some possible indications of sexual difference in advertising calls. For example, an analysis by H. H. Bergmann of a recording by K. Hinrichs showed strong harmonics and monosyllabic fundamentals in a female's advertising call, in contrast to the male's disyllabic fundamentals (Cramp 1985). We found that in confirmed examples of advertising calls given by females (n=7 from 4 birds), the first element was softer and lower pitched and subsequent elements remained fairly evenly pitched, in contrast to confirmed male calls. However, in a pair recorded between April and June 2022, the female's advertising calls were longer (9 elements compared to 7.5 on average) and faster (7.4 elements per second compared to 6.1) with short final elements (female n=29, male n=15). They were also 0.3 kHz higher in the overall frequency of the first element (2.3 kHz compared to 2.0 kHz) and did not decelerate. Once these differences were identified, the birds were easy to tell apart by ear. These are small samples, and any overall rule must remain speculative until a full study of positively gender-identified recordings can be obtained. We did not attempt a statistical comparison of call characteristics between our two principal study areas (France and England). Variation was far greater within each area than between them. There is likely to be considerable value from increasing the number of available acoustic recordings of woodpecker species from across their ranges in developing methods for species and individual recognition algorithms (Florentin & Verlinden 2017, Stowell *et al.* 2019, Vidaña-Vila *et al.* 2020).

An interesting change in the seasonal use of the advertising call and hence the breeding cycle is indicated by comparing our finding of a March to May peak with a survey from 1961 which showed the greatest intensity from February to April (Blume 1962). One possible explanation for this might be a later availability of ants during a period of rising global temperatures, possibly explained by levels of rainfall and grass length (Cramp 1985) but this warrants further study. Juveniles were still being fed in the middle of August in the UK in 2021. However, if we have correctly identified what has been referred to as the 'autumn call', the majority of the 49 examples that we found were heard in summer – 10 in the second half of July, 33 in August and only 6 in September, although the call was still occasionally heard towards the end of September 2022. The call appeared to be associated with the move by juveniles towards independence, indicating increased excitement or antagonism and may be exclusive to them. In our study, there was a clear structural similarity to the flight call, with which it was sometimes combined, rather than the advertising call (Cramp 1985).

Variations in what we refer to as the 'Regular Call' within individuals appear to indicate different meanings. An in-depth behavioral study of several individual's repertoires would be needed to establish the degree to which the variables in element structure relate to their function or to the birds as individuals. Irregular forms of tapping described as 'excitement pecking' (Blume & Jung 1958) were heard during this study but we do not consider them to have constituted ritualised signals.

Conclusion

In our study, we found that the instrumental signals, including drumming, of Eurasian Green Woodpecker were always very soft and were used predominately in the vicinity of nests during courtship interactions. No evidence was found for the use of drumming as a territorial signal. The repertoire of vocal signals consisted almost entirely of calls containing simple, repeated elements with stress typically given on the first element and a gradual deceleration thereafter. In all but three calls, modulation within elements involved a rise and fall of pitch – the typical shape shown in spectrograms of other European woodpecker calls (Winkler & Short 1978, Blume 1996). In the advertising call, the peak appeared before the middle of the element, in contrast to other loud calls where it came after. While there was an overall tendency toward deceleration and reduction in element lengths, familiarization with the combination of differences in; element shape, call duration and speed, appeared to provide an effective way to separate individuals. Differences in element lengths found in the Regular call also indicated a range of meanings related to movement and alarm. Motivation also affected call characteristics, in particular, a higher pitched second, or alternating element indicated disturbance. We found the peak of advertising calls to be from March to May, a month later than a survey conducted in 1961 (Blume 1962).

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Effects of local climate on nest cavity characteristics of a North African endemic woodpecker

Mehdi Badis[1*] & Nabil Hamdi[1,2]

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Abstract Levaillant's Woodpecker *Picus vaillantii* is a primary cavity nester, endemic to the forests of northern Africa, including the cedar forest in Aurès Mountains. This species, similar to all woodpeckers, is important for the integrity of ecosystems, especially as it provides nesting cavities and contributes to the availability of habitats for several secondary cavity nesters that cannot excavate their hollows. This work aim to characterise the Levaillant's Woodpecker's nest cavities and to test the effect of local climatic conditions on the size and orientation of these cavities. Surveys were carried out in the breeding seasons of 2018 and 2019 using the point count method to search for the nests. Based on nest measurements conducted on a total of 52 available nest cavities, our results reveal that entrances are dominated by round shapes (94.2%) as compared to oval shapes. The mean height and width values of the cavity entrances were found to be 7.26 ± 1.51 centimetres and 7.11 ± 1.44 centimetres. The depth of the internal chamber and its width were estimated to be 35.42 ± 7.82 centimetres and 17.95 ± 4.01 centimetres, respectively. Unlike the average values of the volumes of the internal chamber, those relating to the entrance area and orientation vary significantly according to altitude and climatic conditions. Indeed, when climbing towards the summits, the cavities widen and turn to the west-southwest. This behaviour of the Levaillant's Woodpecker seems to help it to benefit from maximum sunshine at high altitudes and to avoid predators and competitors more abundant at medium or low altitudes.

Keywords: *Picus vaillantii*, nest cavity, behaviour, bioclimatic level, cedar, Aurès

Összefoglalás Az Atlasz-küllő *(Picus vaillantii)* elsődleges odúköltő, azaz odúkészítő faj, amely Észak-Afrika erdeinek endemikus madárfaja. Elterjedési területe magában foglalja az Aurès-hegység cédruserdeit. A vizsgált faj, hasonlóképpen más harkályfajokhoz, fontos szerepet játszik az adott ökoszisztéma integritásának megőrzésében, mivel fészkelőodúkat készít, és így számos másodlagos odúköltő számára biztosít fészkelőhelyet. Észak-Kelet Algériában első alkalommal mértük föl az Atlasz-küllő költőodúk méreteit és tájolását a 2018–2019-es költési időszakban, különböző bioklimatikus zónákban. A terepmunka során pontszámlálást és odúkeresést alkalmaztunk. Az 52 odún végzett mérések eredményei alapján a bejárati nyílásoknál dominált a köralak (94.2%) az ovális alakkal szemben. A bejárati nyílások átlagos magassága és szélessége 7.26 ± 1.51 cm-es, valamint 7.11 ± 1.44 cm-es értékeket adott. A belső kamra mélysége és szélessége 35.42 ± 7.82 cm-esnek, valamint 17.95 ± 4.01 cm-esnek adódott. A belső kamra térfogatának átlagos értékeitől eltérően, a bejárat területe és orientációja szignifikáns kapcsolatban van a tengerszint feletti magassággal és klimatikus változókkal. A hegycsúcsok felé haladva az odúk egyre szélesebbek és egyre inkább nyugat-délnyugati irányba fordulnak. Az Atlasz-küllőnek ezen stratégiáját feltehetőleg az magyarázza, hogy nagy tengerszint feletti magasságokon előnyös számára a napfény maximális kihasználása, míg a ragadozók és kompetítorok kerülésének stratégiája gyakoribb közepes és alacsony tengerszint feletti magasságokon.

Kulcsszavak: *Picus vaillantii*, fészkelőodú, viselkedés, bioklimatikus kényszer, cédrus, Aurès

[1] *Research Laboratory of Diversity, Management and Conservation of biological systems (LR18-ES06), Faculty of Sciences of Tunis, Tunis El Manar University, Tunis 2092, Tunisia*
[2] *Higher Institute of Applied Biological Sciences of Tunis, Tunis El Manar University, Tunis 1006, Tunisia*
** corresponding author, e-mail: mehdi.badis@fst.utm.tn*

Introduction

Mediterranean forests host many specialists in cavity-nesting birds (Devictor *et al.* 2010). Primary cavity nesters include woodpeckers which deploy considerable efforts, especially in terms of energy, to excavate their nest cavities. Secondary cavity nesters such as nuthatches (Sittidae) and tits (Paridae) exploit cavities previously created by primary nesters or those generated by the decaying of trees. (Martin & Li 1992, Blanc & Walters 2008).

Woodpeckers are important for the equilibrium of forest ecosystems (Drapeau *et al.* 2009, Damoc *et al.* 2014). They provide suitable habitats for the nesting of secondary cavity nesters. They provide the same resources with other bird species (Pakkala *et al.* 2006, Smith 2006), regulate the density of their prey, especially insects (Fayt *et al.* 2005), and participate in the transmission of wood-decaying fungi (Jackson & Jackson 2004). Owing to their highly selective ecological requirements, these species are frequently considered excellent bioindicators of the forest ecosystems' health (Angelstam & Mikusiński 1994, Mikusiński *et al.* 2001, Virkkala 2006).

The reproductive success of woodpecker populations is influenced by the nature and morphology of the cavities used mainly to protect the chicks against predation and the hostile conditions of their environment (Short 1979, Nilsson 1986, Li & Martin 1991, Newton 1994, Huhta *et al.* 1998, Ćiković *et al.* 2014). Key environmental drivers of nest cavities include the size of the interior chamber of the cavities, the type of bark, the thickness and density of the surrounding wood, the angle and the shape of the entrance, and the orientation of the cavities (Ricklefs & Hainsworth 1969, Austin 1974, Conner 1975, Inouye *et al.* 1981, Wachob 1996, Hooge *et al.* 1999). The number, size, and shape of cavities also influence the total number of cavity nesters in forest stands (Evans *et al.* 2002, Lõhmus & Remm 2005).

The cedar, oak and pine forests of the Maghreb countries are home to various associations of cavity-nesting birds dominated by the Levaillant's Woodpecker *Picus vaillantii* (Isenmann *et al.* 2005, Touihri *et al.* 2015, Badis & Hamdi 2022) a vicariant of the Green Woodpecker *Picus viridis* (Blondel 1999, Pons *et al.* 2010, Perktas *et al.* 2011). It is widespread in northwest Africa. In Tunisia, it frequents the forests of the central to the western parts of the country (Isenmann *et al.* 2005). In Algeria, its habitats extend from the sea to the high forests, reach the Saharan Atlas and the Aurès region (Isenmann & Moali 2000) southwards. However, in Morocco, it is found in forest areas at all altitudes (Heim de Balzac & Mayaud 1962). The diet of the Levaillant's Woodpecker is essentially based on adult ants and pupae, in particular those belonging to the genus *Formica* (Gillmen *et al.* 1998, Henine-Maouche *et al.* 2017). The study species is a sedentary breeder, whose egg-laying begins at the beginning of May. The clutch size amounts to 6–7, white, very shiny and quite pear-shaped eggs (Snow *et al.* 1998, Bougaham 2016). Literature resources show that on the North African scale, the characteristics of its cavities remain unknown. Only Bougaham (2016) studied briefly the dimensions of seven cavities located in the Babors Mountains in northern Algeria.

In this context, the main objective of this work is to provide new ornithological information, especially for the size and orientation of the cavities excavated by the Levaillant's Woodpecker, resident of the forest of Aurès Mountains in northeast Algeria. It is also a question of highlighting the potential relationships between the local climatic conditions and the entrance area, the chamber volume, and the cavity entrance orientation.

Material and Methods

Study area

This study was carried out in the eastern part of the Aurès Forest massifs in northeast Algeria *(Figure 1)*, precisely in the Ouled Yagoub natural cedar forests (35°19'N, 6°76'E at 35°45 'N, 7°01'E). These ecosystems have altitudes ranging from 1,400 m to 2,173 m and are formed of pure cedar forests on the summits and mixed cedar forests (Atlas cedar *Cedrus atlantica*, Holm oak *Quercus ilex*, Aleppo pine *Pinus halepensis*, and Dimorphic ash *Fraxinus dimorpha*) on medium and low altitudes (B.N.E.D.E.R. 2010), which span three bioclimatic levels: cold humid, cold subhumid, and cool subhumid level *(Table 1)*.

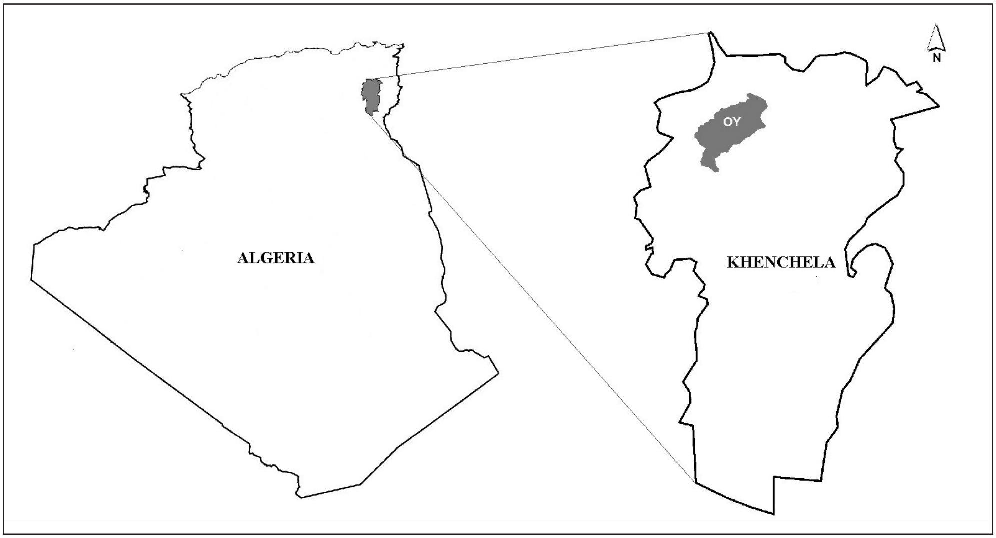

Figure 1. Location of Ouled Yagoub cedar forests in Khenchela – Algeria
1. ábra Az Ouled Yagoub cédrus erdő elhelyezkedése az algériai Khenchela tartományban

Table 1. Distribution of the bioclimatic levels of the study area according to altitude and local climatic conditions
1. táblázat A három különböző bioklimatikus zóna (hideg humid, hideg szubhumid, hűvös szubhumid) tengerszint feletti magasság, évi csapadékmennyiség és évi hőingás adatai

Bioclimatic level	Altitude (m)	Rainfall (ml)	T (°C min-max)
Cold humid	1950 – 2173	837	-1.22 – 32.08
Cold subhumid	1700 – 1950	777	-0.72 – 32.96
Cool subhumid	1450 – 1700	672	0.15 – 34.50

Nest cavity search and measurements

During two breeding seasons (March to July) of 2018 and 2019, using the point count method with playback (De Rosa *et al.* 2016), woodpeckers were searched in 75 stations, randomly chosen, and separated by at least 300 m to avoid double counting. Once the species was heard or seen, a systematic search for nests was launched within a radius of 150 m measured from the listening station. Identified nest cavities were located with a GPS.

Using a ladder, we were able to reach 52 cavities located at a height of less than 5.4 m, 44 in 2018 in the cedar forests and 8 in 2019 in the pine forests. The parameters we measured included: entrance height, entrance width, chamber diameter, chamber depth, using a tape measure in the reachable cavities. We measured the entrance orientation with a compass. Sizes of the interior chamber were taken for 20 reached nest cavities *(Table 2)*. All these measurements were recorded in the autumn to avoid disturbing the nesting process (Tamungang *et al.* 2016).

Entrance height and entrance width measures were used to calculate the entrance area for each cavity according to the formula defined by Kosinski and Ksit (2007):

Entrance Area = π ab (Where a and b were the half height and the half width of entrance). Similarly, chamber diameter and chamber depth measures were used to calculate the chamber volume according to the formula of Kosinski and Ksit (2007):

Chamber Volume = π (Chamber diameter/2)^2 Chamber depth.

The estimation of cavity entrance shape was based on the ratio between entrance height and entrance width (Baral *et al.* 2018) depending on the calculated proportions: round shape (proportion = 1–1.5); oval shape (1.6–3.5), and elongated shape (> 3.5).

Statistical analyses

To estimate the importance of the potential relationships established between the climatic conditions and the morphometric variables, we performed analysis of variance (ANOVA). The normality of these variables was verified by the Shapiro-Wilk test. The minimum level of probability allowed was treated as $P \leq 0.05$. The software used for the statistical calculations was IBM SPSS Statistics 23 (IBM 2015)

Based on circular statistics (Batschelet 1981), the Rayleigh uniformity test allowed us to identify the predictors of the cavities' entrances orientation. Indeed, a random distribution indicated the absence of preference, unlike the selective distribution which designated a predilection of the species for precise orientation. Circular orientation data was analysed by Oriana software version 4, Kovach Computing Services (Kovach 2011).

Results

Morphologic characteristics of nest cavities

The 52 available nest cavities of the Levaillant's Woodpecker detected in the Ouled Yagoub cedar forest in 2018 and 2019 were unevenly distributed over the different bioclimatic levels:

Table 2. Size and orientation of the Levaillant's Woodpecker cavities in the Ouled Yagoub cedar forest

2. táblázat A vizsgált odúparaméterek adatai. Az oszlopok: mintaszám, minimum-maximum, átlag, szórás. A vizsgált paraméterek fentről lefelé: a röpnyílás magassága, szélessége, területe, irányszöge, az odú belső átmérője, mélysége és űrtartalma

Parameter	N	Min – Max	Mean	SD
Entrance Height (cm)	52	4.2 – 11.7	7.26	1.51
Entrance Width (cm)	52	4.05 – 10.8	7.11	1.44
Entrance Area (cm^2)	52	13.35 – 78.5	41.93	15.27
Entrance Orientation (°)	52	0 – 320	263.65	117.54
Chamber Diameter (cm)	20	12 – 24.5	17.95	4.01
Chamber Depth (cm)	20	20.5 – 45.5	35.42	7.82
Chamber Volume (l)	20	2.71 – 18.53	9.98	5.64

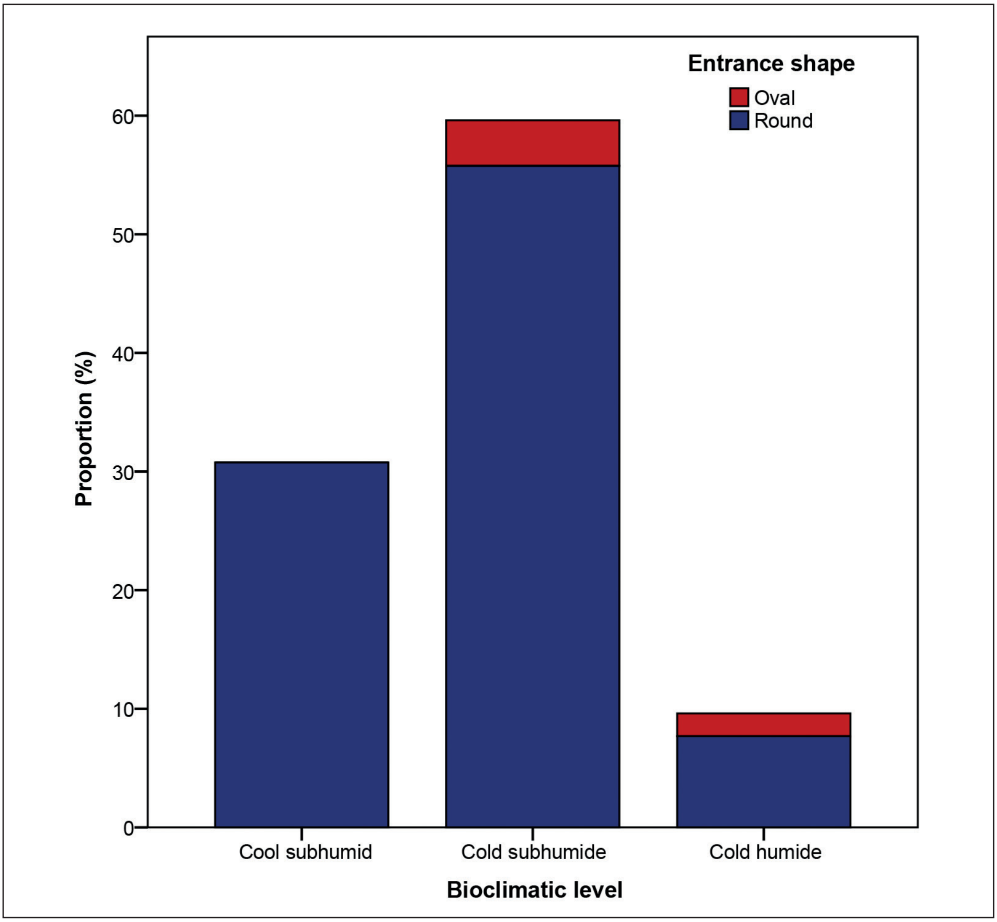

Figure 2. Distribution of the cavity entrances shapes over the three bioclimatic levels

2. ábra A röpnyílás alakok eloszlása a három bioklimatikus zónában (lásd *1. táblázat*)

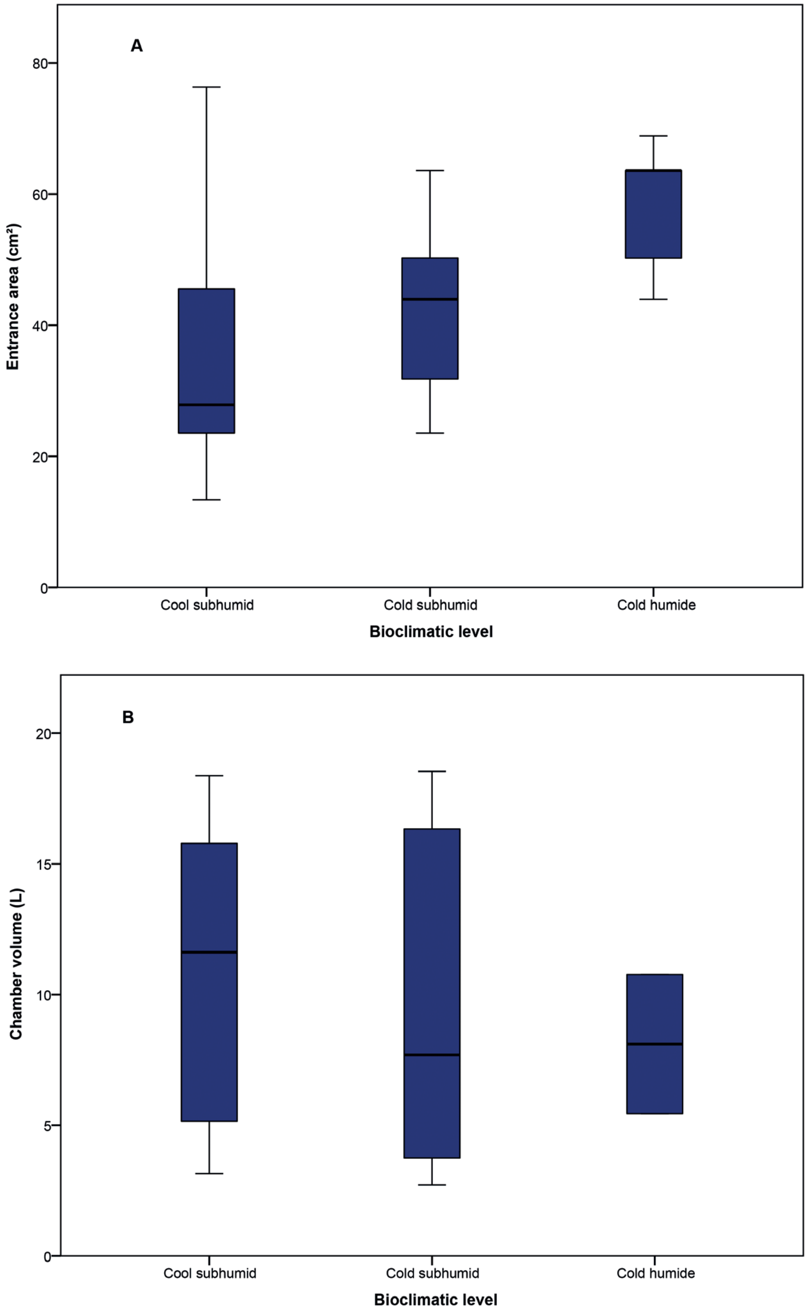

Figure 3. Variability of the sizes of Levaillant's Woodpecker nest cavities according to the bioclimatic levels: (A) cavity entrance area; (B) interior chamber volume

3. ábra Az odúméretek eloszlásai a három bioklimatikus zónában (lásd *1. táblázat*): (A) a röpnyílás területe; (B) az odú űrtartalma

5 at the cold humid level, 31 cavities at the cold subhumid level, and 16 cavities at the cool subhumid level.

Considering all bioclimatic levels combined, the values calculated for the cavity measurements were highly fluctuating *(Table 2)*. For example, the mean values recorded for cavity entrance height and width were 7.26 ± 1.51 cm and 7.11 ± 1.44 cm, respectively. The entrance area presented an average of 41.93 ± 15.27 cm² *(Table 2)*. In terms of cavity entrance, the ratio between the height and the width revealed a significant dominance of round shapes (94.2%) as compared to oval shapes (5.8%). No elongated entries have been found *(Figure 2)*.

The average diameter of the interior chamber was 17.95 ± 4.01 cm, whereas the depth of the chamber was found to be 35.42 ± 7.82cm. The calculated chamber volume was 9.98 ± 5.64 L.

Climate influence on cavity size and orientation

The ANOVA test revealed a significant effect of the bioclimatic level on the cavity entrance area (F = 4.64; df = 2; P = 0.01). Indeed, the Levaillant's Woodpecker decreased the entrance area from the cold humid level with 58.04 ± 10.46 cm² to the cool subhumid

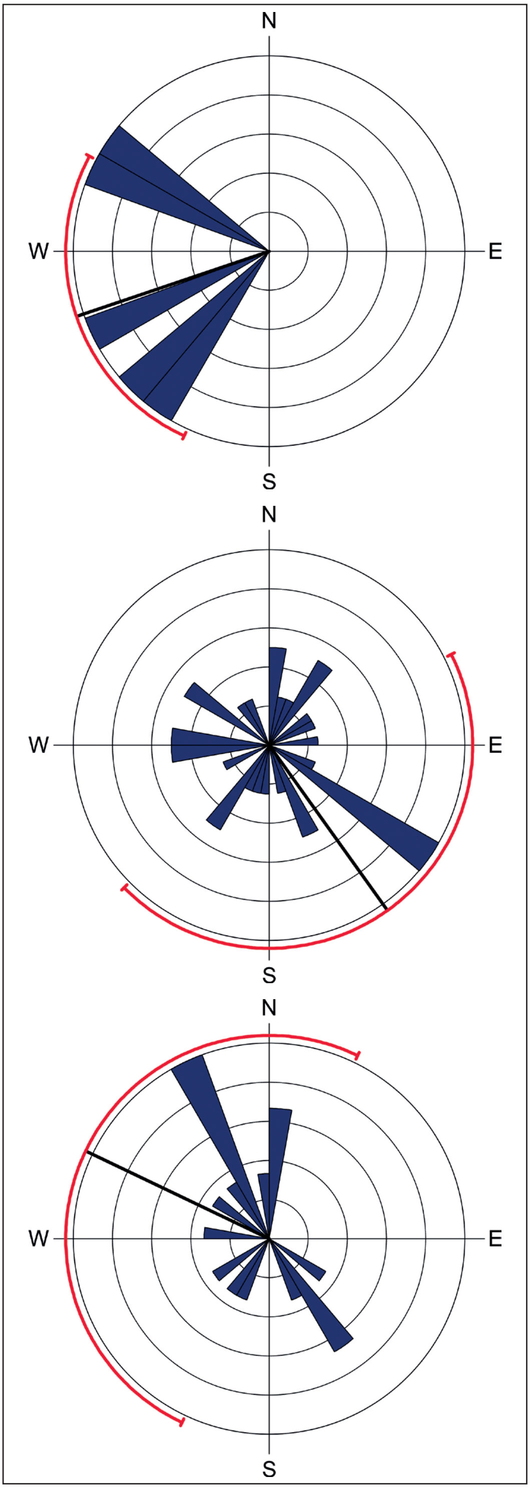

Figure 4. Orientation of entrances to Levaillant's Woodpecker nest cavities in three bioclimatic levels in the study area: (A) cold humid bioclimatic level; (B) cold subhumid bioclimatic level; (C) cool humid bioclimatic level

4. ábra A röpnyílások tájolása a három bioklimatikus zónában (a sorrendhez lásd *1. táblázat*) level with 35.873 ± 18.22 cm², passing by the cold subhumid level being 42.46 ± 12.35 cm² *(Figure 3A)*. The values of the chamber volume were independent of local climate variability (F = 0.186; df = 2; P = 0.832). Indeed, its mean values were found to be 8.1 ± 3.76 L at the cold humid level, 9.6 ± 6.5 L at the cold subhumid level, and finally 10.67 ± 5.6 L at the cool subhumid level *(Figure 3B)*.

The Rayleigh test of uniformity showed a preference for the west-southwest direction at high altitude characterised by a cold humid climate (Mean = 251.31° ± 37.7; Rayleigh test z = 3.24; P = 0.03) *(Figure 4A)*. In contrast, the species randomly chooses the direction of its cavities in the cold subhumid climate (Rayleigh test z = 0.04; P = 0.96) and in the cool subhumid level (Rayleigh test z = 0.75; P = 0.47) *(Figure 4B,C)*.

Discussion

The results of this work reveal that the mixed cedar forests of cold subhumid bioclimatic level represent a favourable environment for the survival of Levaillant's Woodpecker in the Aurès Mountains in Algeria. These ecosystems have a varied vegetation cover dominated by Atlas cedar and holm oak trees, which provides wooden structures to excavate nest cavities for Levaillant's Woodpecker (Badis & Hamdi 2022). They offer optimal and safe conditions for the implementation of cavities such as the low flammability and consistency of cedar woods, as well as its tolerance to various water and climatic stress (Valette 1990, Epron 1997, Ladjal *et al.* 2000, Brunetti *et al.* 2001, Moussouni & Boubaker 2015).

In woodpeckers, the dimensions, and shapes of the entrances to their nest cavities are adapted to body size (Kerpez & Smith 1990, Kosinski & Ksit 2007, Wan *et al.* 2008). This study showed that the cavity entrances of Levaillant's Woodpeckers in the Aurès Mountains are mostly round (94.2%). This observation is consistent with those specific to its European counterpart, the Green Woodpecker, while oval entrances remain reserved for exceptionally large individuals (Gorman 2015, Bütler *et al.* 2020). The absence of the elongated shape is consistent with the results of Baral *et al*. (2018), which linked this shape to non-excavated cavities resulting from mechanical damage and ageing structures of the tree.

Among our studied variables, only the cavity entrance area is significantly influenced by local climatic conditions. At the cold humid level, at a very high altitude, the cavities have larger average entrances compared to those of the cold subhumid and cool subhumid levels. Indeed, it seems that it is a response to the relatively hostile climatic conditions that prevail at high altitudes. This woodpecker adopts this choice to receive maximum solar radiation, reduce humidity and increase the temperature inside the cavities (Wiebe 2001). The reduction of entrance area at medium and low altitudes constitutes, in contrast, a mode of adaptation to avoid predators and competitors (Li & Martin 1991). In this context, various forestry studies confirm that cavity nester species occur in lower abundances with increasing altitude (Jansson & Andren 2003, Moussouni & Boubaker 2015, Bertuzzo *et al.* 2016).

The variability of the chamber volume of Levaillant's Woodpecker cavities in the Aurès Mountains is random and has no significant relationship with the local climate. Indeed, this parameter is most often determined by the number of chicks, which varies from five to seven

(Bougaham 2016), but probably by the body size of the parents and the consistency of the nesting tree.

In general, cavity-nesting birds have a preference for cavity entrance orientation (Mennill & Ratcliffe 2004). This choice is maintained to ensure optimal conditions, in particular a microclimate of the internal chamber favourable to the hatching and the viability of the chicks and therefore, to reproductive success (Conway & Martin 2000, Hartman & Oring 2003, Mainwaring *et al.* 2016). Concerning the present study, only at the cold humid bioclimatic level, at very high altitudes, the Levaillant's Woodpecker excavates cavities oriented in the west-southwest direction. This is a relatively effective strategy for receiving the most sunshine and warming the brood sufficiently. In addition, such an orientation promotes morning warming (Gorman 2021). This warming is associated with reproductive success as mentioned by Wiebe (2001) in a study on Northern Flicker *Colaptes auratus.* However, in the cool and cold subhumid levels, at low and medium altitudes, the orientation of the cavities is random. This observation is the same as concluded by previous studies on other forest and ecologically related species (Inouye *et al.* 1981, Ćiković *et al.* 2014). In this case, the Levaillant's Woodpecker seems to orient its cavities depending on the consistency of the wooden supports. It prefers to excavate in the decayed parts of the tree (Gorman 2021).

The results of this study represent the first scientific documentation of the nesting cavities measurements of this unknown endemic woodpecker species. The analysis of the influence of the local climate on the variability of the sizes and the orientation of the cavities of Levaillant's Woodpecker, endemic to northwest Africa, reveals an adaptive behaviour of the species towards local climatic conditions. Despite the reduced number of samples studied, especially on mountain peaks, these findings constitute an interesting database for understanding the ecology and reproduction of this woodpecker. It is an initiation to other studies that can form a basis for the development of strategies for the management and conservation of forest massifs in the Aurès Mountains.

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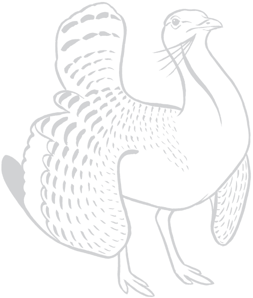

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Allometric inter-relationships between jaw musculature mass, skull size and body mass in *Psittaciformes*

Shannon L. Harrison, Gregory P. Sutton & D. Charles Deeming*

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Abstract Functional characteristics of the jaw apparatus, for example bite force, in vertebrates is a combination of the skeleton and the musculature. In birds, bite force has been measured directly or calculated using various methods including summation of forces generated by the different elements of the jaw musculature. However, there have been no reports of the relationships between body size with the mass of the different muscle groups in a closely related group of birds. This study explored allometry in the different jaw muscle masses from parrot (Psittaciformes) species differing in body mass by 40-fold. It was hypothesised that the different muscle masses would exhibit isometry with body mass and skull size. Parrot heads were dissected and the masses of the individual muscle complexes were recorded. Data were subjected to phylogenetically-controlled regression analysis to document scaling effects with body mass and skull size. Most, but not all muscles, exhibited positive allometry with body mass but most were isometric with skull size. Consequently, as parrots get bigger, their skulls get proportionally longer, but that the muscles within the head isometrically scaled relative to the size of these proportionally larger skulls. The large muscles imply greater bite forces in parrots than have been reported to date, which seems to be associated with an increase in skull size to accommodate more muscles. It is unknown whether this pattern is applicable to other birds within specific orders or even across birds as a whole. There needs to be further investigation into the allometry of the morphological and functional properties of the avian jaw musculature.

Keywords: parrot, anatomy, jaw, jaw muscles, skull, skull size, allometry, bite force

Összefoglalás Az állkapocs funkcionális jellemzői, mint például a harapási erő, a gerinceseknél a csontváz és az izomzat kombinációjából adódnak. Madaraknál a harapási erőt közvetlenül mérték vagy különféle módszerekkel számították ki, beleértve az állkapocs izomzatának különböző elemei által generált erők együttesét is. Ennek ellenére nem készültek kutatások a testméret és a különböző izomcsoportok tömege közötti összefüggésekről közeli rokon madárcsoportok esetében. Ez a tanulmány az állkapocs izmok tömegének allometriáját vizsgálta papagájoknál (Psittaciformes), mely csoportban a testtömegbeli különbség akár 40-szeres is lehet a fajok között. A kiindulási hipotézis az volt, hogy a különböző izmok tömegei izometriát mutatnak a testtömeggel és a koponyamérettel. A papagájfejek boncolása után az egyes izomcsoportok tömegét mértük. Az adatokat filogenetikai elemzésnek vetettük alá, hogy megvizsgáljuk a méretkülönbségből adódó hatásokat a testtömeggel és a koponyamérettel kapcsolatban. A legtöbb (azonban nem az összes) izomcsoport pozitív allometriát mutatott a testtömeggel, de a legtöbb izometrikus volt a koponya méretével. Következésképpen, minél nagyobb az adott papagáj testtömege, koponyája arányosan hosszabb, de a fej izmai izometrikusan arányosan nagyobbak a koponyához mérten. A nagyobb izmok nagyobb harapási erőt jelentenek, mint ahogyan azt korábban feltételezték, ami arra enged következtetni, hogy a koponyaméret növekedésével több izomnak biztosítható tapadási felület. Nem ismert, hogy ez a minta alkalmazható-e a madarak más rendjein belül, vagy akár a madarak egészére. További vizsgálatokra van szükség a madarak állkapocs izomzatának morfológiai és funkcionális tulajdonságainak allometriáját illetően.

Kulcsszavak: papagáj, anatómia, állkapocs, állkapocs izmok, koponya, koponyaméret, allometria, harapás erősség

Department of Life Sciences, School of Life and Environmental Sciences, University of Lincoln, Joseph Banks Laboratories, Lincoln, LN6 7DL, UK;
** corresponding author, e-mail: cdeeming@lincoln.ac.uk*

Introduction

Jaw function and associated bite force are important for animals because they determine the range of dietary items an organism can consume (Nogueira *et al.* 2009, Maestri *et al*. 2016, Sakamoto 2021). The anatomy of the jaw apparatus of birds is commonly reported but often only as a qualitative description of the anatomy of the jaw (e.g. Burton 1974a). Other studies have taken a quantitative approach and report the size of the muscles jaw apparatus (e.g. Burger 1978), whereas other studies have a more functional approach exploring bite force, which is an ecologically relevant performance trait (Deeming *et al*. 2022). Bite force is a function of the force exerted by muscle contraction applied via the skeleton. It is often measured *in vivo* with animals biting down on force transducers (Herrel *et al*. 1999, Sustaita & Hertel 2010, Verma *et al*. 2017) but can also be calculated from the morphometrics of skulls (Anderson *et al*. 2008), or using finite element analysis of 3D images generated by computerised tomography (e.g. Cost *et al.* 2020). In addition, skulls can be dissected to reveal muscle masses, which can be used to calculate bite force in birds (Sustaita 2008, Soons *et al*. 2015). Recently, Deeming *et al.* (2022) showed that the relationship between muscle mass and bite force in birds exhibited positive allometry but in reptiles this relationship was isometric (Deeming 2022). Although this difference may reflect taxonomic variability, one possible reason for this discrepancy could be the limited and biased range of species represented in the avian dataset compared to that for reptiles. Deeming (2022) had values for over 275 species of reptile but for birds, 46 of the 122 species were from the Passeriformes and were no larger than 70 g (Deeming *et al*. 2022).

Muscle dissection is a way of calculating bite force, but muscle masses in birds are only reported in a relatively few species, including (but not exclusively): cormorants Suliformes, (Burger 1978), birds of prey Accipitriformes and Falconiformes (Sustaita 2008 and see Hull 1991, 1993, Wang *et al.* 2017, Deeming *et al.* 2022), waterfowl Anseriformes, (Goodman & Fisher 1962), and songbirds Passeriformes, (e.g. van der Meij & Bout 2004). However, within these taxa the spread of data can be limited. For instance, data for muscle mass is available from only 7 different families of songbirds (see Deeming *et al*. 2022) and often these data represent values for all jaw muscles combined. However, the jaw musculature of birds is a complex of different muscle groups, which all have differing roles in the operation of the jaw (Burger 1978, Bhattacharyya 2013): depressors (that open the jaw); adductors (that raise the mandible); protractors (which lower the upper jaw); and retractors (which simultaneously raise the mandible and lower the upper jaw). In passerines, data for masses of these different muscle groups are limited to 10 species from two bird families, which only vary in body mass between 9–33 g (Soons *et al*. 2012, 2015). However, even across a limited size range van der Meij and Bout (2004) showed that total jaw muscle mass, and individual functional muscle groups, exhibited positive allometry with body mass in the Fringillidae and Estrildidae. This paucity of data, and limited ranges in body size for muscle masses in birds, leave little scope for exploring allometric scaling relationships for different jaw muscle types and how these could impact on the functional properties of the jaw apparatus, that is bite force.

The Psittaciformes are noted for their strong bite force (Carril *et al.* 2015, Cost *et al.* 2020) and dexterity in processing food items with the beak (Auersperg *et al.* 2012, Toft & Wright 2015). Body masses (Dunning 2008) in parrots range from around 12 g for pygmy-parrots (*Micropsitta* spp.) through to over 1300 g for the Hyacinth Macaw *(Andorhynchus hyacinthinus)* for 2000 g for the male, flightless Kakapo *(Strigops habroptila)*. This range of body sizes offers scope to investigate the relationships between body size with the mass of the different muscle groups in a closely related group of birds. This study, therefore, explored allometry in the different jaw muscle masses from a variety of parrot species ranging in body mass by 40-fold. Given the similarity in skull and beak morphology seen in the Psittaciformes (Zusi 1993), because earlier studies in reptiles showed that muscle mass isometrically scaled with body mass and showed marginal positive allometry with skull size (Deeming 2022), we hypothesized that this would also be true in Psittaciformes. The results will provide an insight into how body size impacts on the myology of the jaw apparatus in this order and how this may impact on the functional properties of the jaw apparatus, i.e. the production of bite force.

Methods

Parrot cadavers of nineteen species were obtained from the Lincolnshire Wildlife Park, Friskney, Lincolnshire, UK. All birds had died of natural causes and sample sizes varied according to species *(Table 1)*. The birds were stored in plastic bags and frozen at –20 ºC until required. The cadavers were often not intact and so body mass (in g) used for the parrots was the average reported by Dunning (2008) rather than the mass of the bird at the time of dissection. The range of body masses *(Table 1)* was from 29 g for the Budgerigar *(Melopsittacus undulatus)* to 1215 g for the Red-and-green Macaw *(Ara chloropterus)*.

Birds were defrosted for 24 hours prior to dissection. The heads of the parrots were cut from the bodies before being skinned, exposing the muscles. Each muscle complex was identified and dissected away from the skull. Subdivisions of the muscles (Homberger 2017) were not considered because the contraction of the elements of a muscle complex would have the same physical effect. Muscle tissue was then blotted dry and the wet mass recorded (in g) using a digital Sartorius® micro balance. Where possible, both sides of the head were dissected but in some specimens the muscles were damaged, so data were only available from one side. Therefore, data are presented as an average muscle mass of one side of the head.

To expose the skull for measurement, the head was de-fleshed by soaking in Tergazyme at 15% concentration at 40 ºC. The skulls were then soaked in a solution of concentrated washing up liquid and water, to remove any Tergazyme residue and any residual grease from the bones before drying for 2–3 days in an incubator at 20 ºC. Using digital callipers (RS Pro, 2020), the total length of skull was measured (in mm) from a dorsal view and was the distance between the supraoccipital crest and the tip of the maxilla.

Table 1. Mean (± SE) body mass (in g, as reported by Dunning, 2008), skull length (in mm), and masses of individual single muscle complexes (in g) per species. Number of individuals in the dataset are indicated in parenthesis. Standard error values were calculated for species values where there were 3 or more individuals present

1. táblázat Átlagos (± SE) testtömeg (g-ban, Dunning, 2008 után), koponyahossz (mm) és az egyes izomcsoportok tömege (g) fajonként megadva. A vizsgálatban szereplő egyedek száma a zárójelben van feltüntetve. A sztenderd hibaértékeket azokra a fajokra számítottuk, ahol 3 vagy annál több egyed szerepelt

Species	**Body mass (g)**	**Skull length (mm)**	***Depressor mandibulae* (g)**	***Adductor mandibulae externus* (g)**	***Pseudomasseter* (g)**	***Pterygoideus ventralis* (g)**	***Pterygoideus dorsalis* (g)**	***Ethmomandibularis* (g)**
Cacatua alba (N = 3)	570.0	78.0 ± 2.2	1.00 ± 0.12	0.70 ± 0.08	0.99 ± 0.43	1.71 ± 0.22	0.69 ± 0.04	0.68 ± 0.09
Cacatua galerita (N = 3)	720.4	76.9	1.22	0.91	1.39	2.32	0.74	1.49
Cacatua moluccensis (N = 1)	835.0	91.3	1.10	0.89	1.65	2.19	0.95	0.97
Melopsittacus undulatus (N = 1)	29.0	27.3	0.03	0.01	0.01	0.02	0.01	0.02
Psittacula eupatria (N = 1)	214.0	59.0	0.42	0.25	0.64	1.05	0.30	0.43
Psittacula krameri (N = 4)	116.1	45.8 ± 0.9	0.10 ± 0.02	0.07 ± 0.01	0.10 ± 0.01	0.24 ± 0.02	0.08 ± 0.01	0.17 ± 0.01
Ara ararauna (N = 3)	1125.0	106.4 ± 5.3	1.27 ± 0.06	1.02 ± 0.07	0.63 ± 0.25	2.31 ± 0.17	1.30 ± 0.14	1.81 ± 0.61
Ara chloropterus (N = 3)	1214.0	117.8 ± 1.5	2.07 ± 0.20	1.98 ± 0.41	0.44 ± 0.12	4.99 ± 0.71	2.33 ± 0.23	2.04 ± 0.58
Ara macao (N = 1)	1015.0	103.9	1.26	1.30	0.37	2.94	1.13	0.81
Amazona aestiva (N = 2)	451.0	65.6	0.35	0.18	0.31	0.62	0.25	0.43
Amazona amazonica (N = 3)	370.0	67.6 ± 2.0	0.34 ± 0.04	0.20 ± 0.01	0.30 ± 0.02	0.76 ± 0.10	0.21 ± 0.02	0.36 ± 0.03
Amazona auropalliata (N = 1)	476.9	65.6	0.32	0.28	0.61	0.79	0.22	0.47
Amazona autumnalis (N = 2)	416.0	72.2	0.31	0.19	0.46	0.77	0.25	0.35
Amazona farinosa (N = 1)	626.0	79.8	0.51	0.25	0.38	1.21	0.52	0.95
Amazona ochrocephala (N = 3)	476.9	65.3 ± 2.2	0.34 ± 0.01	0.20 ± 0.03	0.28 ± 0.05	0.80 ± 0.10	0.22 ± 0.02	0.58 ± 0.03
Amazona oratrix (N = 1)	517.0	72.4	0.26	0.28	0.18	0.53	0.19	0.29
Myiopsitta monachus (N=3)	120.0	41.8 ± 2.8	0.10 ± 0.02	0.10 ± 0.01	0.05 ± 0.01	0.14 ± 0.02	0.08 ± 0.01	0.11 ± 0.01
Poicephalus senegalus (N = 2)	147.0	49.6	0.10	0.11	0.16	0.33	0.14	0.22
Psittacus erithacus (N = 5)	333.0	71.5 ± 1.8	0.46 ± 0.04	0.52 ± 0.10	0.44 ± 0.09	1.01 ± 0.15	0.25 ± 0.03	0.52 ± 0.09

Mean values were calculated for those species which had repeated samples *(Table 1)*. Unless stated otherwise, mass and linear measurments were $\log_{10}$-transformed prior to analysis and analysis was performed in R (version 4.0.3; R Development Core Team 2021). Linear models were used to compare logit-transformations (Warton & Hui 2011) of the proportions of the different muscles in the three genera where there were three or more representatives, i.e. the macaws *(Ara)*, amazons *(Amazona)* and cockatoos *(Cacatua)*.

Allometric relationships among body mass, skull length and muscle masses were explored using phylogenetically controlled general linear modelling (pglm) performed in R. This analysis used the statistical packages "*ape*" (Paradis *et al*. 2004), "*MVTnorm*" (Genz & Bretz 2009), and "*MASS*" (Venables & Ripley 2002), with additional code supplied by Dr Carl Soulsbury (personal communication) to run the phylogenetically controlled generalised linear models to test for the linear relationship between variables. To control for phylogeny, a time calibrated phylogeny was constructed using a subset downloaded from the Hackett all species backbone birdtree.org (Jetz *et al*. 2012) and was identical to the tree presented by Provost *et al*. (2018). The phylogenetic signal, λ, indicated that the observed covariance in residuals was similar to that expected under a Brownian motion model of trait evolution (Freckleton *et al.* 2002). By contrast, a low value for λ indicated that this relationship exhibited no discernible evolutionary signal (Freckleton *et al.* 2002). Comparison of exponents against expected isometric slopes was performed using one-sample t-tests based on the method of Bailey (1981).

Results

Muscle complexes

Six muscle complexes were identified in the jaw musculature of the parrot species investigated following previous descriptions (Homberger 2003, 2017, Tokita 2003, Carril *et al*. 2015). These are briefly described here in terms of their physical location and characteristics *(Figure 1)*.

Depressor mandibulae (DM, *Figure 1*, grey): The *depressor mandibulae* muscle was the main depressor of the jaw and originated caudal to the occipital region on the skull, running downwards along the occipital crest. The upper portion of the muscle was wider than its insertion. This sheet of muscle inserted onto, and along the posterior edge of, the mandible on the dorsal aspect of the articular.

Adductor mandibulae externus complex (AME, *Figure 1*, red): This was the larger of the three adductor muscle complexes, which consisted of highly integrated muscle subdivisions. In general, this complex had a large area of origin over the skull associated with the *adductor mandibulae externus superficialis* that originated at the *fossa temporalis* and through the fossa beneath the orbit. In macaws (*Ara* spp.), this muscle covered a large area of bone around the dorsal aspect of the occipital process, whereas in the Budgerigar there was very little external coverage of this muscle. The AME complex then appeared to convert from surface to point attachment whereby a portion of the muscle suspended internally

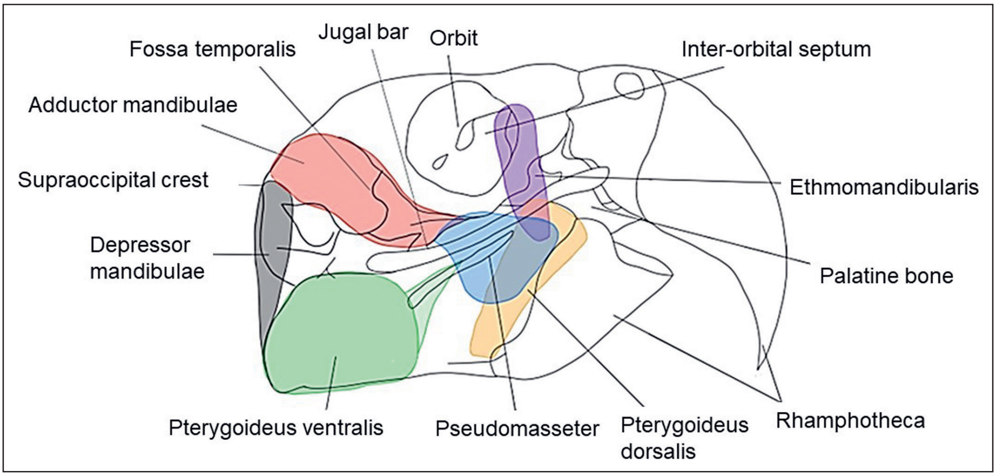

Figure 1. An outline of an *Ara chloropterus* skull with the various jaw muscles illustrated by different colours. See text for more details

1. ábra Egy *Ara chloropterus* koponyájának körvonala az egyes állkapocsizmokkal, különböző színekkel jelölve. További részletek a szövegben

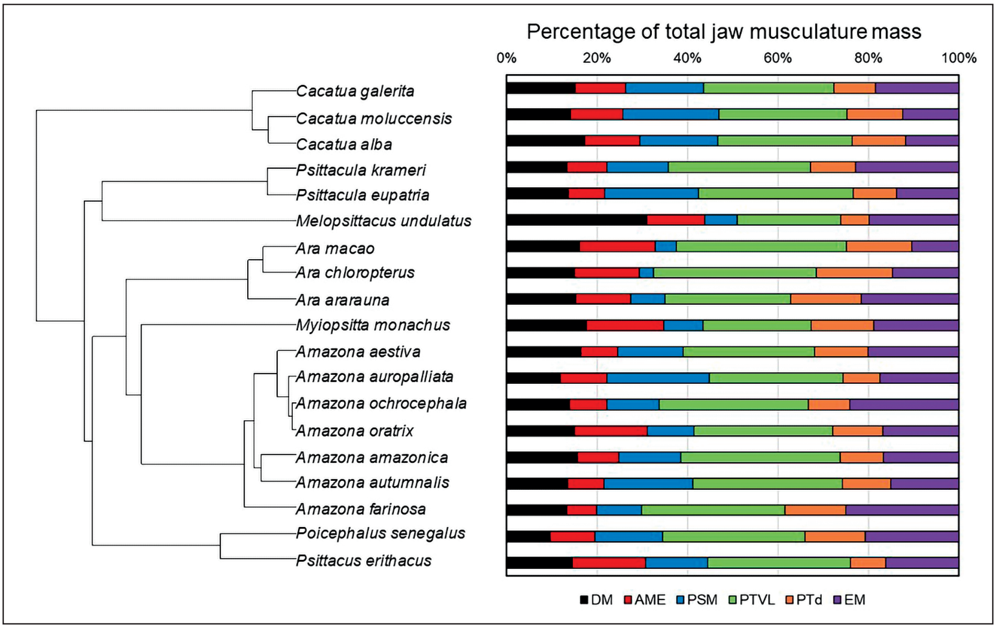

Figure 2. Phylogenetic tree showing the relatedness of the species within this dataset (generated by birdtree.org) alongside each individual muscle mass expressed as a mean percentage of the total muscle mass. DM – *Depressor mandibulae*, AME – *Adductor mandibulae*, PSM – *Pseudomasseter,* PTVL – *Pterygoideus ventralis,* EM – *Ethmomandibularis*, PTd – *Pterygoideus dorsalis*

2. ábra A tanulmányban szereplő fajok filogenetikai viszonya (forrás: birdtree.org), valamint az egyes fajokhoz tartozó átlagos izomtömegek százalékos aránya. DM – *Depressor mandibulae*, AME – *Adductor mandibulae*, PSM = *Pseudomasseter,* PTVL – *Pterygoideus ventralis,* EM – *Ethmomandibularis*, PTd – *Pterygoideus dorsalis* within the cranium attaching to the lower jaw between two ridges on medial edge of the mandible.

Pseudomasseter (PSM, *Figure 1*, blue): The *pseudomasseter* muscle was a second adductor muscle found on the exterior lateral surface of the skull and mandible, originating from the mid-distal end of the *arcus suborbitalis* seen in some species, especially cockatoos (Cacatuidae). The PSM was a sheet of muscle that attached to the surface of the mandible at the anterior region, extending antero-dorsally outwards both towards the superior and inferior regions of the mandibular rhampotheca. Species of *Ara* and *Psittacula* had undeveloped *pseudomassester* muscles compared with those observed in species of *Cactua* and *Amazona*.

Ethmomandibularis (EM, *Figure 1*, purple): This substantial adductor muscle lacked subdvisions and originated from a large region ventral to the inter-orbital septum and followed downwards the length of the *os ectethmoidale*. The EM inserted onto the inside of the lower mandible towards the cranial aspect of the jaw.

Pterygoideus ventralis (PTVL, *Figure 1*, green): This muscle complex was the largest retractor and was closely associated with the *pterygoideus dorsalis* muscle (see below). However, the *pterygoideus ventralis* was a sheet of muscle predominantly located on the external surface of the mandible. The PTVL originated from the pterygoid bone and then extends downwards to the bottom of the mandible. It then wrapped around the ventral edge of the mandible, eventually inserting on the outer lateral surface of the mandible in a fan-like manner. Superficially this muscle is covered by an aponeurosis. This muscle exhibited some variability not only in mass but in its association with surrounding structures. For example, in the Cacatuidae the PTVL was superficially robust, extending outwards away from the edge of the mandible and closely

Table 2. Results from phylogenetically-corrected linear regression models testing the relationships between average body mass (g), average skull length (mm) and average total jaw muscle mass (g), for 19 species of parrot. All data were $\log_{10}$-transformed before analysis and the intercepts presented at log-values

2. táblázat Az átlagos testtömeg (g), az átlagos koponyahossz (mm) és a teljes állkapocs izomtömegének átlaga (g) közötti összefüggéseket bemutató táblázat, amelyek értékei filogenetikailag korrigált lineáris regressziós modellek eredményei a vizsgálatban szereplő 19 papagájfaj esetében. Az elemzés előtt minden adat 10-es alapú logaritmus értékét vettük, az így kapott tengelymetszetek log-értékeit tüntettük fel

Relationship		**Exponent (SE)**	**t (p-value)**	**$F_{1,17}$**	**R^2**	**λ**
Skull length vs Body mass	Intercept Slope	0.832 (0.054) 0.389* (0.020)	15.28 (<0.0001) 19.60 (<0.0001)	384.3	0.957	0.911^{A}
Jaw muscle mass vs Body mass	Intercept Slope	-2.984 (0.278) 1.339** (0.105)	-10.73 (p<0.0001) 12.81 (p<0.0001)	164.1	0.958	$0.676^{A,B}$
Jaw muscle mass vs Skull length	Intercept Slope	-5.577 (0.444) 3.283 (0.242)	-12.56 (p<0.001) 13.60 (p<0.0001)	184.8	0.916	0.241^{B}

Slope values with * and ** indicate significant departures from isometry for skull length against body mass (isometric slope = 0.333), or jaw muscle mass against body mass (isometric slope = 1.0), at P = 0.05 and P = 0.01, respectively. The slopes for jaw muscle mass against skull length did not significantly depart from an isometric slope of 3.0. For λ values, superscript A and B indicate a significant difference from a value of 0 or 1, respectively at least P < 0.05

A *-al és **-al jelölt iránytangens értékek szignifikáns eltéréseket mutatnak az izometriát tekintve a koponyahossznak a testtömeghez (izometrikus meredekség = 0,333), illetve az állkapocs izomtömegének a testtömeghez viszonyítva (izometrikus meredekség = 1,0), P = 0,05 és P = 0,01. Az iránytangensek az állkapocs izomtömegének a koponya hosszához viszonyítva nem mutattak szignifikáns eltérést a 3,0 izometrikus meredekségtől

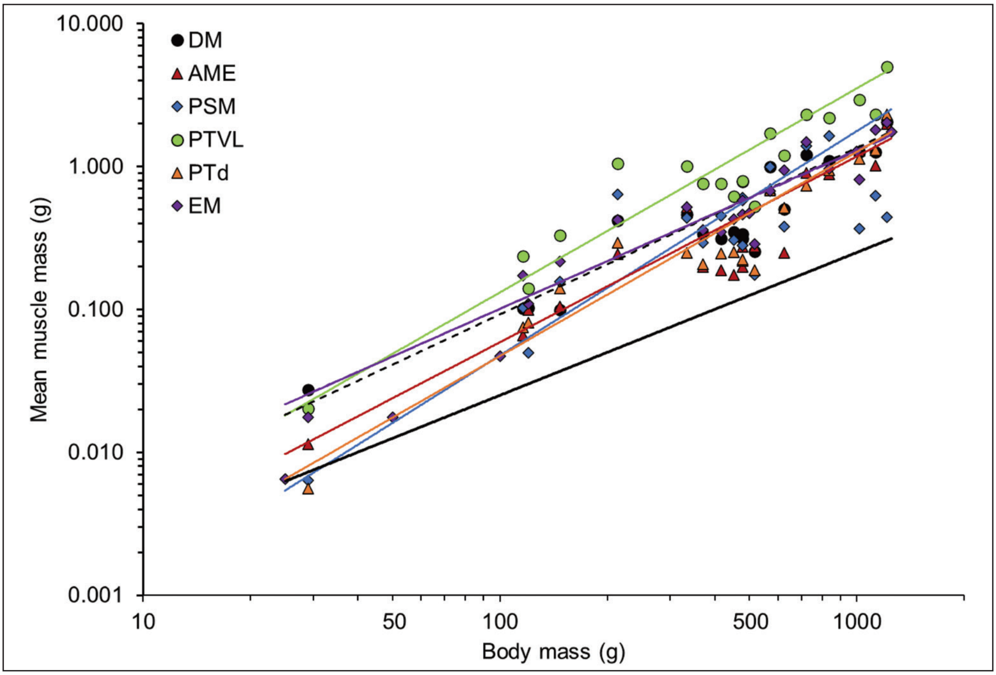

Figure 3. Relationships between mean values for body mass and individual jaw muscle masses for each parrot species. Colour of trendlines equates to the equivalent muscle symbol (except for DM, which is a dashed line), and were generated using phylogenetically controlled linear models calculated in R (see *Table 3*). The solid black line at the bottom is to illustrate a line with a slope of 1.0

3. ábra A testtömeg átlagértékei és az egyes papagájfajok állkapcsát alkotó izmok tömege közötti összefüggés. A trendvonalak színe megegyezik az egyes izmok szimbólumaival (ez alól kivételt képez a DM, ezt szaggatott vonal jelöli), az ábrát R-ben filogenetikailag kontrolált lineáris modellekkel hoztuk létre (lásd a *3. táblázat*). A legalsó folytonos fekete vonal az 1-es meredekséget szemlélteti

aligning with the equally substantial *pseudomasseter* (discussed earlier). In the Budgerigar and the Rose-ringed Parakeet *(Psittacula krameri)* the PTVL was relatively small, with very little definition between the outline of the lower jaw and the muscle itself.

Pterygoideus dorsalis (PTd, *Figure 1*, orange): The *pterygoideus dorsalis* was a substantial retractor muscule that originated from the edge of the dorsal element of the palatine and pterygoid bones and attached along the length of the bone's lateral surface. It inserted onto the mandible, past the quadrate and along a medial ridge which sat below the caudal mandibular fenestra.

The mass of each muscule complex varied between species *(Table 1)* and formed different proportions of the total jaw muscle mass *(Figure 2)*. The PTVL muscle formed the majority (on average 30.8%) of the total muscle mass in the parrots but other muscles varied between taxa. In particular, the PSM formed a significantly higher proportion of the total jaw muscle mass ($F_{2,10}$ = 15.24, P < 0.001) in cockatoos (*Cactua* sp., 18.6%) and amazons (*Amazona* sp., 14.6%) compared with macaws (*Ara* sp., 5.1%). By contrast, the PTd muscle formed a

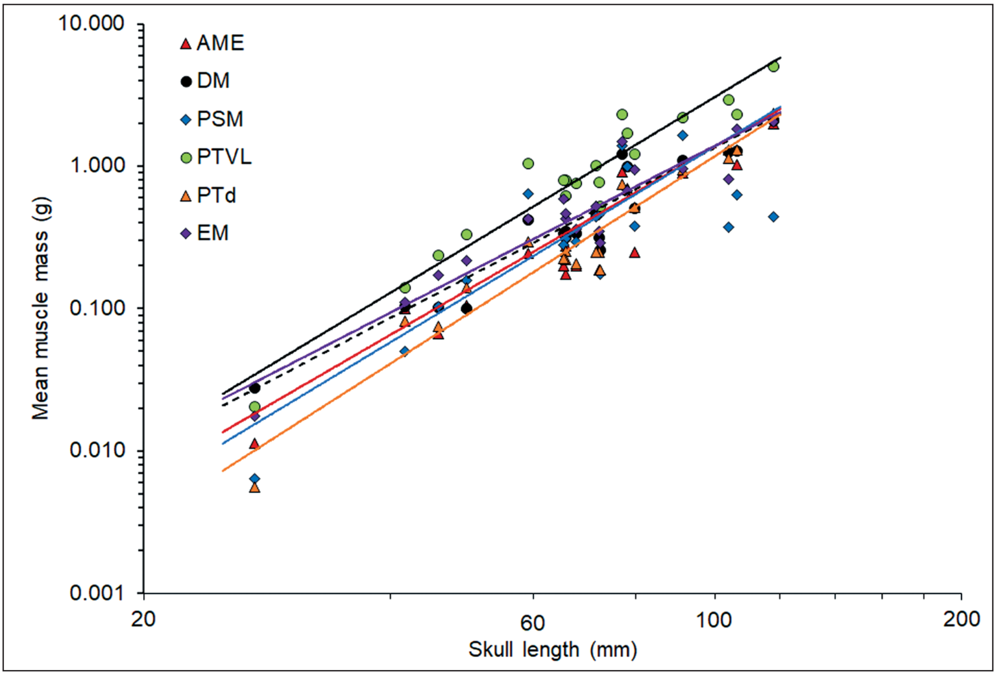

Figure 4. Relationships between mean values for skull length and individual jaw muscle masses for each parrot species. Colour of trendlines equates to the equivalent muscle symbol (except for DM, which is a dashed line), and were generated using phylogenetically controlled linear models calculated in R (see *Table 3*). The solid black line at the bottom is to illustrate a line with a slope of 3.0

4. ábra A koponyahosszok átlagértékei és az egyes papagájfajok állkapcsát alkotó izmok tömege közötti összefüggés. A trendvonalak színe megegyezik az egyes izmok szimbólumaival (ez alól kivételt képez a DM, ezt szaggatott vonal jelöli), az ábrát R-ben filogenetikailag kontrolált lineáris modellekkel hoztuk létre (lásd a *3. táblázat*). A legalsó folytonos fekete vonal a 3-as meredekséget szemlélteti

significantly greater proportion of the total muscle mass in macaws compared to cockatoos and amazons (15.6%, 11.1% and 10.5% respectively; $F_{2,10} = 7.96$, $P < 0.01$). No significant differences were observed between these genera for the other muscle types.

Allometric relationships

There was a highly significant positive relationship between body mass and skull length *(Table 2)*. The phylogenetically-controlled slope was 0.39, which was significantly higher than the predicted isometric slope of 0.33 ($t_{18} = 2.82$, $P = 0.012$) with a high R^2 and high phylogenetic signal *(Table 2)*. Total jaw muscle mass also had highly significant relationships with body mass and skull length, and although the R^2 values were high, the phylogenetic signal was high for body mass but low for skull length *(Table 2)*. Total muscle mass showed significant positive allometry with body mass (observed slope of 1.34, which was significantly different from the hypothesized isometric slope of 1.0; $t_{18} = 3.24$, $P < 0.01$)

Table 3. Results from phylogenetically corrected models testing the effect of the body mass (g) and average skull length (mm) against the average individual muscle masses (g) for 19 species of parrot. All data were $\log_{10}$-transformed before analysis and the intercepts presented at log-values

3. táblázat A filogenetikailag korrigált modellek eredményei, amelyek az átlagos testtömeget (g) és az átlagos koponyahosszat (mm) vizsgálták az egyes egyedek átlagos izomtömegének átlagához mérten (g) 19 papagájfaj esetében. Az elemzés előtt minden adat 10-es alapú logaritmus értékét vettük, az így kapott tengelymetszetek log-értékeit tüntettük fel

		Body mass					**Skull length**				
Muscle complex		**Exponent (SE)**	**t (p-value)**	**$F_{1,17}$**	**R^2**	**λ**	**Exponent (SE)**	**t (p-value)**	**$F_{1,17}$**	**R^2**	**λ**
Depressor mandibulae (DM)	Intercept Slope	-3.37 (0.27) 1.17 (0.10)	-12.62 (<0.0001) 11.58 (<0.0001)	134.1	0.887	$0.591^{A,B}$	-5.89 (0.43) 3.01 (0.24)	-13.55 (<0.0001) 12.74 (<0.0001)	162.3	0.905	0.399^{B}
Adductor mandibulae externus (AME)	Intercept Slope	-3.83 (0.34) 1.30* (0.13)	-11.18 (<0.0001) 10.25 (<0.0001)	105.1	0.861	0.829^{A}	-6.48 (0.54) 3.27 (0.29)	-12.00 (<0.0001) 11.15 (<0.0001)	124.4	0.880	0.607
Pseudomasseter (PSM)	Intercept Slope	-4.46 (0.56) 1.57* (0.21)	-7.90 ((<0.0001) 7.55 (<0.0001)	57.0	0.770	0.859	-6.79 (1.03) 3.47 (0.56)	-6.59 ((<0.0001) 6.20 (<0.0001)	38.5	0.693	0.620
Pterygoideus ventralis (PTVL)	Intercept Slope	-3.74 (0.32) 1.43** (0.12)	-11.59 (<0.0001) 11.75 (<0.0001)	137.9	0.890	0.617^{B}	-6.44 (0.46) 3.46 (0.25)	-14.46 (<0.0001) 13.99 (<0.0001)	195.6	0.920	0.053^{B}
Pterygoideus dorsalis (PTd)	Intercept Slope	-4.19 (0.34) 1.43** (0.13)	-12.50 (<0.0001) 11.30 (<0.0001)	127.7	0.883	0.598^{B}	-7.27 (0.47) 3.67* (0.25)	-15.63 (<0.0001) 14.49 (<0.0001)	210.1	0.925	0.012^{B}
Ethmomandibularis (EM)	Intercept Slope	-3.22 (0.25) 1.11 (0.09)	-13.09 (<0.0001) 11.80(<0.0001)	139.3	0.891	0.025	-5.76 (0.48) 2.95 (0.26)	-11.97 (<0.0001) 11.27 (<0.0001)	127.1	0.882	$<0.0001^{B}$

Slope values with * and ** indicate significant departures from isometry for muscle mass against body mass (isometric slope = 1.0) or skull length (isometric slope = 3.0) at P = 0.05 and P = 0.01, respectively. Slopes for all other relationships did not depart from isometry. For λ values, superscript A and B indicate a significant difference from a value of 0 or 1, respectively at least P < 0.05.

A *-al és **-al jelölt iránytangens értékek szignifikáns eltéréseket mutatnak az izomtömegnek a testtömeghez (izometrikus meredekség = 0,333), illetve a koponyahosszhoz viszonyítva (izometrikus meredekség = 3,0), P = 0,05 és P = 0,01. Az iránytangensek az összes többi összefüggésben nem mutattak szignifikáns eltérést az izometriától.

but the slope for total muscle mass against skull length exhibited an isometic relationship (expected slope of 3.0; $t_{18} = 1.17$, P = 0.196).

All of the relationships between muscle mass type and body mass exhibited significant positive relationships with high values for R² *(Figure 3, Table 3)*. The relationships for the *depressor mandibulae* and *ethmomandibularis* were isometric (compared to an expected slope of 1.0) but all of the other muscles exhibited significant positive allometry *(Figure 3, Table 3)*. The phylogenetic signal, λ, was moderate to high for most muscles but by contrast λ was very low for the *ethmomandibularis*, indicating that this relationship exhibited no discernible evolutionary signal.

There were significant positive relationships between the mass of each muscle and skull length *(Figure 4, Table 3)*. These relationships were all isometric (compared to an expected slope of 3.0) with the exception of the *pterygoideus dorsalis*, which exhibited significant positive allometry *(Table 3)*. The phylogenetic signal was relatively low for the *depressor mandibulae* and moderate for the adductor muscles but was very low for each of proractor muscles *(Table 3)*.

Discussion

Contrary to expectations larger parrots had greater total masses of the jaw muscles than smaller parrots and generally each muscle type also exhibited positive allometry with body mass but not skull length. The parrots varied in the relative composition of the muscle in the jaw apparatus with genera varying in their arrangement of the adductor and protractor muscles. Unlike lizards, whose head size scales isometrically with body mass (Deeming 2022), as Psittaciformes get larger, their heads become a proportionally larger part of their body. The jaw muscles, however, scaled isometrically with the size of these proportionally larger heads. Consequently, the high bite forces of the large Psittaciformes is due to them having proportionally larger heads then the smaller Psittaciformes. The muscle geometry within the heads of the Psittaciformes is, however, conserved, with the muscle mass scaling isometrically with the size of the head.

The arrangement of muscle types observed in this study matched that of other studies of the parrot jaw musculature (Burton 1974b, Homberger 2003, 2017, Tokita 2003, Carril *et al.* 2015, Cost *et al*. 2020) although the *protractor pterygoideus et quadrati* reported by Carril *et al.* (2015) was not differentiated here. This may have been because this relatively deep muscle was included with the *pterygoideus dorsalis* or *pterygoideus ventralis* muscles or it was not present, as seemed to be in case in the African Grey Parrot *(Psittacus erithacus)* (Cost *et al.* 2020). The *ethmomandibularis* was found in all species and was a substantial part of the musculature. This muscle has been observed in all parrots examined to date (Burton 1974b, Bühler 1981, Tokita 2003, Carril *et al.* 2015, Homberger 2017, Cost *et al*. 2020) but is not unique to parrots. It was reported in the Hawfinch (*Coccothraustes coccothraustes*, Fringillidae) where it is an adductor muscle (Sims 1955). It is unknown whether this is a feature of other *Coccothraustes* species, or whether other finch species have this muscle, but such possibilities are worthy of further investigation.

Previous reports of the muscles of the parrots the African Grey Parrot (Cost *et al.* 2020) and the Monk Parakeet *(Myiopsitta monachus)* (Carril *et al.* 2015) have values of the jaw muscles that close the jaw (Deeming *et al.* 2022), which are around twice the values recorded in the present study. This may reflect variation between birds or perhaps the published values were for both sides of the jaw combined. Deeming *et al.* (2022) did suggest that there was a lack of clarity in what the published values actually represented and that they were from one side was assumed. It would be more useful if future reports of jaw musculature were explicit in describing what values represent.

The proportions of the adductors and retractors in parrots were approximately equal (on average 0.42 of total muscle mass), which is different to the predominance of the adductors in the Fringillidae and Estrildidae, which form 0.47–0.51 of the total muscle mass compared with 0.34–0.37 for the pterygoid complex (van der Meij & Bout 2004). This may reflect the use of the beak by finches and estrilds to generate high forces to dehusk seeds (van der Meij & Bout 2006). Although bite force has yet to be recorded in the Hawfinch, which has an *ethmomandibularis,* it is anticpated to be high because the similarly sized Yellow-billed Grosbeak *(Eophona migratoria)* has a similar total mass of jaw muscle and generates a bite force of 36.1 N, which is high relative to its body mass (van der Meij & Bout 2004). Parrots seem to be less reliant on simple crushing of hard seeds favouring the use of the lower jaw and their feet to manipulate the food item between the more distal edge of the lower mandible, pushing the food item against the maxilla's palate, which is lined with ridges providing an uneven surface to chisel the seeds and nuts against, aiding in de-husking (Homberger 2003, Martens *et al*. 2013, Bright *et al*. 2019). Cranial kinesis is well developed in parrots (Homberger 2017) and the amounts and arrangement of muscles in the jaw apparatus may help contribute to the efficacy of this. The well-developed retractor muscles may help in the manipulation of food items between the mobile upper beak and the mandible.

Most muscles that are involved with closing the jaw in parrots exhibited positive allometry with body mass. These muscles were thin sheets with broad points of origin and/or insertion. The exception was the *ethmomandibularis*, which appeared to be composed of parallel fibres running between limited points of origin and insertion. If muscle mass is directly proportional to force generated by its contraction (Lieber & Ward 2011), and if the moment arms for the levers associated with jaw action are isometric, then larger parrots with more muscle mass will be able to generate a greater bite force than smaller parrots. This positive allometry has also been observed for total muscle mass in passerines (slope of 1.38) (Deeming *et al*. 2022) and in granivorous songbirds in particular (slope of 1.29) (van der Meij & Bout 2004). Species of the Fringillidae had significantly more jaw muscle mass than species of the Estrildidae (van der Meij & Bout 2004). By contrast, the slope of the relationship for non-passerine species was significantly negatively allometric and it may reflect a more functional aspect of the amounts of jaw muscle that individual species have. However, the analysis by Deeming *et al*. (2022) was limited in species range and only included data for two parrot species. Once bite forces are available for the parrots species described here it would be interesting to see how this changes the patterns described by Deeming *et al.* (2022).

Bite force in lizards has been shown to reflect tooth morphology and hence by association the diet with species dealing with harder food items having the stronger bite force (Jenkins & Shaw 2020). Both granivorous passerines and parrots have diets that include potentially hard seeds and nuts that require greater force to process compared with other food items, such as flesh. To date, only the Monk Parakeet (Carril *et al*. 2015) and the African Grey Parrot (Cost *et al*. 2020) have been studied but bite forces do seem to be relatively high compared to other bird species with comparable body mass. For instance, the Cooper's Hawk *(Accipiter cooperii)*, a bird of prey (Accipitriformes) of a similar size (360 g) to the African Grey Parrot (333 g, Dunning 2008), has a bite force of only 2–3 N (Sustaita & Hertel 2010) compared to the calculated bite force of 63 N for the parrot (Cost *et al*. 2020). The Monk Parakeet, which weighs less than half the mass of the Cooper's Hawk, has an estimated bite force of 16 N (Carril *et al*. 2015). Hawks kill their prey with the talons and use their beaks to tear their prey apart (Sustaita & Hertel 2010) so appear to have no need for a higher bite force, although falcons Falconiformes often kill their prey by biting (Pecsics *et al.* 2019). It is anticipated that calculated bite forces in the parrot species investigated here are also going to be high relative to body mass. Diet may, therefore, be a crucial aspect of defining the relationship between body mass and jaw muscle mass in birds. More research, from a much large dataset from a greater diversity of species, is required to explore the the more functional aspects of the jaw musclature in birds.

By contrast to body mass, the relationship between skull length and individual muscle mass in parrots was isometric in most muscle types, with one exception. Previously unreported, this relationship may reflect the physical limitations for muscle orgin offered by the skull. Bigger parrots need to accommodate more muscle in order to generate a greater bite force and it seems that this is simply achieved by increasing the size of the skull. It is unclear whether this also applies for other species of bird within, or across, orders and is worthy of further investigation. The exception in parrots was the *pterygoideus dorsalis*, which exhibited positive allometry with skull length. This adductor muscle originates on the surface of the palatine bone, which has rotated through 90 degrees and points downwards (Zusi 1993, Homberger 2003, 2017, Carril *et al*. 2015, Pecsics *et al.* 2020). This change in skull morphology appears to have two consequences. The first is that there is a large area of bone for the origin of the muscle and secondly, the distance between the origin and the insertion on the mandible is reduced. Muscle architecture is important in generating force, as the arrangement of the fibres relative to the central axis is a major determinant in how much of the force generated will be transferred efficiently (Lieber & Ward 2011). Shorter muscle fibres can generate higher forces (Biewener & Patek 2018) so this shortening of the *pterygoideus dorsalis* muscle may help increase the amount of force it can generate.

This study demonstrated that the mass of the different muscle types in the jaw apparatus of parrots varies between species. There is some suggestion that this will also be observed in other birds and is worthy of further investigation. To date the strongest bite force in birds has been calculated at 430 N for the Ostrich (*Struthio camelus*; Struthionidae, Struthioniformes) which has a jaw muscle mass of 16.9 g (Gussekloo & Bout 2005). However, the Large Ground Finch (*Geospiza magnirostris*; Thraupidae, Passeriformes) has only 0.664 g of jaw muscle and generates a bite force of 70.8 N (Herrel *et al.* 2005). Relative to body mass this is a bite force of 2.16 N g^{-1}, over 500 times greater than that of the Ostrich (0.0043 N·g^{-1}). However, the Monk Parraket has a jaw muscle mass of 0.92 g but Carril *et al.* (2015) calculated its bite force at only 16 N (0.13 N g^{-1}). The Red-and-green Macaw studied here has a total muscle mass of almost 12 g (~1% of body mass) and so given the relationship between jaw muscle mass and bite reported by Deeming *et al.* (2022), it is predicted that it will have a bite force of 150 N (0.12 N g^{-1}). Given the well-muscled jaw apparatus of this large parrot, and the damage a parrot bite can inflict (King *et al*. 2015), these estimates seem rather low. Although bite force is generally low in birds (Deeming *et al*. 2022) compared to some reptiles (see Deeming 2022), our understanding of this relationship is based on a very relatively small dataset for a limited range of bird species. Moreover, in parrots an increase in bite force seems to be associated with an increase in skull size to accommodate more muscles. It is unknown whether this pattern is applicable to other birds within specific orders or even across birds as a whole. If we are going to be able to understand the evolutionary pressures on beak morphology (Hrabar & Perrin 2002, Bright *et al*. 2016, Cooney *et al*. 2017, Navalón *et al.* 2019) there will need to be further investigation into the allometry of the morphological and functional properties of the jaw musculature in a wider range of species.

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Effects of climate variables on the White Stork (*Ciconia ciconia* L.) productivity in a long term study

Adrienn Gyalus[1*], Péter Lovászi[2], Zsolt Végvári[3] & Tibor Csörgő[4]

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Abstract We analysed the effects of weather and climatic patterns on the productivity of the White Stork in Hungary between 1958 and 2017, using i) linear mixed effect models (LMM), ii) LMM-s extended by a single random effect variable or a nested combination; iii) LMM-s extended by a single fixed effect variable and iv) using an additive model of the selected variables. As a preselection, the following climatic variables were identified with substantial support: March mean temperature, March precipitation, April mean temperature, June mean temperature, June precipitation (negative), July mean temperature. The slight increase of the mean number of fledged chicks over 59 years could be the result of the increasing mean temperature, but in itself it might not be strong enough to prove that climate change will overall benefit White Stork productivity. Higher temperature and precipitation values are favourable, probably because of the higher biomass, providing more prey, but high precipitation is unfavourable until the thermoregulation of chicks is not developed. Decreasing amounts of precipitation may cause loss of wetlands as suitable feeding sites. Extreme weather is important to complement the picture given by climate change.

Keywords: climate change, weather effect, White Stork, productivity

Összefoglalás Az időjárás- és klímamintázatok fehér gólya produktivitására gyakorolt hatásait elemeztük 1958–2017 közötti magyarországi adatsorokon i) lineáris kevert modellekkel (LMM), ii) LMM, kiterjesztve egyetlen random hatású változóval vagy beágyazott kombinációval, iii) LMM, kiterjesztve egyetlen fix hatású változóval és iv) a kiválasztott változókkal additív modellben. Az előzetes szelekció során a következő klimatikus változókat azonosítottuk alapvető jelentőségűnek: márciusi átlaghőmérséklet, márciusi csapadékösszeg, áprilisi átlaghőmérséklet, júniusi átlaghőmérséklet, júniusi csapadékösszeg (negatív előjellel), júliusi átlaghőmérséklet. A kirepült fiókák átlagos számának 59 év során bekövetkezett enyhe emelkedése lehet az átlaghőmérséklet emelkedésének következménye, de önmagában nem elég erős bizonyítéka annak, hogy a klímaváltozás általában pozitív hatással van a fehér gólya produktivitására. A magasabb hőmérséklet és a több csapadék kedvezőbb, valószínűleg a magasabb biomassza miatt, ami több táplálékkal szolgál, de a sok csapadék kedvezőtlen addig, amíg a fiókák hőszabályozása nem elég fejlett. A csökkenő csapadékmennyiség okozhatja az alkalmas táplálkozóterületnek számító vizes élőhelyek eltűnését. Az extrém időjárás hatásairól alkotott ismeretek fontosak abban, hogy kiegészítik a klímaváltozás által alkotott képet.

Kulcsszavak: klímaváltozás, időjárás hatása, fehér gólya, költési siker

[1] Department of Plant Systematics, Ecology and Theoretical Biology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c, Hungary
[2] MME/BirdLife Hungary, 1121 Budapest, Költő utca 21., Hungary
[3] Institute of Aquatic Ecology, Centre for Ecological Research, 1113 Budapest, Karolina út 29., Hungary
[4] Department of Anatomy, Cell- and Developmental Biology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c, Hungary
** corresponding author, e-mail: adrienn.gyalus@gmail.com*

Introduction

The strong ecological effects of climate change has been demonstrated in a large number of studies (Doran & Zimmerman 2009, Scheffers *et al.* 2016, Sheldon 2019) and also its anthropogenic origin is widely supported (IPCC 2021). Responses of affected ecosystems manifested in phenological changes: flowering and leaf unfolding occur earlier in plants (Mo *et al.* 2017), migratory birds arrive earlier in spring (Csörgő *et al*. 2009, Pautasso 2011, Harnos *et al*. 2015), mismatch occurs in interacting species whose life cycle asynchronically shifted, which acts at community level (Nakazawa & Doi 2012), distribution of species changes in latitude (Tryjanowski *et al*. 2005b, Chamberlain *et al*. 2012, Moren-Ruenda *et al*. 2012, Chodkiewicz & Sikora 2020) and altitude (Popy *et al*. 2009, Freeman 2018), both in terrestrial and marine ecosystems (Poloczanska 2013).

The White Stork *(Ciconia ciconia)* is a large, long-distance migratory bird, a model species of population and breeding ecology with long-term datasets available (BirdLife International 2015, Kaatz *et al*. 2017, Lovászi *et al*. 2020), which makes it a perfect candidate to study climate change at different spatial scales. The European population increased in the last two decades of the 20th century, since then the smaller western populations increase and the Eastern core population decrease (Kaatz *et al*. 2017, PECBMS 2022).

Hungary is a particularly suitable area for such a study, as three climatic regimes (Mediterranean, continental, oceanic) influence the weather to a constantly varying extent and duration, therefore, significant differences in weather may occur despite the relatively small area and flat surface of the country. The absolute minimum temperature is –35 °C, the absolute maximum is +41.9 °C, the local annual precipitation varies between 203 and 1554.9 mm (Hungarian Meteorological Service 2022).

The aim of our study was to analyse whether there are differences in productivity (mean number of nestlings) between the regions, are the differences due to weather effects or caused by independent geographical factors, are the differences caused by mixed effects of these above mentioned factors, how extreme weather conditions affects the productivity.

Materials and Methods

We analysed White Stork breeding data recorded between 1958 and 2017, retrieved from two resources. For the 1958–1989 period, censuses were conducted every five years via printed questionnaires. Two types of protocols ran in parallel: simplified forms (po) sent out to post offices, filled out by post workers; and more detailed questionnaires (qu) sent out to amateur ornithologists, forestries, hunting companies, high schools, etc., filled out by their members or volunteers (Lovászi 1998). These data are archived in the Móra Ferenc Múzeum, Szeged. For the 1994–2017 period, volunteers of the MME/BirdLife Hungary collected the data. This database is now fully available in electronic format, provided by the Monitoring Centre of the MME/BirdLife Hungary. Since the repetition of observations were not expected and 100% coverage was not ensured, the number of White Stork pairs is probably underestimated and there could be also differences in productivity, but these estimates do not differ significantly from real values, as this study states (Aguirre & Vergara 2009).

For our study, we chose six out of the 19 Hungarian counties (namely Győr-Moson-Sopron, Somogy, Bács-Kiskun, Békés, Hajdú-Bihar and Szabolcs-Szatmár-Bereg County). We considered the following criteria: 1. data available from every year, 2. there are enough breeding pairs for the analysis, 3. they represent different geographical and socio-economical regions of Hungary.

Water permeability of soil types affects the amount of water covered areas which is in relation to the distribution of White Storks, therefore we present the soil types of the counties along with the main water bodies, the typical agricultural use and the human population density (Mezősi & Bata 2011, https://www.ksh.hu/).

- Győr-Moson-Sopron (GYMS): soil types: fluviosols, gleysols, phaeozems, chernozems (near rivers), luvisols (Transdanubian Mountains). Main waters: Danube, Rába, Rábca. Agricultural usage: 4.8% grassland, 53.5% arable land, 19.2% forest. Density: 107/km^2.
- Somogy: soil types: fluviosols, gleysols, phaeozems (near rivers and lakes), luvisols, arenosols, cambiosols. Main waters: Dráva, lake Balaton. Agricultural usage: 5.2% grassland, 42.2% arable land, 29.5% forest. Density: 52/km^2.
- Bács-Kiskun (BK): soil types: regosols, solonchaks, fluviosols (along Danube), chernozems (Bácska region). Main waters: Danube, alkaline, saline lakes. Agricultural usage: 12.3% grassland, 41.3% arable land, 20.9% forest. Density: 61/km^2.
- Békés: soil types: chernozems, rendzinas, phaeozems, vertisoils. Main waters: Körös, Berettyó. Agricultural usage: 5.5% grassland, 67.7% arable land, 4.6% forest. Density: 63/km^2.

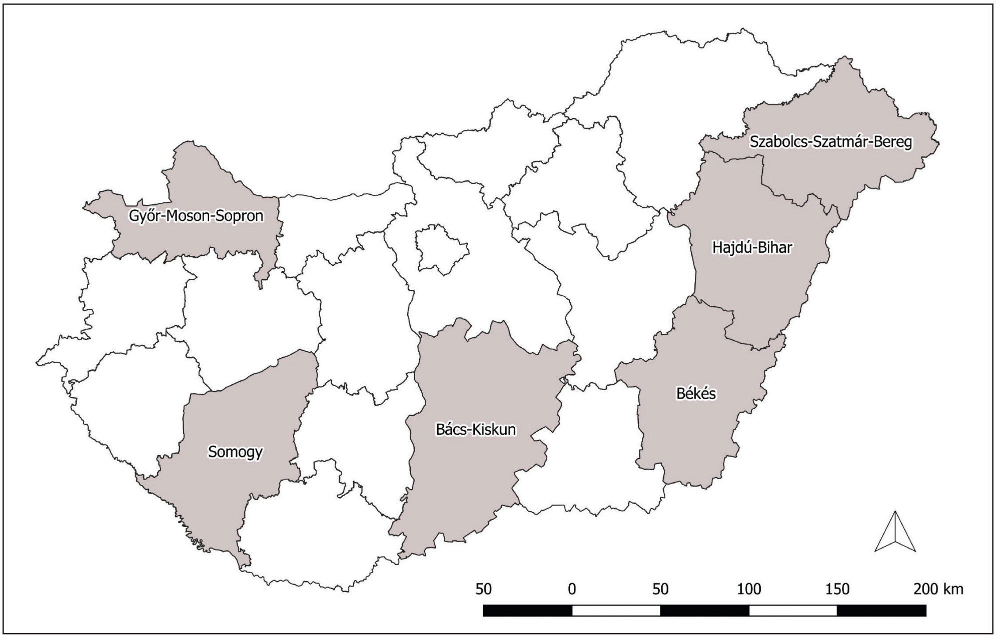

Figure 1. Map of Hungarian counties studied
1. ábra A vizsgált magyarországi megyék

- Hajdú-Bihar (HB): soil types: chernozems, solonetzes (Közép-Tisza region). Main waters: Tisza, Berettyó, alkaline-saline lakes. Agricultural usage: 17.7% grassland, 53.1% arable land, 11.1% forest. Density: 86/km^2.
- Szabolcs-Szatmár-Bereg (SZSZB): soil types: regosols, arenosols; phaeozems, fluviosols (along rivers). Main waters: Tisza. Agricultural usage: 10.8% grassland, 44.4% arable land, 21.1% forest. Density: 94/km^2 *(Figure 1).*

Questionnaire data were digitized in MS Office Excel 2003 in .csv format, by county. The following variables were derived from the forms: year, settlement, address, number of adults, chicks hatched, chicks fledged, date. The postal forms up to 1989 only asked the number of nests (in the postal district) and their nest site and occupancy, but since many reported detailed breeding information, the exactly identifiable ones were included. We also marked the nesting status (successful pairs, pairs without young fledged, lonely stork, unoccupied) and redundancy (is the record identical to a previous one) for easier analysis. In case of the latter, the record with the most exact information was marked as nonredundant. The nonredundant successful pairs and pairs without young fledged were filtered from the paper data and merged with the successful pairs and pairs without young fledged from the electronic data (which was already nonredundant and in suitable format). The next step was to sum the presence of data by settlement and year. To examine the long-term effect of climate, we selected settlements which have data from at least 15 years. The productivity – the mean number of fledged chicks – was calculated for each settlement. To investigate whether there are regional differences in productivity, medium and microregions were assigned to each settlement (Marosi & Somogyi 1990). Number of records of the final dataset was assessed per year and county *(Table 1).*

For the climate variables, we used the data of the following meteorological stations: Baja and Kecskemét (BK); Békéscsaba (Békés); Győr and Sopron (GYMS); Debrecen (HB); Siófok (Somogy); Nyíregyháza (SZSZB). Station data were retrieved from two sources: from the Hungarian Meteorological Service (HMS) for the 1958–1974 period, and from the Ogimet weather information service portal (http://www.ogimet.com/gsodc.phtml.en#est) for the 1979–2017 period. For analysis related to the breeding period, we used the mean temperature (°C) and the sum precipitation (mm) of months March–July, averaged (in case of mean temperature) and summed (in case of precipitation) for a whole month. Since HMS provided weekly, not daily data, the following month boundaries were made: 01.03–04.04., 05.04–02.05., 03.05–30.05., 31.05–27.06., 28.06–25.07. Otherwise, it was processed the same way as Ogimet data. In case of Bács-Kiskun and GYMS, where two stations were available, regions were assigned to the following stations: Bácskai-löszös síkság, Mohácsi-sziget, Kalocsai-sárköz to Baja; Kiskunsági-löszöshát, Solti-sík, Kiskunsági-homokhát and Dél-Tiszavölgy to Kecskemét; Kapuvári-sík, Ikva-sík, Répce-sík, Soproni-hegység, Fertő-medence and Fertőmelléki-dombság to Sopron; Csornai-sík, Mosoni-sík, Pápa-Devecseri-sík, Pannonhalmi-dombság, Szigetköz and Igmánd-Kisbéri-medence to Győr.

As an initial step, the same monthly temperature and precipitation values of the different stations were compared with Pearson's correlation. After that, we used linear mixed effect models to further investigate the effects of climate variables (which were the fixed effects,

Table 1. Number of White Stork productivity records per year and county
1. táblázat A fehér gólya produktivitási adatsorok száma évre és megyére lebontva

year	Békés	BK	GYMS	HB	Somogy	SZSZB	sum / year
1958	6	0	57	1	3	14	81
1963	15	4	44	1	5	43	112
1968	22	0	38	3	3	29	95
1974	18	10	46	2	6	33	115
1979	29	9	47	3	3	59	150
1984	33	6	47	2	9	66	163
1989	40	8	65	3	10	57	183
1994	0	2	51	0	7	76	136
1999	0	5	54	5	7	92	163
2000	0	1	0	0	1	67	69
2001	1	6	54	0	1	73	135
2002	33	1	1	2	1	85	123
2003	6	4	9	2	10	87	118
2004	16	9	62	5	11	111	214
2005	14	6	62	3	11	97	193
2006	36	5	59	5	11	110	226
2007	42	9	6	5	11	108	181
2008	42	7	4	2	10	114	179
2009	42	8	54	5	9	109	227
2010	41	6	50	4	8	108	217
2011	42	10	61	5	9	50	177
2012	42	10	59	3	9	102	225
2013	42	8	60	2	4	115	231
2014	41	10	63	5	7	111	237
2015	41	9	60	4	10	89	213
2016	41	10	62	4	3	83	203
2017	41	8	64	5	1	74	193
sum /county	726	171	1239	81	180	2162	
total sum							4559

along with the year variable) and spatial variables (which were the random effects) on productivity. Before building more complex models, a preselection was made by applying a Linear Mixed Model (LMM). lmer(productivity ~ year) was considered a null model (Bates *et al.* 2015). Models extended by a single random effect variable or a nested combination of those were compared to find the one with the lowest AIC value. Models extended by a single fixed effect variable were investigated and the ones with a |t-value| > 2 – as a rule of thumb for significance, using a conservative approach (Siegel 2012) – were considered. As a final step, an additive model of the selected variables were build and investigated. Models were tested in R programming environment (R Core Team 2015).

Table 2. The Pearson's correlation of climatic variables between the studied weather stations
2. táblázat A klimatikus változók Pearson-korrelációja a vizsgált meteorológiai állomások között

	Tmean.mar	**Prec.mar**	**Tmean.apr**	**Prec.apr**	**Tmean.may**	**Prec.may**	**Tmean.jun**	**Prec.jun**	**Tmean.jul**	**Prec.jul**
Baja_Bekes	0.899	0.804	0.902	0.836	0.840	0.224	0.842	0.463	0.823	0.623
Baja_BK	0.938	0.820	0.889	0.899	0.849	0.476	0.909	0.419	0.886	0.537
Baja_GYMS	0.933	0.642	0.874	0.565	0.813	0.391	0.899	0.135	0.828	0.652
Baja_HB	0.875	0.687	0.920	0.684	0.786	0.522	0.829	0.406	0.802	0.343
Baja_Somogy	0.945	0.745	0.881	0.674	0.803	0.506	0.869	0.340	0.839	0.163
Baja_Sopron	0.907	0.357	0.797	0.421	0.788	0.505	0.860	0.315	0.800	0.350
Baja_SZSZB	0.862	0.606	0.893	0.673	0.750	0.278	0.808	0.433	0.829	0.062
Bekes_BK	0.947	0.869	0.939	0.654	0.971	0.253	0.960	0.363	0.954	0.380
Bekes_GYMS	0.859	0.802	0.913	0.539	0.902	0.143	0.927	0.057	0.901	0.559
Bekes_HB	0.973	0.819	0.981	0.669	0.976	0.578	0.964	0.712	0.958	0.634
Bekes_Somogy	0.931	0.868	0.903	0.572	0.918	0.330	0.947	0.380	0.929	0.209
Bekes_Sopron	0.829	0.521	0.836	0.625	0.899	0.165	0.900	0.248	0.828	0.178
Bekes_SZSZB	0.957	0.766	0.953	0.639	0.928	0.057	0.923	0.323	0.914	0.170
BK_GYMS	0.913	0.661	0.939	0.509	0.898	0.947	0.955	-0.040	0.917	0.284
BK_HB	0.962	0.844	0.958	0.740	0.965	0.408	0.932	0.465	0.945	0.212
BK_Somogy	0.963	0.883	0.935	0.457	0.920	0.361	0.960	0.402	0.939	0.150
BK_Sopron	0.900	0.370	0.894	0.323	0.888	0.508	0.920	0.192	0.881	0.207
BK_SZSZB	0.959	0.844	0.933	0.655	0.892	0.372	0.876	0.388	0.934	0.133
GYMS_HB	0.870	0.649	0.917	0.743	0.916	0.370	0.885	0.103	0.926	0.235
GYMS_Somogy	0.955	0.779	0.944	0.522	0.941	0.334	0.980	0.258	0.967	0.527
GYMS_Sopron	0.970	0.837	0.962	0.710	0.973	0.553	0.977	0.331	0.962	0.634
GYMS_SZSZB	0.884	0.588	0.899	0.678	0.893	0.401	0.837	0.139	0.909	0.087
HB_Somogy	0.944	0.776	0.902	0.590	0.925	0.727	0.920	0.526	0.961	0.031
HB_Sopron	0.857	0.502	0.846	0.627	0.907	0.246	0.844	0.397	0.870	0.026
HB_SZSZB	0.989	0.863	0.967	0.884	0.964	0.491	0.977	0.569	0.969	0.347
Somogy_Sopron	0.948	0.612	0.946	0.483	0.967	0.316	0.965	0.378	0.930	0.049
Somogy_SZSZB	0.942	0.818	0.901	0.541	0.852	0.494	0.875	0.232	0.922	0.018
Sopron_SZSZB	0.871	0.411	0.838	0.457	0.872	0.137	0.800	0.305	0.871	0.208
mean	0.921	0.705	0.909	0.620	0.893	0.396	0.905	0.330	0.900	0.286

Table 3. Comparison of null models with different random spatial variables. npar = number of parameters, AIC = Akaike information criterion, BIC = Bayesian information criterion, logLik = log-likelihood, Chisq = Chi-square test statistic, Df = degree of freedom, Pr(>Chisq) = significance of Chi-square test statistics, reg.med = medium region, reg.small = microregion

3. táblázat Nullmodellek összehasonlítása különböző random térbeli változókkal. npar = paraméterek száma, AIC = Akaike-kritérium, BIC = Bayes-kritérium, logLik = log-likelihood, Chisq = khí-négyzet próba, Df = szabadságfok, Pr(>Chisq) = a khí-négyzet próba szignifikanciaszintje, reg.med = középtáj, reg.small = kistáj

random variable	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
county	4	12668	12694	-6330.1	12660			
reg.med	4	12654	12679	-6322.8	12646	11.6182	0	
reg.small	4	12687	12713	-6339.5	12679	0	0	
settlement	4	12725	12751	-6358.6	12717	0	0	
county/reg.med	5	12653	12685	-6321.6	12643	73.9936	1	< 2.2e-16 ***
county/reg.small	5	12663	12696	-6326.7	12653	0	0	

Results

The average correlation coefficients between two meteorological stations for temperatures and precipitation are: Tmean.mar = 0.9208, Prec.mar = 0.7050, Tmean.apr = 0.9094, Prec.apr = 0.6202, Tmean.may = 0.8927, Prec.may = 0.3961, Tmean.jun = 0.905, Prec.jun = 0.3299, Tmean.jul = 0.8997, Prec.jul = 0.286 (for the full table for each individual pairs, see *Table 2*). The preselection on the random effects in the linear mixed effect models showed that among spatial variables, the medium region nested within the county has the lowest AIC value: 12643 (for table of all models, see *Table 3*). As for the preselection of fixed effects, the following climatic variables were found with t values > 2: year = 13.38, Tmean.mar = 7.025, Prec.mar = 7.233, Tmean.apr = 8.342, Tmean.jun = 9.099, Prec.jun = –5.310, Tmean.jul = 4.659. The final full model was: m_full = lmer(fled.mean ~ Tmean.mar + Prec.mar + Tmean.apr + Tmean.jun + Prec.jun + Tmean.jul + (1 | county/reg.med)). The t values for the fixed effects were: Tmean.mar = 5.359, Prec.mar = 9.313, Tmean.apr = 5.868, Tmean.jun = 4.090, Prec.jun = –3.693, Tmean.jul = –1.771. The variance for the random effects was: regmed:county = 0.05057, county = 0.05835 with total variance = 1.0033 (see *Table 4*).

Discussion

Climate is one of the stochastic environmental factors affecting populations: unpredictable, uncontrollable and involves all individuals. It can influence individuals directly, for example through their development or survival, or indirectly, for example through the availability of food (Kaatz *et al*. 2017). The White Stork, as a large, long-lived bird species, is mainly affected through its prey (Nevoux 2008), however, weather has a direct influence for the survival of the chicks up until their thermoregulation fully develops at three weeks old (Denac 2010).

Table 4. The statistics of model with the preselected fix and random variables. AIC = Akaike information criterion, BIC = Bayesian information criterion, logLik = log-likelihood, residual df = residual degree of freedom, std. error = standard error, rel. variance = relative variance

4. táblázat A kiválasztott fix és random változókat tartalmazó modell statisztikái. AIC = Akaike-kritérium, BIC = Bayes-kritérium, logLik = log-likelihood, residual df = reziduális szabadságfok, std. error = standard hiba, rel. variance = relatív variancia

Model criterions					
	AIC	BIC	logLik	deviance	residual df
	12408.2	12478.8	-6193.1	12386.2	4515
Number of observations					
medium region:county					22
county					6
total					4526
Fixed effects					
	estimate	confidence intervals		std. error	t value
intercept	-15.174	-20.074	-10.274	2.498	-6.074
year	0.008	0.005	0.010	0.001	6.040
march mean temperature	0.085	0.054	0.116	0.016	5.359
march sum precipitation	0.141	0.111	0.171	0.015	9.313
april mean temperature	0.096	0.064	0.128	0.016	5.868
june mean temperature	0.075	0.039	0.111	0.018	4.090
june sum precipitation	-0.056	-0.085	-0.026	0.015	-3.693
july mean temperature	-0.031	-0.066	0.003	0.018	-1.771
Random effects					
			std deviation	variance	rel. variance
medium region:county			0.225	0.051	0.050
county			0.242	0.058	0.058
residual			0.946	0.894	0.891

The food supply of the White Stork is also influenced by various descriptors of climatic variability on its breeding and wintering grounds and on the migration route as well. There is a connection between the NDVI (the most commonly used vegetation index to estimate phytomass) and the survival of individuals on the wintering grounds (Schaub *et al*. 2005, Nevoux 2008). There is a difference between the sexes in how much weather affect the timing of arrival: females are more dependent on temperature (Gordo 2013). The outcome of spring migration affects breeding success of the population: the ratio of successful breeding pairs is lower in years with delayed arrival. Adverse weather circumstances during migration result weaker condition and lower body mass at arrival, so fewer pairs start to breed, and breeding pairs have fewer eggs (Profus 1991). Storks breeding in Hungary use the eastern migration route (Lovászi & Rékási 2009), where bird are more exposed to weather conditions during wintering and migration compared to western populations (Kaatz *et al*. 2017). The influence of the Sahel on the western stork population has decreased in recent decades (Nevoux 2008).

The amount of food that can be collected by storks also depends upon the density of prey animals and the vegetation cover. Warmer temperatures in March and April facilitates the earlier development of the vegetation and thus the higher amount of insects and rodents as prey animals. Warmer June and July weather may increase the activity of prey. Models showed no significant correlation between May mean temperature and productivity of storks, maybe because of the very variable weather of this month. Precipitation is also important for the development of the vegetation, but with two possible opposite impact. Higher precipitation in March facilitates vegetation. Precipitation in June regularly occurs together with colder weather, causing increased mortality of the offspring.

The climate correlations between stations within Hungary showed that differences were higher in the precipitation than in the temperature. According to IPCC predictions, precipitation patterns will become more unpredictable and variable due to climate change (IPCC 2021), which means the differences will more likely grow, so it is crucial to consider spatial variation at various scales to see how it affects the White Stork population. The slight increase in mean number of fledged chicks over 59 years (estimate: 0.008, see *Table 4*) could be the result of the increasing mean temperature, but in itself it might not be strong enough to prove that climate change will overall benefit White Stork productivity. Moreover, the results of Martín *et al*. (2021) show that there has been a gradual decrease in survival of Western European populations as a result of climate change, affecting juvenile birds more strongly.

The weather of the breeding areas determines the local food conditions, which mainly affects productivity. Winter precipitation is positively correlated with the mean number of chicks (Lovászi 2013), as the number and size of areas covered with shallow water preferred by storks increase. The correlation between the May and June NDVI values of the feeding areas around the 1.5 km radius of the nest and the average number of chicks is also positive (Kosicki 2010). The temperature and precipitation conditions of the spring-summer months affect small mammals, e.g. for the behaviour of the Common Vole *(Microtus arvalis)*: they move more in warmer weather, so storks are more likely to prey on them. However, in rainy years earthworms can be found in larger masses, that are more favorable for young chicks (Thomsen 1995).

Habitat quality can also modify the impact of weather on productivity: more chicks hatch in a better habitat, they can heat each other more efficiently, and as they are in better condition, reach the body weight needed for homeothermality sooner, the weather has less effect on them (Denac 2006). Due to the unpredictability, the effect of precipitation out of the climatic factors is more critical: while temperature rise steadily each year (regardless of baseline), a heavy storm, more rainfall can occur at any stage of breeding (Bert & Lorenzi 1999). Depending on latitude, the temperature conditions of which month have the greatest effect on productivity may vary, but the role of May precipitation is equally important in each region (Moritzi *et al*. 2001, Jovani & Tella 2004).

According to research in Poland and Slovakia, global warming reduce the differences in altitude for storks: higher, cooler regions's climate become milder and thus more habitable by storks (Tryjanowsky *et al*. 2005a, Gordo 2013). The same is true for latitude: in the last 30 years, the White Stork may have spread in the Baltic States due to global warming

(Kosicki 2010, Kaatz *et al*. 2017). Moreover, the impact of weather on productivity may diminish, as storks feed more and more on landfills (both in their breeding and wintering grounds), making their survival less and less dependent on local natural vegetation (Djerdali *et al*. 2016, Gilbert *et al*. 2016, López-Garcia *et al.* 2021), although number of breeding pairs affected mainly by anthropogenic environmental factors do not automatically reflects for the breeding success (Bachir 2013).

One of the reasons for the increase in the mean number of offsprings in our study is climate change: the positive effect of temperature variables on productivity is clear in all climate models. According to our results, the maximum temperature is the strongest explanatory variable among the temperature components. In previous studies, a relationship was found with the mean temperature (Moritzi *et al*. 2001, Jovani & Tella 2004, Kosicki 2010). While this is a good indicator of the temperature throughout the day, extreme values are likely to be of even greater biological significance. It is possible, for example, that during the heat-sensitive period it is particularly important how well the chicks can warm up, which is determined by the maximum temperature.

Precipitation also proved to be a significant positive variable in the three strongest models, which was also expected from the results of previous studies, as local precipitation conditions affect the vegetation index of the breeding area and thus the number of hatching chicks through the food supply (Schaub *et al*. 2005). However, the interaction of precipitation with each temperature variable is negative, i.e. the higher the temperature, the less the precipitation. An increase in temperature and precipitation is also favourable for storks, but they do not usually rise at the same time. While higher temperatures are likely to be favourable at all stages of breeding, high precipitation can be detrimental in the heat-sensitive period of the chicks. Examining the months of extreme weather is therefore important to complement the picture given by climate change. The distribution of precipitation has a significant effect on productivity, but with different signs for each month: in March, for example, rainy weather is strongly positive and drought is strongly negative (Cuadrado *et al*. 2016). Storks are not yet in the breeding area for most of March, arriving at the end of the month: the cold may delay the arrival of storks, but does not affect breeding success (Kosicki 2010). The rains in March establish the food base of storks as in Hungary there are a lot of temporary wet grasslands and other wetlands with shallow water, which in certain years can be dry all year round.

The warmth of early spring also has a positive effect: it accelerates the development of vegetation and the appearance of herbivorous insects. The key role of early spring temperatures may be indicated by that the effect of the extreme cold was only significantly negative in March; chicks are not affected, negative effects affect only vegetation. At first glance, the positive correlation of cold extremes of the other months, especially the significant values in April and May, seem surprising. A possible explanation for this is that cold extremes are rarely coupled with rainfall, and low temperatures alone do not risks chicks (hatching is typical during this period and small chicks can be covered by the parents to keep them warm). Nevertheless, it is true that the effect of warm extremes is more favourable than that of cold, as less energy is needed to heat eggs or chicks (Denac 2010). An exception to this is July, when the positive effect of cool weather is significantly greater than heat: probably because higher temperatures in this month tend to reduce the amount of food by increasing the evaporation and the vegetation can dry out without rainfall, which has a negative effect on the food supply. However, our results do not support that the lack of rainfall in the summer months would have an overall negative effect on the average number of hatching chicks through the vegetation index (Schaub *et al*. 2005), but the positive trend in dry weather is declining from May onwards. It is more favourable for the chicks if the rainfall conditions tend to shift towards dry land, but they require more and more food, that can only be provided by a habitat in the right condition. Extreme heat is therefore harmful to the habitat, not to the chicks: the heatwave is not only tolerated by the chicks, but we have a significantly positive effect according to our results. Studies in Spain show that extremely high temperatures do not affect their survival, as they occur at the end of the breeding season, when the mortality of the chicks is already low (Jovani & Tella 2004). In Poland, the growth rate of chicks was different in particular years affected by temperature and precipitation (Kosicki & Indykiewicz 2011), and the most critical period during the breeding period was the time of incubation and the first days after hatching (Kosicki 2012).

Climate models for the entire breeding period show that the level of significance of climate variables and their interactions decreases compared to the original climate model: the weather of the months of the breeding period together better explains productivity than the maximum temperature, precipitation, and their interaction together. This shows that different weather conditions are optimal for storks at different stages of their development. Based on our results, for example, a higher precipitation in March, a lack of precipitation in May, a cold in April, and a warm in June plays key role, and cooler period in July is also important (for good vegetation conditions).

Overall, the average number of nestlings has increased in most of the counties studied since 1958, and our models suggest that this may be due to the warming of recent decades. The higher the temperature, the higher the productivity of the storks: the relationship with the minimum, average and maximum temperatures is significantly positive, but the effect of the maximum temperature is the strongest. This is an important result as it draws attention to the importance of extreme values. In the case of precipitation, productivity in generally better with increasing amount, but its distribution is significant: more precipitation is favourable in March because it establishes the water supply of the vegetation, thus increasing the area's food base, but rains in May and June can perish chicks. A more detailed examination of the weather in the months of the breeding season reveals how extreme the various stages of spending affect productivity: in July and April, for example, the influence of precipitation is significantly smaller than in the other months. The variance between counties is low for all climate models: this means that the influence of weather is independent of the region.

On a large scale, warming is predicted, which is favourable for productivity; however, on a small scale, extreme weather events are expected to become more frequent and, as our results show, even a short period extreme weather can significantly reduce the productivity. If there are more frequent years in which very few young fly out due to an extreme weather period, the age group dynamics of the population will change.

It should be noted, however, that the present study only examines the effects of weather on productivity and therefore its results may in themselves be misleading for future population developments. During the period under review, Hungary's stork population decreased from about 16,000 pairs to 4,000 pairs, presumably due to unfavourable changes in nesting sites and feeding grounds (Lovászi *et al*. 2020), and population development of the last two decades is similar to other East-European populations (Lovászi 2022).

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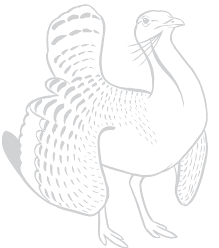

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Monitoring population change using ’citizen science’ data: case study of the Hungarian White Stork *(Ciconia ciconia)* population between 1999 and 2021

Péter Lovászi[1]*, Károly Nagy[1], Zoltán Görögh[1] & Tibor Szép[2]

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Abstract In Hungary, changes in the White Stork population are monitored using two methods that involve a large number of volunteers: nest surveys since 1941, and since 1999 within the framework of the Common Bird Monitoring Scheme (MMM) programme. In our article, we briefly present the results of the nest survey data between 1999 and 2021, the population trend calculated on the basis of them, and the comparison of the latter with the trends shown by the MMM programme, which – among other species – counts all stork individuals on 2.5×2.5 km sample areas. Both sets of data show a decreasing trend, but there is a significant difference between them, which may be partly due to the inaccuracies of the nest database, considering the fact that the MMM also counts non-breeding adult and immature individuals. However, both methods have the characteristics that make them suitable for monitoring population trends.

Keywords: White Stork, national census, breeding population, citizen science

Összefoglalás Magyarországon két, önkénteseket nagy számban bevonó módszerrel is zajlik a fehérgólya-állomány változásainak nyomon követése: az 1941 óta végzett fészekfelmérésekkel és 1999 óta a Mindennapi Madaraink Monitoringja (MMM) program keretében. Cikkünkben röviden bemutatjuk a fészekfelmérések 1999 és 2021 közötti adatainak összesített eredményeit, az ezek alapján számított populációs trendet, és utóbbit összevetjük a 2,5×2,5 km-es mintaterületeken – többek közt – valamennyi gólyaegyedet felmérő MMM-program által mutatott trendekkel. Mindkét adatsor csökkenő trendet mutat, de közöttük szignifikáns eltérés mutatkozik, ami részben a fészekadatbázis pontatlanságaiból fakadhat, részben abból, hogy az MMM a nem költő öreg és a még nem ivarérett egyedek számlálását is végzi. Jellegzetességeiket figyelembe véve azonban mindkét módszer alkalmas a populációs trendek nyomon követésére.

Kulcsszavak: fehér gólya, országos felmérés, költőállomány, csökkenés, közösségi tudomány

[1] *MME/BirdLife Hungary, 1121 Budapest, Költő utca 21., Hungary*
[2] *University of Nyíregyháza, 4400 Nyíregyháza, Sóstói út 31/b Hungary*
** corresponding author, e-mail: lovaszi.peter@mme.hu*

Introduction

Large datasets collected by volunteers are generally suitable for carrying out scientific research (Fraisl *et al*. 2002). There are good examples of large and/or long scale bird studies involving volunteers, such as the more than hundred years old Christmas Bird Count (Bock & Root 1981), or the continent-wide mapping activities of the European

Bird Atlas 2 (Chokiewicz & Sikora 2020). The White Stork has been a popular and a well monitored bird species for a long time as the first international census was organised almost a century ago, in 1934 and further international nest counts were organised in 1974, 1984, 1994/1995 and 2004/2005 (Thomsen 2013, Kaatz *et al*. 2017). Citizen ornithologists collect a lot of information on the species in several countries every year, but as the White Stork population stabilized, the focus of researchers and conservationists seems to have shifted to other priority species, so these data collected by the wide public are not fully analysed and published. Only a few scientific articles were published on the annual changes of national or regional populations in the last decade, for example in Germany (Kaatz *et al*. 2017), Poland (Kaługa *et al*. 2016, Kopij 2017, Sikora 2017, Bialas *et al*. 2020), Slovenia (Denac 2010), Turkey (Onmuş *et al*. 2012), Ukraine (Grischenko & Yablonovska-Grishchenko 2019). The last international analysis was published on the 2004/2005 census (Thomsen 2013).

In Hungary, the first national White Stork census was organised in 1941, it was repeated in 1958, 1963, 1968, then in 1974 (in the year of the international census) and since then, in every five years. Data were collected by teachers and students, postmen, volunteer ornithologists, national parks staff members and since the foundation of the MME/BirdLife Hungary in 1974, the members of the national ornithological society (Homonnay 1964, Marián 1962, 1968, 1971, Jakab 1978, 1985, 1987, 1991, Lovászi 1998, 2004, Lovászi *et al.* 2013, 2016, 2020). The Monitoring Centre of the MME created an online stork database in 2005 (www.golya.mme.hu). Approximately 2,000 volunteers uploaded data of almost 14,000 nesting sites and more than 117,000 breeding data. These records were collected by a wide range of people, not in a framework of a preliminary designed monitoring. In spite of the immense amount of information, only the regular, five-year national censuses have been analysed and published so far (Lovászi *et al.* 2013, 2016, 2020).

The MME/BirdLife Hungary started a monitoring programme of common birds in 1999 (Szép *et al*. 2012, Nagy 2022), involving trained volunteers, using a standard protocol.

Our goal in this study was to analyse whether the White Stork data collected by volunteers was suitable to monitor the trends of the species and to compare the usability of a big, but lower quality database to a dataset collected using a well-designed protocol.

Materials and Methods

We analysed data of the online White Stork database of the MME/BirdLife Hungary, collected and uploaded by volunteers. This database was established in 2005, but it was possible to upload archive data also. Data collection is based on nesting sites: registered users can create a new nesting site with its location (‘address’) and can add information on the nest basement, geographical coordinate, presence or lack of nest holder ‘basket”, quality of the nest holder, presence of dangerous electric poles around, type of the electric pole holding the nest, and other comments. Photographs can be uploaded to the nesting site. The system allows the upload of annual data to the nesting sites (empty nest holder without nest material, unoccupied nest, lonely stork, unsuccessful pair, successful pair, number of young hatched and fledged). Daily observation can also be uploaded, which provide data on e.g. the presence of storks, egg laying, fighting, mortality cases. It is important that nesting site can be an empty nest holder facility without any nest material.

We used data of years between 1999 and 2021, aligned with the dataset of the Common Bird Monitoring Scheme (see below). Local coordinators organise regional nest counts every year, involving volunteers, regularly covering all nests in a village or district. As data can be uploaded by independent volunteers also, in many cases we have data on single nests within a settlement (for example beside a main road), but there are no information on other nesting sites of the same settlement. In addition, the coverage of settlements is substantially different between years. As a result, we have a large number of nests and settlements without information in particular years (there are lot of lacking data in the database).

Our analysis was based on the number of breeding pairs in settlements. As we do not have data from each year from all the nests, before the analysis, we deleted data of years when number of reported pairs was less than 80% of the average of the given settlement between years to decrease the effects of partially covered settlements. Nesting sites without valid breeding data were excluded from the analysis. We analysed data of 2,221 settlements (covering 82.5% of the area of Hungary). During trend analysis, we excluded further three settlements where breeding was not detected.

As a comparison, we used the dataset of the Common Bird Monitoring Scheme (MMM) of the MME/BirdLife Hungary. This programme is a point-based counting method using grid cells with a semi-random sampling design. The survey is based on randomly selected 2.5×2.5 km UTM squares (Universal Transverse Mercator geographic coordinate system). Observers count birds for five minutes at 15 points; these points are randomly selected out of 25 central points of 0.5 km segments of the 2.5×2.5 km UTM square. Surveys were carried out from 1999, twice between mid-April and mid-June, counting birds within 50, 100 and 200 m radius circles (Szép *et al.* 2012, Nagy 2022). We considered data of 220 pieces of 2.5×2.5 km UTM squares, which were surveyed at least in two separate years during 1999–2021 using standard protocol and White Stork was observed at least in one year. The observers in the MMM programme able to survey White Storks both at their nests and their foraging areas. Because of the random sampling protocol of the MMM programme, the surveyed areas covered dominantly by agricultural and forest habitats (85%), but the coverage of two habitats (wetlands and urban) frequently used by White Stork was low (<15%) (Szép *et al.* 2012).

The package rtrim (Pannekoek & van Strien 2001, Bogaart *et al.* 2016) was used to analyse the trend of number of breeding pairs in the settlements and the number of individuals surveyed in the 2.5×2.5 km UTM squares in the frame of the MMM monitoring. The package implements a variety of log-linear models (including Poisson regression) which can handle data of sites in year(s) when observations were missing, by the use of models that make assumptions about the structure of the counts and considering imputed counts, time-total and indices. In the case of the analysed data series, we investigated overdispersion and serial correlation and considered specific models when its level was high. We investigated trend changes by considering models expecting changepoint for each years as a full model and using stepwise model selection to indentify significant changepoints based on Wald statistics. Model goodness of fit-test and comparison of models by the use of Akaike's Information Criterion (AIC) were made. Overall trends for the entire period was estimated. Modelling and statistical testing was run in R v4.2.1 (R Core Team 2022).

Table 1. Breeding results uploaded to the database (HO: unoccupied nest, HE: lonely stork, HPo: unsuccessful pair without fledged nestling, HPm: successful pair, HPa: all breeding pairs reported)

1. táblázat Az adatbázisba feltöltött költési eredmények (HO: lakatlan fészek, HE: magányos gólya, HPo: sikertelen pár kirepült fióka nélkül, HPm: sikeres pár, HPa: összes felmért költőpár)

Year / Év	Empty nest holder / Üres fészektartó	Nest attempt / Fészek kezdemény	HO	HE	HPo	HPm	HPa
1994	12	7	140	26	158	1,241	1,399
1995	16	2	36	4	78	406	484
1996	21	1	51	8	68	553	621
1997	25	1	127	35	165	390	555
1998	25	4	86	10	86	624	710
1999	160	7	268	38	273	1,848	2,121
2000	142	2	159	15	105	1,157	1,262
2001	186	2	224	38	271	1,255	1,526
2002	261	2	439	44	239	1,360	1,599
2003	447	4	572	58	340	1,921	2,261
2004	1,013	13	788	85	367	3,423	3,790
2005	658	8	1,198	158	766	1,527	2,293
2006	919	39	1,352	115	574	2,515	3,089
2007	968	40	1,078	108	273	2,552	2,825
2008	872	31	637	53	195	2,121	2,316
2009	1,849	89	1,269	121	601	2,858	3,459
2010	1,475	96	848	68	875	2,198	3,073
2011	1,442	93	668	48	284	2,964	3,248
2012	1,623	71	742	74	389	2,669	3,058
2013	1,628	59	793	62	361	2,917	3,278
2014	2,441	128	986	93	680	4,050	4,730
2015	1,764	51	1,015	84	531	2,527	3,058
2016	1,272	42	880	78	401	2,000	2,401
2017	1,393	60	879	63	380	2,082	2,462
2018	1,415	71	958	88	329	1,987	2,316
2019	2,528	80	1,386	83	609	3,017	3,626
2020	1,725	73	929	57	359	2,411	2,770
2021	1,285	40	647	39	333	1,932	2,265

Results

Our dataset included 111,778 nest occupation data in the White Stork database from the years 1999–2021 (including empty nest holders and unoccupied nests, *Table 1*). In total, 62,826 data were reported about real nesting (successful or unsuccessful nesting pairs, *Table 2*).

Table 2. Breeding success uploaded to the database (JZG: total number of nestlings fledged, JZa: average number of nestlings for all nests, JZm: average number of nestlings for successful nests)

2. táblázat Az adatbázisba feltöltött költési siker adatok (JZG: kirepült fiókák száma, JZa: összes költőpár fészkenkénti fiókaátlaga, JZm: sikeres párok fészkenkénti fiókaátlaga)

Year / Év	Number of fledglings / Fiókaszám						JZG	JZa	JZm
	1	2	3	4	5	6			
1994	50	281	475	339	72	2	3,765	2.73	3.09
1995	16	101	171	96	11		1,170	2.47	2.96
1996	36	139	201	131	38	6	1,667	2.69	3.03
1997	58	166	110	50	4		940	1.70	2.42
1998	32	166	264	127	18		1,754	2.53	2.89
1999	113	417	626	526	150	10	5,739	2.71	3.12
2000	49	200	398	356	131	10	3,782	3.03	3.31
2001	157	434	491	147	8		3,126	2.07	2.53
2002	104	445	578	214	12		3,644	2.29	2.69
2003	135	594	840	305	17		5,148	2.31	2.72
2004	207	767	1,421	883	120		10,136	2.69	2.98
2005	235	615	501	152	16		3,656	1.60	2.41
2006	341	741	944	408	66	1	6,623	2.15	2.65
2007	142	566	1,010	679	130	3	7,688	2.74	3.04
2008	111	464	872	542	111	1	6,384	2.78	3.04
2009	236	879	1,222	441	37		7,609	2.23	2.70
2010	433	809	655	220	27		5,031	1.67	2.35
2011	122	466	880	900	437	17	9,581	3.08	3.40
2012	215	830	1,189	331	31		6,921	2.32	2.67
2013	206	649	1,088	755	164	9	8,662	2.68	3.02
2014	321	942	1,416	1,086	249	10	12,102	2.57	3.01
2015	244	852	1,005	365	43		6,638	2.18	2.65
2016	166	608	803	323	38	2	5,285	2.26	2.72
2017	170	630	886	326	38	1	5,588	2.30	2.72
2018	126	395	673	543	190	3	6,075	2.69	3.15
2019	331	747	1,081	627	66		7,906	2.28	2.77
2020	146	642	1,070	458	34		6,642	2.45	2.83
2021	173	578	721	342	29	1	5,011	2.30	2.72

Trends of the number of breeding pairs in settlements

The overdispersion (0.485) and serial correlation (0.373) value were low and the general model expecting different change at each year fits to the data (χ^2=14,421.95, df=29,147, P>0.9, AIC=-42,704.91). Using the stepwise procedure for selection of changepoints of rtrim, the final model which expect change in the trends for 13 different periods, has the lowest AIC value (-42,717.07) and this was used for trend analysis.

The overall change of the number of breeding pairs has a weak non-significant decline (slope=0.999, SE=0.0008, P=0.085) during 1999–2021 *(Figure 1)*. The population showed several declining periods (1999–2002, 2004–2005, 2008–2009, 2011–2013, 2014–2015, 2015–2020) and the same number of increasing periods (2002–2004, 2005–2008, 2009–2011, 2013–2014, 2020–2021). The highest decline was found during 1999–2000 (slope=0.773, SE=0.024, P<0.001) and 2004–2005 (slope=0.772, SE=0.018, P<0.001) periods, the highest increase during 2002–2003 (slope=1.162, SE=0.017, P<0.001) and 2013–2014 (slope=1.118, SE=0.025, P<0.001) periods *(Table 3)*. The estimated mean number of pairs in the settlements which data was considered in the trend analysis was 4,205 pairs (SD=402.583, range=3,577–5,227, n=23).

Figure 1. Population indices of White stork in Hungary based on nest survey (NEST) and MMM data (MMM), comparing to 1999 (100%)

1. ábra A magyarországi fehérgólya-állomány változását bemutató populációs indexek, amelyek a fészekfelmérések (NEST), illetve az MMM adatokon alapulnak, 1999 tekintve bázis évnek (100%)

Table 3. Significant changes between years (periods) (slope: trend in the given period (1: no change, <1: decrease – red, >1: increase – green), SE: SE of slope, – : no significant change)

3. táblázat Egyes évek (időszakok) közti szignifikáns változások (change from: kezdő év, change upto: záró év, slope: adott időszakban a trend értéke (1: nincs változás, <1: csökkenés – piros, >1: növekedés – zöld), SE: slope SE értéke, – : nincs szignifikáns változás)

Year / Év	**Number of pairs – settlements model Párok száma – települések szerinti modell**						**Number of individuals – MMM model Egyedek száma – MMM alapú modell**					
change from	change upto	slope	SE	Wald test	df	p	change upto	slope	SE	Wald test	df	p
1999	2000	0.773	0.024	68.185	1	**0.000**	–					
2000	2002	0.942	0.018	18.394	1	**0.000**	–					
2001	–						–					
2002	2004	1.162	0.017	50.024	1	**0.000**	–					
2003	–						–					
2004	2005	0.772	0.018	155.229	1	**0.000**	–					
2005	2008	1.042	0.010	96.643	1	**0.000**	–					
2006	–						–					
2007	–						–					
2008	2009	0.952	0.023	8.694	1	**0.003**	–					
2009	2011	1.064	0.013	12.151	1	**0.000**	–					
2010	–						2011	0.581	0.150	4.409945	1	**0.036**
2011	2013	0.976	0.012	16.430	1	**0.000**	2012	1.229	0.363	2.151699	1	**0.142**
2012	–						2013	0.640	0.163	1.986028	1	**0.159**
2013	2014	1.118	0.025	19.493	1	**0.000**	2015	1.490	0.181	6.165506	1	**0.013**
2014	2015	0.896	0.019	35.815	1	**0.000**	–					
2015	2019	0.979	0.006	12.496	1	**0.000**	2016	0.577	0.120	11.557824	1	**0.001**
2016	–						2017	1.478	0.330	5.997047	1	**0.014**
2017	–						2019	0.603	0.090	8.159412	1	**0.004**
2018	–						–					
2019	2020	0.905	0.026	6.213	1	**0.013**	2021	1.179	0.205	5.128366	1	**0.024**
2020	2021	1.086	0.039	10.058	1	**0.002**	–					
2021	–						–					

Trends of the observed individuals in the MMM programme

The overdispersion (1.64) was high and considered during the modelling, the serial correlation (-0.054) value were low. The general model expecting different change at each years did not fit to the data (χ^2=2,217.41, df=1,279, P<0.001, AIC=-846.26). Using the stepwise procedure for selection of changepoints of rtrim, the final model has eight periods with different change of trends with the lowest AIC value (-861.53) and was used for trend analysis.

The overall change of the number of breeding pairs has a significant decline (slope=0.958, SE=0.009, P<0.001) during 1999–2021, regarded as a moderate decrease *(Figure 1)*. On the base of the final model, the population showed several declining periods (2010–2011, 2012–2013, 2015–2016, 2017–2019) and increasing periods (2011–2012, 2013–2015, 2016–2017, 2019–2021), however Wald test (still be used when model fit is weak, Bogaart *et al*. 2016) did not show significant changes for two periods of 2011–2012 and 2012–2013 (P>0.14). The highest decline was found during 2010–2011 (slope=0.581, SE=0.150, P=0.036) and 2015–2016 (slope=0.577, SE=0.12, P=0.001) periods, the highest increase during 2013–2015 (slope=1.49, SE=0.181, P=0.013) and 2016–2017 (slope=1.478, SE=0.33, P=0.014) periods *(Table 3)*. The estimated mean number of individuals in the surveyed UTM squares in the trend analysis was 167 individuals (SD=51.904, range=60–216, n=23).

Discussion

Based on formerly published results, the estimated national population of White Stork amounted 5,600 pairs in 1999 (Lovászi 2004), in 2001 a lower value was found (5,000 pairs) (Lovászi 2004), and 5,200 pairs in 2004 (Lovászi *et al*. 2013). In 2014, only a breeding population of 4,950 pairs was estimated (Lovászi *et al.* 2016), and then the number of breeding pairs dropped down to around 4,000 pairs (Lovászi *et al.* 2020, Lovászi & Nagy 2022). These numbers fits the trend calculated by rtrim using nest count data.

The data of Common Bird Monitoring Scheme showed stable population between 1999 and 2010, than indicated rapid decline. The number of birds observed in 1999 halved by the end of the period. The index fluctuated more hectically than the number of breeding pairs, but the peaks in 2004 and 2014–2015 were detected.

Similar peaks was found in Slovenia in 2004 (Denac 2010), and in 2004 and 2014 in Ukraine (Grischenko & Yablonovska-Grishchenko 2019) and Poland (Sikora 2017, Wardecki *et al*. 2021). As these populations also migrate on the same eastern route, it suggests the effect of conditions on the wintering grounds or during the migration (Wuczyński *et al*. 2022).

The difference between the trend indicated by the nests surveys and the data of the MMM programme may be caused by several reasons. The online White Stork database actually provided data for 13,958 nesting sites (7,600 active nests, 4,227 empty nest holder facilities (former nests) and 2,117 destroyed nests) and 117,771 annual data on nest occupancy. It is possible to specify the year of building and cessation of a nest (or a nest holder facility), but observers usually upload only annual breeding data, so we have no information on real actual number of nests. In addition to this, not all nests are covered by observers in each year. To decrease the effects of this inaccuracy of the database, analysis of breeding data combined with environmental databases could be a good basement for a GIS modelling procedure to calculate trends or population sizes.

The participants of the Common Bird Monitoring Scheme count birds on fixed points of randomly selected 2.5×2.5 km UTM squares. The White Stork is the 43rd most common species, observed in 31.7±3.6% of the UTM squares, mainly on agricultural areas, out of the four main habitat types. Forests are not suitable habitats for the species, and fewer counts are conducted on urban areas and wetlands. Due to it, a low number of White Storks (60–216) was observed on the 220 UTM squares involved in the analysis, often in flocks (in 9.4% of the UTM squares more than 4 individuals, max. 42), which can largely explain the poor fit of the full model. In addition, observers detect both breeding and non-breeding individuals. Number of immature storks depends on former years' weather of breeding sites via breeding success (Gyalus *et al*. 2022), on the weather of the wintering grounds via survival rate (Schaub *et al.* 2005) and the rate of individuals summering on non-breeding grounds (Antczak & Dolata 2006). The number of actually non-breeding adult birds is correlated with fitness after wintering, among others (Martín *et al.* 2021). Unsuccessful pairs spend more time far from their nests (as do not lay eggs or defend chicks for example against the weather), increasing the number of observed birds on sample squares. These factors should be involved into the model calculation.

Considering their characteristics, both methods are suitable for monitoring population trends of the White Storks. However, monitoring of population trends based on annual observation of all breeding pairs in settlements could provide more detailed information when large areas, representative to the country, frequently surveyed. In the case of the White Stork in Hungary, the existing online database and network based on large number of participating voluntary people let to follow the trend of the breeding population. Further improvement of the data collection by using the same 2.5×2.5 km UTM grid system, as the MMM program, to measure the density of breeding pairs in the surveyed UTM squares could let to model the spatial distribution, population size and spatial trend of the breeding population in the country on the base of recent experience in this fields (Szép 2022).

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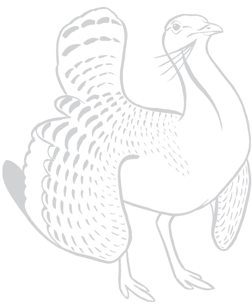

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Ecology and "bird-habitat" relationship in the cedar forest of Aurès mountain (Eastern Algeria)

Abdenour Moussouni[1*], Zoubir Boubaker[2] & Amin Chaffai[3]

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Abstract This work aims to compile the birds breeding in the cedar forest of Aurès and to study the "Bird – Habitat" relationships. The data was collected using the progressive frequency sampling method that served as the basis for the diagnosis build on an analytical approach designed around three tools (mutual information, ecological profiles, modelling). Information theory tools allowed us to identify the indicator values of species as well as the most important descriptors. Habitat modelling has been prepared for species with a high indicator value. The logistic models are shown to be well adapted to the nature of the ornithological data. They related the occurrences of the species with the dendro-ecological descriptors. The 70 surveys carried out enabled us to identify 32 bird species. The ecological analysis revealed the most active descriptors and the species with high indicator value. The best-fitting models are those of Short-toed Treecreeper with positive effect of dead wood, density of trees and variability of distances between trees, and European Robin with negative effect of anthropization and general coverage, and positive effect of crown parametres. We conclude that promoting forest structural complexity by diversifying management regimes will be key to maintain avian biodiversity in cedar forests.

Keywords: bird, endemic forest, ecological profiles, modelling, logistic regression

Összefoglalás A cédrus erdők Algéria és Marokkó hegységein előforduló nagyon változatos, őshonos ökoszisztémák. A szerzők az aurès-i cédruserdőben költő madárfajok „madár – élőhely" kapcsolatait vizsgálták. Az adatokat progresszív frekvenciás mintavételi módszerrel gyűjtötték, az elemzéshez három megközelítést használtak: ezek a kölcsönös információ, az ökológiai profilok és a modellezés. Az információelméleti eszközök lehetővé tették a fajok indikátorértékeinek, valamint a legfontosabb erdőállomány-szerkezeti háttérváltozóinak azonosítását. Az élőhely-modellezést magas indikátorértékű fajok esetében végezték. A logisztikus modellek jól illeszkednek az ismert ornitológiai adatokhoz. A magas indikátorértékű fajok előfordulását erdőállomány-szerkezeti változókkal hozták összefüggésbe. Az elvégzett 70 felmérés 32 madárfaj azonosítását tette lehetővé. Az ökológiai elemzés feltárta a magas indikátorértékű fajokat és a legjobb magyarázó értékkel rendelkező háttérváltozókat. A vizsgált faj-élőhely modellek közül a legjobban a rövidkarmú fakusz és a vörösbegy modellje illeszkedett. A kapott eredmények a cédruserdők természetvédelmi kezeléséhez is hozzájárulhatnak.

Kulcsszavak: madár, őshonos erdő, ökológiai profilok, modellezés, logisztikus regresszió

[1] *National Center for Prehistoric, Anthropological and Historical Research (CNRPAH) 03, Rue Franklin Roosevelt, Algiers, 16500*
[2] *Laboratory Research in Conservation, Management and Improvement of Forest Ecosystems (LRCGAEF). Department of Forestry and Nature Protection, National Agronomic School, Avenue Hassan Badi – El Harrach, Algiers*
[3] *Laboratory of Dynamics and Biodiversity, Faculty of Biological Sciences, University Science and Technology, Houari Boumediene, Bab Ezzouar, Algiers*
**corresponding author, e-mail: mous.abdenour@yahoo.fr*

Introduction

The diversity of the fauna represents an important dimension of global biodiversity through contributing to the proper functioning of ecosystems and by enhancing their resistance (Franklin *et al.* 2002). The importance of its maintenance stems from our efforts invested in the identification of essential species for the continued functioning of ecosystems (Burton *et al.* 1992). At the current state, knowing and understanding the long-term capacity of Mediterranean forests in maintaining their multifunctionality through their different roles, in particular as a refuge for biodiversity, are of major concerns in the ecology of forest conservation (Rykowski 2002).

The Atlas cedar *(Cedrus atlantica)*, an endemic species in North Africa, offers through the various formations that constitute, favourable habitats for a diversified flora and fauna. However, in Algeria, until recently, there has been no work concerned to study the cedar groves as a reservoir of faunistic biodiversity, neither in general nor from the perspective of ornithological biodiversity in particular, even less regarding the species-habitat relationships.

Biodiversity is almost impossible to measure exhaustively, so it is generally accepted to employ its state indicators. However, there is not yet a comprehensive forest biodiversity monitoring system. In parallel with data from forest inventories (height of trees, diameter, basal area, volume of wood, density, etc.), researchers are nevertheless gradually adding data on the abundance of particular species or groups of species, in particular vascular plants, bryophytes, lichens, saproxylic fungi, birds, carabids, etc. Biodiversity monitoring is therefore most often based on data from national forest inventories to organize reporting on forest biodiversity (Burley 2002, Nivet *et al.* 2012).

These biological indicators must satisfactorily reflect the entity they target for analysis, i.e. a taxonomic group, an ecological guild, or even an ecosystem as a whole, which includes the relationships between the different taxa that compose it (Levrel 2007). Moreover, the choice of these bioindicators is also largely subordinated to other considerations, such as the cost of monitoring, the amount of data already available and the technical capacity to monitor taxonomic groups (Dale & Beyeler 2001, Nivet *et al.* 2012).

The "birds" model is justified by the fact that they are the most approved class in bioindication (Bonardi *et al.* 2010). Their ecological characteristics and their sensitivity to habitat modifications (Blondel 1975) make these species good biological indicators (Bibby *et al.* 1992, Drapeau *et al.* 2001).

A multitude of techniques is available to model the distribution of species. They vary in principle by the type of response expected, the adjustment of the model, the weighting of observations, the integration of interactions and the type of prediction (Elith *et al.* 2006). Nevertheless, despite the performance of certain methods, none is effective in all situations (Marini *et al.* 2012).

Logistic regression is a recommended statistical tool for analyzing binary data, such as the presence and absence of avian species. The logistic model belongs to the family of generalized linear models and relates, by a linear combination, the environmental variables to the variable to be predicted by means of a logistic link function (McCullagh & Nelder 1989, Guisan & Zimmermann 2000). Logistic regressions have been used to model the probability of occurrence of many species (Tobalske & Tobalske 1999, Zimmermann & Kienast 1999, Villard & Guénette 2005). Therefore, we applied this approach to our data.

Each bird species may be characterized by a general habitat type, however many species use different features of a forest, requiring a various set of behaviour. For this purpose, we propose to study the population of birds breeding in Algerian cedar forest by analysing their interactions with the environment through a combination of methods inspired by information theory and autecological modelling. This will provide managers with appropriate models for the management and the conservation of the species and the natural environments as well as the development and implementation of protection strategies for these endemic habitats.

Material and Method

Study sites

The Aurès cedar forest, located in Eastern Algeria, is directly influenced by the Sahara. It presents the only cedar stations in North Africa with a semi-arid bioclimate on their southern border. On the northern slopes, the subhumid bioclimate dominates (Abdessemed 1981).

Figure 1. Aurès cedar forest
1. ábra Az Aurès cédrus erdő

Annual rainfall varies between 700 and 1,000 mm depending on altitude and exposure. The maximum is recorded during spring (119 mm). Summer is the least rainy season (73 mm), the rains of which are mostly stormy. The average annual temperature is 12 °C. The lowest average temperature is recorded in January (2.3 °C) and the highest average temperature is recorded in July (22.7 °C).

Attached to the Mauritanian steppe domain, sector of southern Constantine (Yahi *et al.* 2008), it represents a specific vegetation *(Figure 1)* on limestone, dominated by old stands, which develop in a pure or mixed state. The area of the Aurès cedar forests estimated at 17,000 ha is decreasing due to massive tree mortality. The drying out is intense especially in the southern areas subject to Saharan influences, in clumps or entire bands that can reach up to 95% (Kherchouche *et al.* 2012).

Bird survey

The semi-quantitative progressive frequency sampling method was adopted for the bird count. This method can help to make an ecological diagnosis at different levels of precision fixed in advance and which depends on the research objective, the available time for the observer, the spatial extension of the territory to be studied and the ecological characteristics of the area (Blondel 1975).

It is a method of recording in presence-absence which consists in counting the birds observed or heard during a period of 15 to 20 minutes from a fixed point within a fictitious circle of radius fixed or unlimited centred on the observer (Blondel *et al.* 1970, Hutto *et*

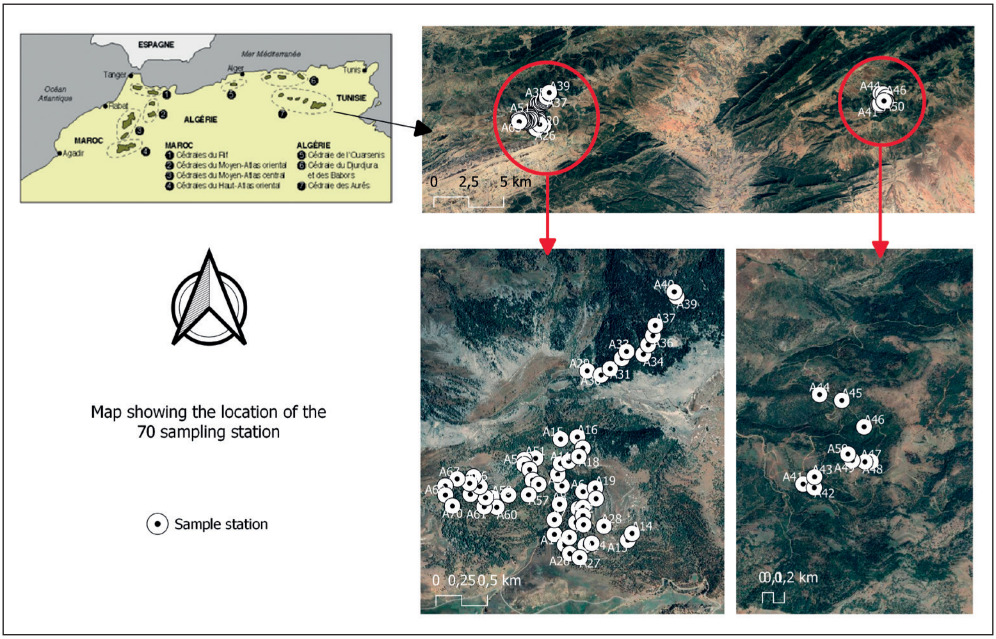

Figure 2. Map showing the location of the 70-sampling station
2. ábra A 70 mintavételi helyszín térképe

Table 1. List of measured and calculated descriptors with indication of their abbreviations
1. táblázat A leíró változók listája, azok rövidítéseivel

Descriptor category	Code	Descriptors	Details
Ecological descriptors 7	ESANT	Trees health status	Visual detection of signs of disease (defoliation, discoloration, parasitic attacks, etc.)
	ANTH	Degree of anthropization	Indications of any actual and/or potential anthropogenic disturbance coded according to their intensity: "0" no disturbance; "1" weak disturbance; "2" medium disturbance; "3" high disturbance.
	EAU	Presence of watercourses	Water bodies, wadi, stream, small ponds, areas of water stagnation. "0" absence, "1" presence.
	ROCH	Presence of rocks	"0" absence, "1" presence.
	CAVT	Presence of cavities on trees	Cavity, cracks, hollow. "0" absence, "1" presence.
	MOSSL	Presence of moss and lichen	"0" absence, "1" presence.
	BMORT	Presence of dead wood	The ratio of dead trees (standing or on the ground) to the total number of trees per station.
Overall vegetation structure 6	RECGRL	General plot cover	Standardized stratification of the vegetation with visual estimation of the leaf index of each stratum (tree, shrub, herbaceous). The general recovery is also estimated. The visual estimation of vegetation cover rates being subjective, it required the use of a cover chart.
	RECARBR	Coverage of the tree layer	
	RECARBU	Shrub layer cover	
	RECHERB	Covering of the herbaceous layer	
	REGEN	Regeneration rate	Percentage of cedar regeneration per station.
	FEUIL	Deciduous trees rate	Number of deciduous trees calculated on the total number of trees per plot.
Vertical stand structure 7	HTARBMoy	Average trees height	All measured trees and averaged data per plot (measurement unit: m).
	HTFUTMoy	Average trunk height	
	HTHOPMoy	Average crown height	
	VOHOPTot	Total crown volume	All measured trees crown and sum data per plot (measurement unit: m^3).
	VOHOPMoy	Average crown volume	All measured trees crown and averaged data per plot (measurement unit: m^3).
	VTot	Total wood volume	All measured trees volume and sum data per plot (measurement unit: m^3). The wood volume per tree is calculated as follows: $V = g * H_{trunk}$ with g = basal area of the tree, H_{trunk} = trunk height.
	VMoy	Average wood volume	All measured trees volume and average data per plot (measurement unit: m^3).
Spatial stand structure 7	DENSARB	Trees density	Number of trees per hectare (trees/ha), calculated by the formula: DENSARB= (N*10000)/s With: N = number of trees counted in the plot, s = area of the plot (in m^2).
	DISARBMoy	Average distance between trees	/
	DIMARBMoy	Average shaft diameter at breast height	/
	SUHOPTot	Total crown area	All measured trees crown area and sum data per plot (measurement unit: m^2/plot). The crown area of a tree (Su_{hop}) is calculated as follows: $Su_{hop} = [\pi * (D_{hop})^2]/4$. With D_{hop} = average diameter of the crown of the tree.
	SUHOPMoy	Average crown area	All measured trees crown area and average data per plot (measurement unit: m^2/trees).
	GTot	Total wood basal area	Sum of the cross-sections at 1.30 m height from the ground, of all the trees inventoried in the plot (measurement unit: m^2/plot). The basal area (g) of a tree is calculated as follows: $g = (\pi/4) * DIMARB^2$ With DIMARB= shaft diameter at breast height.
	GMoy	Average wood basal area	Average of the cross-sections at 1.30 m height from the ground, of all the trees inventoried in the plot (measurement unit: m^2/trees).

Descriptor category	Code	Descriptors	Details
Stand structural variability descriptors 18	DISARBEty	Standard deviation of the mean distance between trees	/
	DISARBCV	Coefficient of variation of the average distance between trees	/
	DIMARBEty	Standard deviation of average diameter per tree	/
	DIMARBCV	Coefficient of variation of average diameter per tree	/
	HTARBEty	Standard deviation of the average height of the trees	/
	HTARBCV	Coefficient of variation of average tree height	/
	HTFUTEty	Standard Deviation of Average Barrel Height	/
	HTFUTCV	Coefficient of variation of average trunk height	/
	HTHOPEty	Standard deviation of average crown height	/
	HTHOPCV	Coefficient of variation of average crown height	/
	SUHOPEty	Standard deviation of the average crown area	/
	SUHOPCV	Coefficient of variation of the average crown area	/
	VOHOPEty	Mean Crown Volume Standard Deviation	/
	VOHOPCV	Coefficient of variation of average crown volume	/
	GEty	Standard deviation of the average basal area of wood	/
	GCV	Coefficient of variation of mean basal area of wood	/
	VEty	Standard Deviation of Mean Wood Volume	/
	VCV	Coefficient of variation of average wood volume	/

al. 1986). In our case, the birds were counted using the fixed circular plot technique with a radius of 150 m for a period of 15 min. Thus, 70 count stations *(Figure 2)* were carried out during the breeding period (April – June). 5 to 8 counting points/day are carried out during the peak of daily activity which corresponds, for diurnal birds, to the first hours after sunrise (from 6 a.m. to 10 a.m.). Each station was sampled only once (one count/station). All birds heard and/or seen were noted.

Eco-dendrometric variables

The study of bird-habitat relationships involves the search for habitat characteristics that are closely related to variations in the abundance and distribution of species. These characteristics should be measured at the same stations and time of taking the bird survey (Bradbury *et al.* 2005).

All the stations of bird surveys were accompanied by an eco-dendrometric description of the habitat. For sampling of habitat characteristics, the circular plot of 20 m radius is used. It is considered fairly representative for the description of bird habitats (Young & Hutto 2002). Inside the plot, all the trees were measured. We were interested in the general environmental conditions of the station, the overall structure of the vegetation, the vertical and spatial structures of cedar stands and the description of their structural variability *(Table 1)*. The eco-dendrometric measurements concerned 2,501 trees including 2,471 cedars.

Data analysis

Before starting the analytical approach, we calculated the specific richness (total number of species contacted at least once), the heritage richness taking into account the protection status of the birds identified by referring to the national legislative texts of Algeria, to the IUCN Red List and the Bern Convention.

We calculated the taxonomic diversity (number of species per family) (Jastrzębska *et al.* 2011). Also, birds were assigned to functional groups based on their diet (insectivorous, granivorous, omnivorous). Similar groupings have been used for the functional classification of birds (De Souza *et al.* 2013, Prajapati & Prajapati 2013).

The analytical approach adopted focused on the principles and tools of the theory of information, initially developed in phyto-ecology by Guillerm (1971), Daget *et al.* (1972), Godron (1968, 1975), and Daget and Godron (1978). This enables the analysis of the distributions of species by using the concepts below.

The profiles of the relative frequencies "F_R" correspond to the profile of the centesimal frequencies used in ornithology. It represents the number of the species present in each class by a factor "L" divided by the number of records made in each class, multiplied by 100.

$$F_R = \frac{FA}{N} * 100$$

FA: Number of individuals or absolute frequency, N: Number of avian surveys.

The distribution of species in different classes of ecological factors corresponds to a set of probabilities of their presence when the number of records becomes sufficiently large (Godron 1968). These probabilities allow us to estimate numerous information: entropy, the quality of the sampling, mutual information, and the most active variables (the most important variables influencing species distribution) (Mangara *et al.* 2010).

Species entropy H(E) is a measurement of the ability of a species to respond to a variable. It grants the possibility of measuring the potential information that each species can relatively provide to a variable (Blondel *et al.* 1978). The species entropy is calculated by the following formula (Guillerm 1971):

$$H(E) = \frac{\sum_I^{NK} U(K)}{NR} log_2 \frac{NR}{\sum_I^{NK} U(K)} + \frac{\sum_I^{NK} V(K)}{NR} log_2 \frac{NR}{\sum_I^{NK} V(K)}$$

NK: number of distinguished classes for the factor L, U(K): number of records in class K within the presence of species E, V(K): number of records in class K where species E is absent, NR: total number of readings.

Entropy factor H(L) determines the quality of sampling and is used in the determination of the most active ecological variables (Guillerm 1971, Daget *et al.* 1972). The overall profile for a factor L, presents a NK number of classes (1, 2, … NK). It is calculated as follows:

$$H(L) = \sum_{I}^{NK} \frac{R(K)}{NR} log_2 \frac{NR}{R(K)}$$

R(K): number of records carried out in class K, NR: total number of records.

The maximum entropy factor, which corresponds to the best sampling is (Guillerm 1971):

$$H(L)max = \sum_{I}^{NK} \frac{1}{NK} log_2 NK = \frac{NK}{NK} log_2 NK = log_2 NK$$

The sampling quality for the factor considered can be assessed by comparing the maximum entropy linked to the factor with that resulting from the sampling data (Touaylia *et al.* 2011). It is given by the report:

$$Q = H(L)/H(L)_{max}$$

Q is the value reflecting the quality of the sampling.

Mutual species-factor information detects the most active factors in the distribution of species and highlights the amount of information provided by the distributions of frequency of each species for the considered descriptor (Blondel *et al.* 1978). It also enables the classification of species according to their sensitivity to the factor considered (Legendre & Legendre 1984). For each factor studied, mutual information is established for all the species encountered in the surveys. Thus, for a species E and a factor L, the mutual information is denoted by H(L, E) and is defined as follows (Daget *et al.* 1972):

$$H(L,E) = \sum_{I}^{NK} \frac{U(K)}{NR} log_2 \frac{\frac{U(K)}{R(K)} * NR}{U(E)} + \sum_{I}^{NK} \frac{V(K)}{NR} log_2 \frac{\frac{V(K)}{R(K)} * NR}{V(E)}$$

NK: number of distinguished classes for the factor L, U(K): number of records of class K in which species E is present, V(K): number of records of class K in which species E is absent, R(K): number of records in class K, U(E): total number of records in which species E is present, V(E): total number of records in which species E is absent, NR: total number of readings.

Global species indicator value: To detect the index value of each species in relation to all the factors, we calculated the average mutual information $H(L, E)_{moy:}$

$$H(L,E)moy = \frac{H(L1,E) + H(L2,E) + \cdots H(LN,E)}{N}$$

E: species, L1, L2, ….: factors, N: number of factors.

The modelling of bird-habitat interactions was addressed according to an autecological approach. We have selected the species which have a high indicator value and whose frequency is greater than 20% to minimize the biases caused by the detectability of the species (Williams 2003).

The 45 potentially effective descriptors included in the regression models were chosen based on the extensive research on the ecological requirements of forest birds. These descriptors underwent a triple selection to highlight their discriminatory power.

Initially, two groups of descriptors were retained during the ecological analysis: those whose mutual information demonstrated relevance and those which were shown to discriminate (Kruskal-Wallis, $\alpha < 0.05$) during the analysis of ecological profiles. Subsequently, through simple regressions, the descriptors were tested individually by logistic regression to identify all the variables statistically linked to the dependent variables. The candidate variables are those whose p-value is less than or equals 0.1. Following these steps, we have retained the descriptors that we deemed relevant by reintegrating some forced descriptors. To overcome the collinearity problem, we have performed a Spearman correlation test for all the selected descriptors. We consider that the two descriptors are strongly correlated when the correlation coefficient is ≥ 0.8.

The regression procedure adopted is the so-called “top-down stepwise” method to maximize the explanation of the dependent variable with the lowest number of independent variables.

All the processing was carried out using IBM SPSS version 19.0 (IBM Corp. Released 2010) and XLSTAT-Pro 7.5 (Addinsoft 2004).

Results

A total of 24 breeding birds species have been identified in Aurès cedar forest with an average richness of 8.03 species per station. Sixteen species are sedentary and eight are migratory. Additionally, 8 species were contacted outside the stations (auditory or visual contacts made beyond 150 metres). The overall 32 bird species are divided into 27 genera and 16 families. The Muscicapidae dominates with 19%, followed by the Accipitridae with 13%.

Fourteen species are protected by executive decree at national level (No. 12-235 of May 24, 2012, setting the list of non-domestic animal species protected in Algeria), 29 are protected under the Bern Convention. All the species listed are considered to be of a least concern according to the IUCN Red List *(Table 2)*. The most common species are the Coal

Table 2. List of bird species recorded in the Aurès cedar forest
2. táblázat A megfigyelt fafajok listája az Aurès cédrus erdőben

Family	Common Name	Scientific Name	Phenological Status (1)	Protection Status (2)
Accipitridae	Golden Eagle*	*Hieraaetus pennatus*	ME	A, LC, B2
	Red Kite*	*Milvus milvus*	S	A, LC, B2
	Bonelli's Eagle*	*Aquila fasciata*	S	A, LC, B2
	Black Kite*	*Milvus migrans*	ME	A, LC, B2
Certhiidae	Short-toed Treecreeper	*Certhia brachydactyla*	S	LC, B2
Columbidae	Stock Dove	*Columba oenas*	ME	A, LC
	Common Wood Pigeon	*Columba palumbus*	S	LC
	European Turtle Dove	*Streptopelia turtur*	ME	LC, B3
Corvidae	Northern Raven*	*Corvus corax*	S	LC, B3
Emberizidae	Rock Bunting	*Emberiza cia*	S	LC, B2
Falconidae	Common Kestrel *	*Falco tinnunculus*	S	A, LC, B2
	Peregrine Falcon *	*Falco peregrinus*	S	A, LC, B2
Fringillidae	Common Chaffinch	*Fringilla coelebs*	S	LC, B3
	European Serin	*Serinus serinus*	S	A, LC, B2
	European Greenfinch	*Chloris chloris*	S	LC, B2
Muscicapidae	Spotted Flycatcher	*Muscicapa striata*	ME	LC, B2
	Europian Pied Flycatcher	*Ficedula hypoleuca*	ME	LC, B2
	European Robin	*Erithacus rubecula*	S	LC, B2
	Common Redstart	*Phoenicurus phoenicurus*	ME	A, LC, B2
	Moussier's Redstart	*Phoenicurus moussieri*	S	A, LC, B3
	Northern Wheatear	*Oenanthe oenanthe*	ME	LC, B2
Paridae	African Blue Tit	*Cyanistes teneriffae*	S	LC, B2
	Great Tit	*Parus major*	S	LC, B2
	Coal Tit	*Periparus ater*	S	LC, B2
Phylloscopidae	Western Bonelli's Warbler	*Phylloscopus bonelli*	ME	LC, B2
Picidae	Levaillant's Woodpecker	*Picus vaillantii*	S	A, LC
Régulidae	Common Firecrest	*Regulus ignicapilla*	S	A, LC, B2
Strigidae	Tawny Owl *	*Strix aluco*	S	A, LC, B2
Troglodytidae	Winter Wren	*Troglodytes troglodytes*	S	LC, B2
Turdidae	Mistle Thrush	*Turdus viscivorus*	S	LC, B3
	Common Blackbird	*Turdus merula*	S	LC, B3
Upupidae	Eurasian Hoopoe	*Upupa epops*	S	A, LC, B2

(1) Phenological status. S: sedentary, ME: summer migrant
(2) Protective status. A: Algerian law, LC: Least Concern on the IUCN red list, B: Bern Convention and its annexes 1, 2 and 3.
* Species contacted off-station

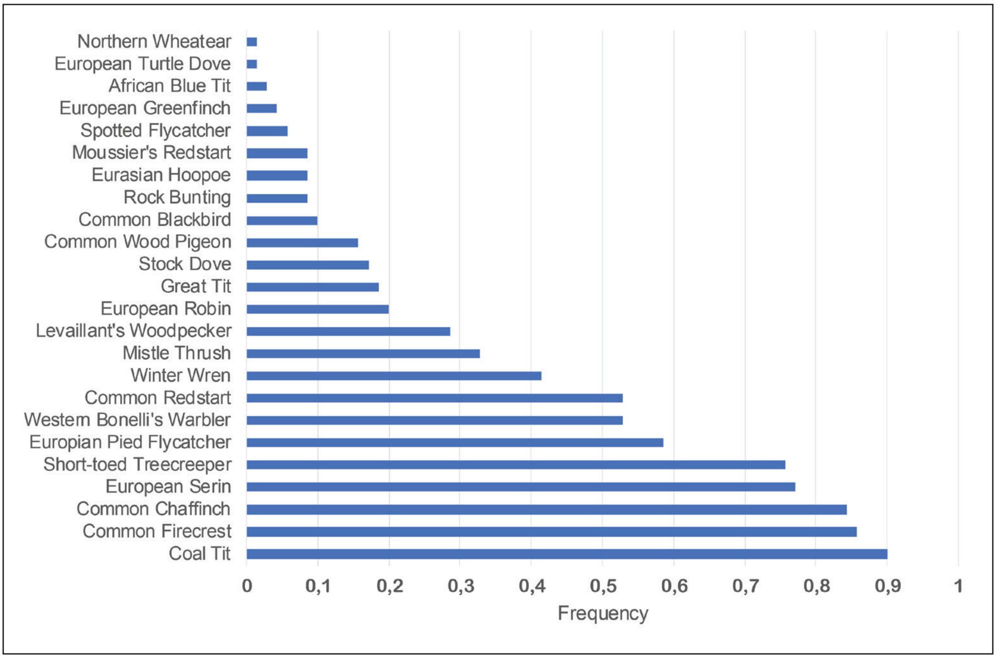

Figure 3. Frequency of bird species in the Aurès cedar forest
3. ábra Madárfajok gyakoriságai az Aurès cédrus erdőben

Tit *(Periparus ater)*, the Common Firecrest *(Regulus ignicapilla)*, the Common Chaffinch *(Fringilla coelebs)*, the European Serin *(Serinus serinus)* and the Short-toed Treecreeper *(Certhia brachydactyla)* (Frequency > 75%). African Blue Tit *(Cyanistes teneriffae)*, European Turtle Dove *(Streptopelia turtur)* and Northern Wheatear *(Oenanthe oenanthe)* are the less frequent (Frequency < 30%) *(Figure 3)*.

Table 4 represents the values of the factor entropy, the maximum factor entropy and the quality of the sampling for all the descriptors selected. Given their respective class number, all the descriptors were well sampled (Q > 0.9).

The species able to respond to variations of the eco-dendrometric descriptors are those with high entropies. These are the ones present in almost 50% of the surveys and for which the indeterminacy in terms of presence/absence is high. Fourteen species show high entropy (> 0.5) *(Table 3)*.

To determine the active eco-dendrometric descriptors in bird species distribution, taken all together, we have calculated the average of the mutual information of each descriptor in relation to its entropy. The most active descriptors are the total crown volume, the total basal area and the average distance between trees (highest average of mutual information) *(Figure 4)*.

The analysis of the bird species selected according to their average mutual information towards all the descriptors informs about the indicator value of each species. Those that have important indicator values in our case are the Stock Dove, the European Robin, the Common Firecrest and the Short-toed Treecreeper *(Figure 5)*.

Table 3. Bird species entropies
3. táblázat Madárfaj entrópiák

Scientific Name	Common Name	FO	Entropy
Emberiza cia	Rock Bunting	0.09	0.422
Muscicapa striata	Spotted flycatcher	0.06	0.316
Ficedula hypoleuca	Europian Pied Flycatcher	0.59	**0.979**
Certhia brachydactyla	Short-toed Treecreeper	0.76*	**0.800**
Turdus viscivorus	Mistle Thrush	0.33	**0.913**
Upupa epops	Eurasian Hoopoe	0.09	0.422
Turdus merula	Common Blackbird	0.10	0.469
Cyanistes teneriffae	African Blue Tit	0.03	0.187
Parus major	Great Tit	0.19	**0.692**
Periparus ater	Coal Tit	0.90	0.469
Picus vaillantii	Levaillant's Woodpecker	0.29	**0.863**
Columba oenas	Stock Dove	0.16	**0.627**
Columba palumbus	Common Wood Pigeon	0.84	**0.627**
Fringilla coelebs	Common Chaffinch	0.53	**0.998**
Phylloscopus bonelli	Western Bonelli's Warbler	0.86*	**0.592**
Regulus ignicapilla	Common Firecrest	0.20*	**0.722**
Erithacus rubecula	European Robin	0.53	**0.998**
Phoenicurus phoenicurus	Common Redstart	0.09	0.422
Phoenicurus moussieri	Moussier's Redstart	0.77	**0.776**
Serinus serinus	European Serin	0.01	0.108
Streptopelia turtur	European Turtle Dove	0.41	**0.979**
Oenanthe oenanthe	Northern Wheatear	0.17	**0.661**
Troglodytes troglodytes	Winter Wren	0.01	0.108
Chloris chloris	European Greenfinch	0.04	0.255

(*) Species selected for ecological profiles and regression. In bold, species with entropy greater than 0.5

To analyse the ecology of bird species through ecological profiles, we treated species with a high indicator value and a frequency greater than 20%, simultaneously. The descriptors retained for each species are those for which the nonparametric test of Kruskal and Wallis is significant ($\alpha = 0.05$).

The descriptors selected for Short-toed Treeceeper are average tree height, average crown surface, total wood basal area and total wood volume. Those selected for Common Firecrest are tree density, total crown surface, total crown volume and total wood volume. For European Robin, the descriptors retained are anthropization degree, shrub cover, the average distance between trees and average wood basal area.

Short-toed Treecreeper showed a marked preference for the upper classes of the various descriptors used. Common Firecrest showed no tendency for wood volume while the middle

Table 4. Logistics regressions models for species with frequencies above 20%
4. táblázat A 20%-nál gyakoribb fajok logisztikus regressziói

		A	E.S.	Wald	ddl	Sig.	Exp(B)	Exp(B) 95% CI		Nagelkerke 's R^2
								Lower	Upper	
Short-toed Treecreeper	BMORT	21.815	10.18	4.589	1	__.032*__	2.980E	6.402	1.39E+18	0.78
	DENSARB	0.038	0.016	5.526	1	__.019*__	1.039	1.006	1.072	
	DISARBCV	28.985	12.17	5.67	1	__.017*__	3.872E	168.52	8.90E+22	
	DIMARBCV	-29.22	12.08	5.851	1	__.016*__	0	0	0.004	
	HTARBCV	-24.85	11.36	4.782	1	__.029*__	0	0	0.076	
	SUHOPTot	-0.024	0.012	4.395	1	__.036*__	0.976	0.954	0.998	
	SUHOPEty	1.591	0.652	5.964	1	__.015*__	4.911	1.369	17.611	
	Constante	-13.93	5.354	6.774	1	0.009	0			
European Robin	ANTH	-2.946	1.186	6.173	1	__.013*__	0.053	0.005	0.537	0.681
	RECGRL	-42.33	19.45	4.735	1	__.030*__	0	0	0.015	
	RECARBR	21.628	11.66	3.444	1	0.063	2.47E+09	0.297	2.06E+19	
	FEUIL	14.533	7.499	3.755	1	0.053	2049256	0.847	4.96E+12	
	BMORT	9.311	4.87	3.655	1	0.056	11056.3	0.791	1.55E+08	
	HTARBCV	-9.66	5.414	3.184	1	0.074	0	0	2.588	
	HTHOPMoy	0.621	0.28	4.913	1	__.027*__	1.861	1.075	3.224	
	SUHOPCV	5.936	2.102	7.974	1	__.005**__	378.257	6.146	23280.1	
	Constante	13.782	9.161	2.263	1	0.132	967314			
Coal Tit	RECARBU	-14.02	6.388	4.813	1	__.028*__	0	0	0.224	0.481
	DENSARB	-0.011	0.005	4.503	1	__.034*__	0.989	0.979	0.999	
	DIMARBEty	-16.79	8.427	3.968	1	__.046*__	0	0	0.764	
	HTARBMoy	0.545	0.257	4.512	1	__.034*__	1.725	1.043	2.854	
	HTFUTEty	-0.45	0.333	1.823	1	0.177	0.638	0.332	1.225	
	HTFUTCV	2.232	1.81	1.521	1	0.218	9.314	0.268	323.224	
	Constante	2.443	3.043	0.645	1	0.422	11.51			
Common Chaffinch	REGEN	-7.084	2.592	7.471	1	__.006**__	0.001	0	0.135	0.451
	HTHOPMoy	-0.419	0.182	5.285	1	__.022*__	0.657	0.46	0.94	
	SUHOPEty	-0.208	0.08	6.733	1	__.009**__	0.812	0.694	0.95	
	Constante	10.369	3.047	11.58	1	0.001	31843.6			
Western Bonelli's Warbler	RECGRL	15.537	6.509	5.697	1	__.017*__	55923.7	16.099	1.94E+12	0.446
	RECHERB	-6.148	2.304	7.121	1	__.008**__	0.002	0	0.195	
	BMORT	-6.206	3.234	3.682	1	0.055	0.002	0	1.142	
	DENSARB	-0.02	0.006	10.63	1	__.001***__	0.98	0.969	0.992	
	HTARBEty	0.539	0.216	6.245	1	__.012*__	1.714	1.123	2.615	
	HTHOPMoy	0.235	0.125	3.522	1	0.061	1.265	0.99	1.617	
	Constante	-6.148	4.987	1.519	1	0.218	0.002			

		A	E.S.	Wald	ddl	Sig.	Exp(B)	Exp(B) 95% CI		Nagelkerke 's R^2
								Lower	Upper	
European Pied Flycatcher	RECGRL	6.219	5.286	1.384	1	0.239	502.434	0.016	15873647	0.338
	RECHERB	3.038	1.657	3.361	1	0.067	20.856	0.811	536.605	
	FEUIL	-12.74	8.936	2.032	1	0.154	0	0	118.647	
	BMORT	-7.429	3.31	5.039	1	**.025***	0.001	0	0.39	
	DENSARB	-0.012	0.005	5.814	1	**.016***	0.988	0.979	0.998	
	DIMARBEty	-8.670	4.246	4.169	1	**.041***	0	0	0.707	
	HTARBMoy	0.081	0.079	1.064	1	0.302	1.085	0.929	1.266	
	Constante	-1.248	4.637	0.072	1	0.788	0.287			
Common Firecrest	DIMARBEty	-14.94	7.501	3.967	1	**.046***	0	0	0.788	0.321
	DIMARBCV	3.923	2.744	2.044	1	0.153	50.547	0.233	10949.4	
	VOHOPTot	0.001	0.001	3.681	1	0.055	1.001	1	1.002	
	VTot	0.027	0.015	3.144	1	0.076	1.027	0.997	1.058	
	Constante	-0.451	1.241	0.132	1	0.716	0.637			
Common Redstart	ANTH	0.683	0.393	3.019	1	0.082	1.981	0.916	4.282	0.296
	RECHERB	2.914	1.439	4.097	1	**.043***	18.425	1.097	309.523	
	DIMARBCV	-2.421	1.417	2.921	1	0.087	0.089	0.006	1.427	
	VOHOPTot	0.001	0	5.06	1	**.024***	1.001	1	1.001	
	Constante	-3.326	1.494	4.959	1	0.026	0.036			
Winter Wren	DISARBEty	-0.612	0.24	6.505	1	**.011***	0.542	0.339	0.868	0.238
	VOHOPTot	0.001	0	5.643	1	**.018***	1.001	1	1.001	
	Constante	0.14	0.892	0.025	1	0.875	1.151			
Mistle Thrush	ESANT	2.215	0.864	6.572	1	**.010****	9.161	1.685	49.823	0.209
	RECGRL	-8.027	4.709	2.906	1	0.088	0	0	3.327	
	DISARBCV	-3.072	1.7	3.264	1	0.071	0.046	0.002	1.298	
	Constante	7.805	4.25	3.373	1	0.066	2452.86			
European Serin	MOSSL	-1.73	0.965	3.231	1	0.072	0.176	0.027	1.17	0.147
	DISARBMoy	0.181	0.151	1.426	1	0.232	1.198	0.891	1.612	
	Constante	0.557	0.795	0.491	1	0.483	1.745			
Levaillant's Woodpecker	RECGRL	4.301	4.526	0.903	1	0.342	73.7	0.01	525569.34	0.119
	REGEN	-2.784	1.523	3.342	1	0.068	0.062	0.003	1.222	
	BMORT	1.906	1.916	0.989	1	0.32	6.725	0.157	287.488	
	Constante	-4.511	4.018	1.261	1	0.262	0.011			

*: significant (α ≤ 0.05) **: highly significant (α ≤ 0.01) ***: very highly significant (α ≤ 0.001)

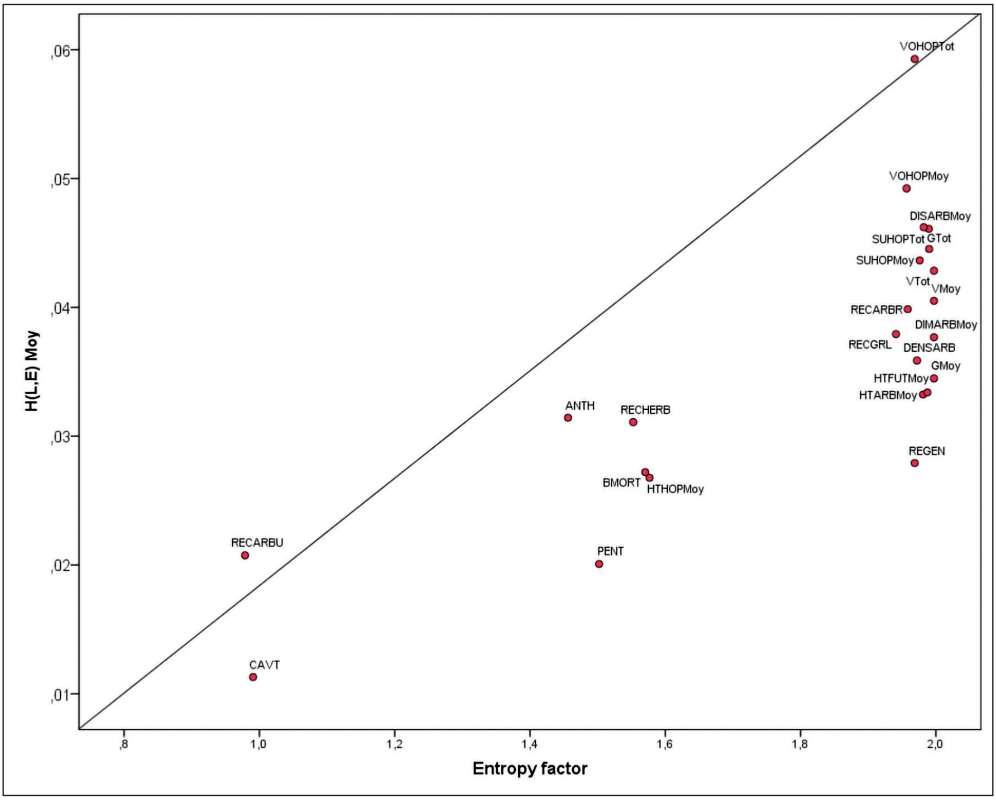

Figure 4. Relationship «Mutual information – Descriptor entropy» defining active descriptors
4. ábra A közös információ és az entrópia kapcsolata

and upper classes of the other descriptors were favourable to it. The European Robin showed a preference for low density and non-anthropogenic forest environments *(Figure 6)*.

The relationship between the twelve species whose frequency is greater than 20% and the eco-dendrometric parameters are described using logistic regression. The models fit assessment are based on Nalgelkerke's R^2. The best-fitting model is the one with a high R^2. We rely on Wald's statistic to assess the statistical significance of the estimated coefficients of the independent variables. The results of the logistics regressions are summarized in *Table 4*.

The best-fitting models are those of Short-toed Treecreeper (Nalgelkerke's $R^2 = 0.78$) and European Robin (Nalgelkerke's $R^2 = 0.68$).

All the descriptors included in the Short-toed Treecreeper model are relevant ($\alpha \leq 0.05$). The rate of dead wood, the density of trees, the variability of distances between trees have a positive effect (Exp (B) > 1) while the variability of diameters and heights of trees, as well as the total surface of the crown and standard deviation of crown surfaces, have negative effects (Exp (B) < 1).

The European Robin model showed a negative effect on anthropization and general coverage, and a positive effect on average crown height and variability of crown surfaces ($\alpha \leq 0.01$).

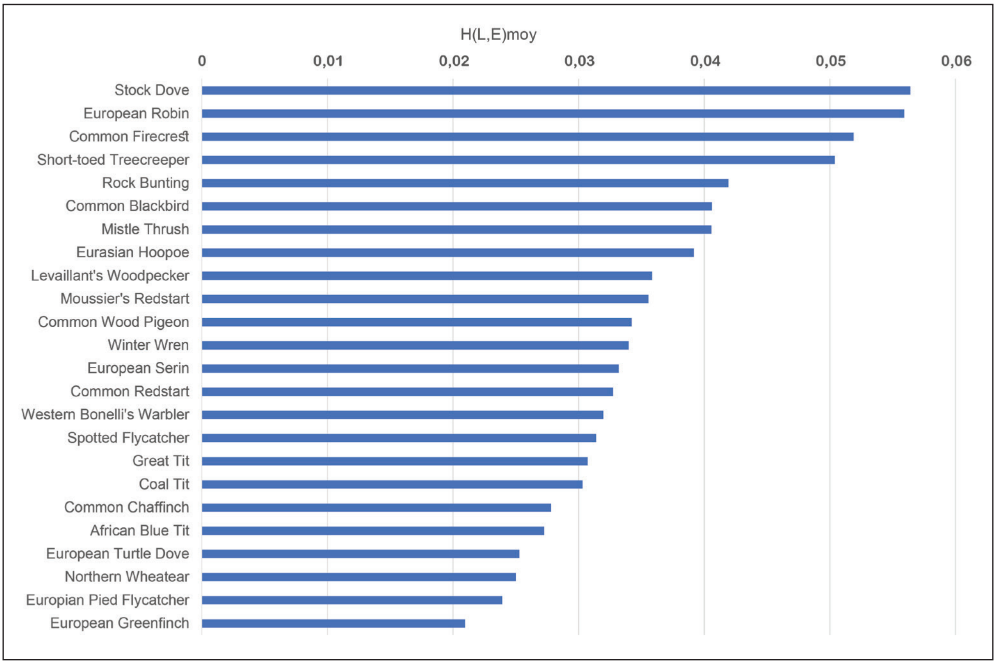

Figure 5. Indicative values of bird species
5. ábra A fajok indikációs értékei

Four effective descriptors (shrub cover, tree density, standard deviation of tree diameter, average tree height) act negatively on the Coal Tit. Common Chaffinch is negatively affected by three descriptors. The average crown height affects its presence significantly ($\alpha \leq 0.05$). The regeneration rate and the standard deviation of crown surfaces affect it highly ($\alpha \leq 0.01$).

In Western Bonelli's Warbler model we note positive effects of general cover and the standard deviation of tree heights, and negative effects of grass cover ($\alpha \leq 0.01$) and tree density ($\alpha \leq 0.001$).

Deadwood rate, tree density and standard deviation of tree diameters negatively affect Europian Pied Flycatcher presence. Only one descriptor (standard deviation of tree diameter) is relevant in the Common Firecrest model with a negative effect.

Common Redstart model contains two relevant descriptors (covering of the herbaceous stratum and the total volume of the crowns) which act positively on the presence of the species. The presence of Winter Wren is negatively affected by the standard deviation of the distance between trees and positively by the total volume of the crown. Tree health is the only descriptor with significant action ($\alpha \leq 0.01$) in the Mistle Thrush model. European Serin and Levaillant's Woodpecker *(Picus vaillantii)* models are very weakly fitted (Nalgelkerke's $R^2 = 0.147$; 0.117, respectively) and do not present any relevant descriptor.

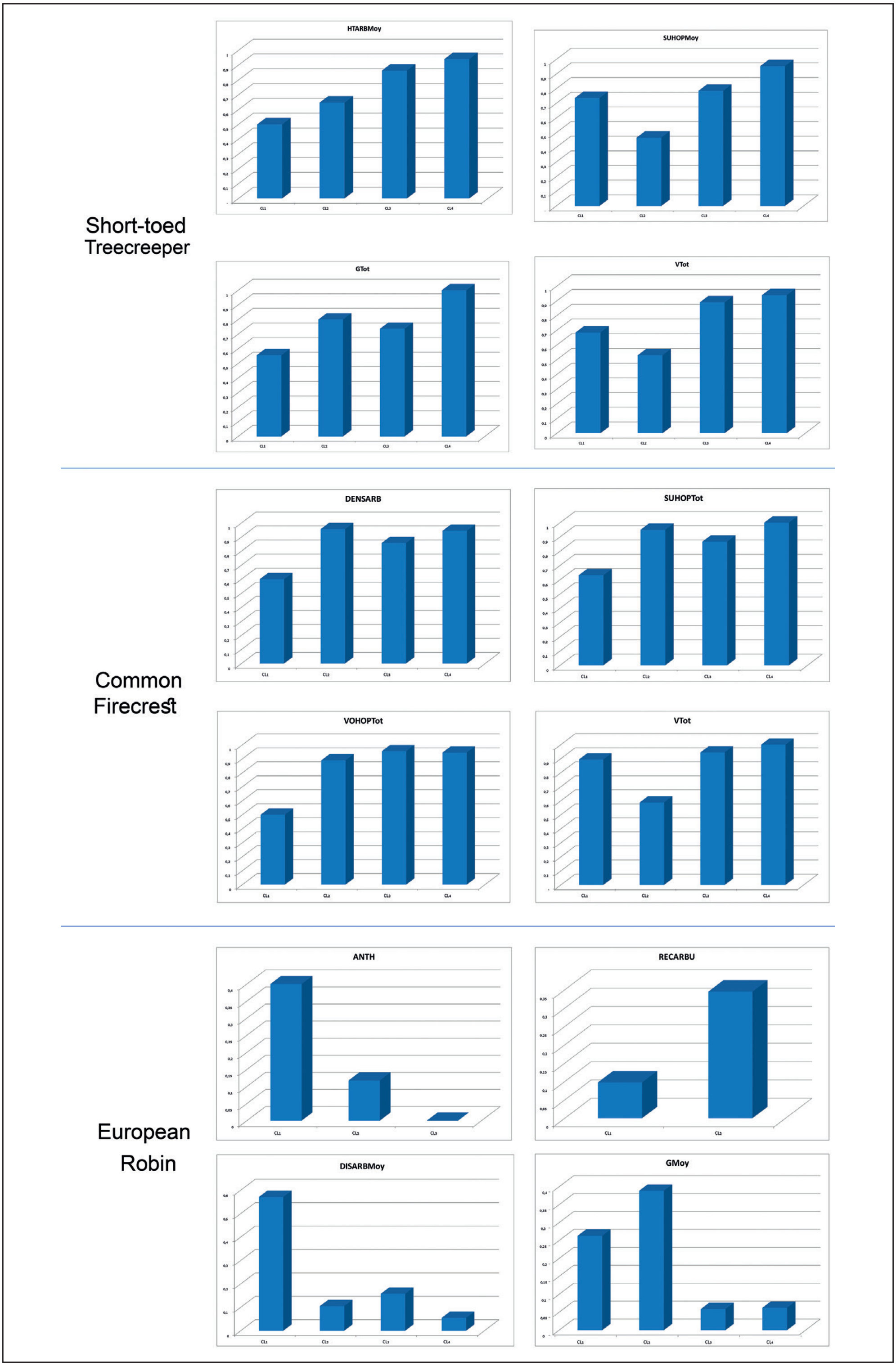

Figure 6. Ecological profiles
6. ábra Ökológiai profilok

Discussion

Our diagnostic was based on establishing an ornithological portrait in an endemic forest in North Africa, based on multiple analytical approaches (exploratory analysis, ecological profiles, mutual information and logistic models). The ornithological diagnosis highlighted the ecological heritage characteristics and peculiarities of the cedar forest birds and their ecological requirements.

The bird species richness of the Aurès cedar forest was estimated at 32 species. However, it should be pointed out that the absence of a species does not necessarily mean that it does not present in this type of habitat in one-visit point counts. Some species may not appear during sampling (Royle *et al.* 2005) or are very discreet and pose the problem of detectability (Alldredge *et al.* 2007, Pacifici *et al.* 2008, Stanislav *et al.* 2010). The habitat structure, as well as the observation period, have a considerable influence on the detection of avian species (Alldredge *et al.* 2007, Brewster & Simons 2009, Simons *et al.* 2009, Basile *et al.* 2020).

The heritage bird's value is reflected by the presence of raptors which constitute excellent biological indicators (Kirk 2003, Farmer *et al.* 2007, Santangeli & Girardello 2021) and also by the number of species with national and international protection status. The analysis of the birds' taxonomic and phenological composition revealed the reception capacity of the cedar forest offering heterogeneity which promotes the coexistence of a multitude of species. This diversity is due to the strategic location of the Mediterranean region (Blondel *et al.* 1978).

Mutual information "species – descriptor" highlighted the most determining descriptors in the cedar forest. The first features of the information collected provide an appreciation of the species' reaction to the descriptors. These findings are further refined by the ecological profiles.

The most active descriptors identified are crown volume, wood basal area and distance between trees. Several authors (Blondel *et al.* 1978, Menard & McNeil 1982, Lebreton *et al.* 1987, Boubaker 1996) using mutual information methods "species-ecological factor" asserted the influences of the quoted descriptors on birds.

The species with high indicator values are sylvatic species restricted to coniferous/mixed forests and cool mountain areas (Blondel 1970, Dronneau 2007).

The Common Firecrest model displays a single relevant descriptor (standard deviation of tree diameter) with a negative effect, which could reflect a preference for regular forest (trees with same age and similar dimension). This conifer specialist bird reaches its maximum abundance in the fir forest of the Morvan in the high forest stage with trees 25 metres high (Marion & Frochot 2001). In the Ardennes oak forest, the average tree circumference affects the Common Firescrest negatively (Delahaye 2006). In El Kala pine forest, the species' presence is linked to the development of the tree layer and its maximum abundance occurs in the old stages of the succession where the cover and the height of the trees determine its presence (Benyacoub 1993).

All the descriptors included in the Short-toed Treecreeper model seem relevant. The rate of dead wood, which is often abundant in old forest stages favourable to corticolous and cavernicolous species, the density of trees and the variability of distances between trees have a positive effect on the presence of the species (Laiolo 2002, Leitao *et al*. 2022).

The large size of the branches constitutes an obstacle hindering access to cortical insectivorous species including Short-toed Treecreeper (Benyacoub 1993, Delahaye 2006). This is reflected in the cedar forest by the negative effect of the variability of the diameters and heights of the trees, the total crown area and the standard deviation of the crown areas. In Ardennes oak-beech forest, the old, high forest is particularly suitable for the species (Delahaye 2006). The relatively low mobility and specialized foraging behaviour of this species may explain its dependence on large trees (Dondina *et al.* 2015). In fact, large trees are likely to contain a high density of arthropods and offer good microhabitats, which lead to low mobility of the species (Osiejuk 1996). In mature oak forests in northwestern Tunisia, the occurrence of Short-toed Treecreeper increased with forest area at the local scale and decreased with the amount of low scrub at the landscape scale (Touihri *et al.* 2017).

The European Robin is negatively influenced by anthropization and general cover, and positively by the average crown height and the variability of crown surfaces. Indeed, the heterogeneity of the environment is favourable to the species (Ferry & Frochot 1970, Marion & Frochot 2001). In the pine forest of El Kala, the species tends to achieve its maximum abundance in the undergrowth of forests where the cover and the height of the trees are significant (Benyacoub 1993). In the oak groves of Burgundy, the European Robin has a slight preference for the intermediate stages of young high forest (Ferry & Frochot 1970, 1974, 1987). The same observation was made by Marion and Frochot (2001) in the ecological succession of the Douglas fir in Morvan. In the Ardennes oak forest, the European Robin does not appear in classes with a gardened and irregular stage (where all diameter classes are well represented) (Delahaye 2006). In Norwagian spruce plantation forests, it was positively associated with the amount of fresh deadwood (Velova *et al.* 2021).

Logistic regression is a recommended statistical tool for analyzing binary data. It has been used to model the probability of occurrence of many species (Tobalske & Tobalske 1999, Zimmermann & Kienast 1999, Villard & Guénette 2005, Dendup *et al.* 2021). By the logistic regression, we have identified the explanatory variables responsible for the presence/absence of the bird species. The results show that the modelled species react differently to different environmental factors. Indeed, birds respond equally well to the composition and structure of the habitat (Fleishman *et al.* 2003, Jentsch *et al.* 2008, Jayapal *et al.* 2009, Holmes 2011), but in a different way (Imhoff 1997, Laiolo 2002, Walker 2008). Depending on the microclimate, vegetation structure and availability of food resources, each natural habitat provides a different environment for birds (Rotenberry 1985, Deppe & Rotenberry 2008, Arya & Gopi 2021).

The role of birds in the elaboration and development of biodiversity conservation strategies is well established (Arinaitwe *et al.* 2007, Brooks *et al.* 2008, Rodrigues & Tristao da Cunha 2012). The semi-quantitative progressive frequency sampling method proved to be very practical given the topographic conditions of the forest habitats studied (cedar forests). The principle of the modelling approach is to relate the occurrences of a species to certain environmental descriptors associated with the observation plots. We therefore necessarily model the realized niche of the species, starting from the observation that its observed distribution is already the result of possible biotic constraints restricting its fundamental niche (Guisan 2003).

Our results suggest that cedar forest provides potentially suitable habitat for many bird species. The birds with high indicator value as well as the key factors impacting their distribution are identified. The bird species considered in our study showed remarkably different responses to forest characteristics. Forest managers must be able to anticipate the impact of their management actions in order to contribute to the conservation of bird diversity. To do this, we propose to incorporate into cedar forest guidelines the result derived from the models applied to Common Firecrest, Short-toed Treecreeper and European Robin, because of their high indicator values.

Overall, the results of the models are in favor of the diversification of management practices favoring heterogeneous habitats with different levels of tree density, variability in diameter and height classes of trees, and a considerable amount of dead wood.

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Annual captures and low apparent survival rates in two tit species in western Hungary

József Gyurácz[1*], Péter Bánhidi[2], József Góczán[2], Péter Illés[2], Sándor Kalmár[2], Péter Koszorús[2], Zoltán Lukács[2], Péter Molnár[1], Csaba Németh[2] & László Varga[2]

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Abstract Adult and juvenile survival are important factors affecting the population dynamics of small passerines. Understanding variation in the population dynamics and survival rates is critical for ecological studies and nature conservation. The aim of this study was to investigate the annual capture-recapture, apparent survival and capture probabilities of the Blue Tit *Cyanistes caeruleus* and the Great Tit *Parus major* occurring in western Hungary. Data from 8,628 Blue Tits and 7,727 Great Tits came from a constant-effort ringing scheme, using three ringing periods, spanning 24 years (1998 to 2021). The annual captures did not show a significant linear trend from 1998 to 2021 in the study site for both tit species. The temporal variation of annual captures and the annual capture-recapture proportions of different ages and sexes of the tit species were similar. This indicated that the migration strategies of these two partial migrant species did not differ significantly. According to the best standard Cormack-Jolly-Seber model, apparent survival of first-year birds was lower than that for adults. The CJS model selection for the dataset indicated that the time and sex had no effect on apparent survival probabilities for both tit species. Capture probability in the juvenile groups was not significantly higher than that in the adult groups for both species.

Keywords: Cormack-Jolly-Seber model, apparent survival, capture-recapture, tits

Összefoglalás A különböző korú egyedek túlélése a madárpopulációk dinamikájának egyik legfontosabb meghatározó tényezője. A populációdinamika és a túlélési arányok változásainak megértése kiemelt jelentőségű az ökológiai vizsgálatokban és a gyakorlati természetvédelemben is. E tanulmány célja a kék cinege *(Cyanistes caeruleus)* és széncinege *(Parus major)* éves fogás-visszafogásainak, látszólagos túlélésének és fogási valószínűségének vizsgálata egy nyugat-magyarországi élőhelyen 1998 és 2021 között. A tanulmányban az Actio Hungarica és az Állandó Ráfordítású Gyűrűzés programokban 24 év alatt (1998–2021) gyűrűzött 8628 kék cinege és 7727 széncinege adatait használtuk fel. Az éves fogások egyik faj esetében sem mutattak lineáris trendszerű változást a vizsgált területen. A két cinege faj éves fogásainak időbeli változása, valamint a különböző korú és nemű egyedek éves fogás-visszafogási arányai hasonlóak voltak, ami arra utal, hogy e két részlegesen vonuló faj vonulási stratégiája nem különbözik jelentősen. A legjobb standard Cormack-Jolly-Seber-modell szerint az elsőéves madarak látszólagos túlélése alacsonyabb volt, mint a felnőtteké. Az adathalmazra vonatkozó CJS modellválasztás azt mutatta, hogy az időpont és az ivar nincs hatással a látszólagos túlélési valószínűségekre egyik cinegefajnál sem. A fiatal madarak fogási valószínűsége nem volt szignifikánsan magasabb, mint az felnőtt madaraké egyik cinegefajnál sem.

Kulcsszavak: Cormack-Jolly-Seber modell, látszólagos túlélés, fogás-visszafogás, cinegék

[1] *University of Eötvös Lorand, Savaria Campus, Department of Biology, 9700, Szombathely, Károlyi Gáspár tér 4. Hungary*
[2] *Local Group of BirdLife Hungary, 9700 Szombathely, Károlyi Gáspár tér 4. Hungary*
** corresponding author, e-mail: gyuracz.jozsef@sek.elte.hu*

Introduction

Annual counts of birds tell us how their numbers are changing, but the capture-recapture method is needed if we want to understand the mechanism of the changes observed. Various types of useful information can be recorded when birds are caught for ringing, including age and sex. If a bird is subsequently recaptured, repeated measurements can be used to study both apparent survival and capture probability (Silkey *et al.* 1999, Newton 2011). Capture-recapture is a powerful and efficient means of collecting critical data on demographic parameters such as survival (Nur *et al.* 2004).

As part of a long-term monitoring study to understand passerines' population dynamics and migration (Gyurácz & Bánhidi 2008, Lukács *et al.* 2015, Gyurácz *et al.* 2021), here we report annual capture-recapture data, and estimate age- and sex-specific survival for one Palearctic and one European cavity-nesting and partial-migrant species of tits: Blue Tit *Cyanistes caeruleus* and Great Tit *Parus major* breed and migrate sympatrically in western Hungary (Gyurácz *et al.* 2017). The European breeding populations of Great Tit and Blue Tit appear to have increased moderately in recent decades (PECBMS 2021). In Hungary, the Great Tit overwintering population has increased, but changes in populations of overwintering Blue Tit were unclear between 1999 and 2018 (Gyurácz 2021, Szép *et al.* 2021). However, even within a country, population trends of tits can vary significantly across regions, as regional environmental factors affecting bird survival may also differ (Perdeck *et al.* 2000). In order to understand the causes of population dynamics, detailed demographic information is required. In bird populations, survival (Tinbergen & Boerlijst 1990, Adriaensen *et al.* 1998), dispersal and site fidelity (Both *et al.* 2012, Mátrai *et al.* 2012) are essential components for understanding the causes of population growth and decline (Jones *et al.* 2021). Survival, or fitness, may depend on the age, sex, behaviour, habitat and seasonal occurrence of the tits (Dhondt 1979, Horak & Lebreton 2008, Class *et al.* 2014).

Survival studies have usually been conducted during the breeding season (Orell & Ojanen 1979, Horak & Lebreton 2008, Bastianelli *et al.* 2021), though migration is the most risky season of the avian lifecycle (Newton 2007). Inclusion of birds captured in the pre- and post-breeding migration in the survival estimate is also needed to better understand the population limitations during the annual cycle (Salewski *et al.* 2013, Ward *et al.* 2018). In the present study, we investigated whether annual capture-recapture, apparent survival and capture probability differed between the two sympatric species, and whether juveniles and adults, and adult males and females have different apparent survival rates and capture probabilities that are linked to variations in behaviour or the role of the sex. First, we predicted that the two tit species have similar annual capture-recapture, apparent survival and capture probability due to their similar breeding, foraging and migratory strategies. Secondly, we predicted that juveniles would have lower apparent survival rates and capture probability than the adults, based on their lower dominance ranking status. Finally, based on different gender strategies in mating systems, parental care and migration, we predicted sex differences in apparent survival and capture probability in both tit species.

Material and Methods

Study area and data collection

The study was carried out at the Tömörd Bird Ringing Station in western Hungary (47°21'N 16°40'E). The study site has a typical continental climate with cold winters and warm summers. There are four natural habitat types around the station of Tömörd.

1. Scrubland: bushes and herbs make up compact, dense vegetation, which is dissected by small grass patches. Its characteristic plant is the blackthorn *(Prunus spinosa)*.
2. Forest edge: broadleaf trees and bushes form a compact, dense edge, forming an ecotone community with the Turkey oak *(Quercus cerris)* as the characteristic plant. These forests are characterized with regular felling and other forestry activities.
3. Grassland with shrubs: this habitat type represents a transition between the wet habitats of the swamp and the steppe communities that used to cover the agricultural land around the marsh. There are a few bushes in the grassland, with two small patches of the dwarf elder *(Sambucus ebulus)*. The grassland is not managed.
4. Marsh: a small (6 ha), permanent, and isolated wetland. The characteristic plant is the reedmace *(Typha latifolia)*.

Bird ringing for this study took place during the spring migration (an Actio Hungarica programme in March-April), the breeding (a Constant Effort Site programme from April to July) and post-fledging (also an Actio Hungarica programme from August to November) periods between 1998 and 2021. We used 23 (spring), 13 (breeding) and 28 (autumn), individually numbered Ecotone mist-nets (12 metres long and 2.5 metres high, with 5 shelves and a mesh size of 16 mm) for trapping. The nets were placed evenly in the four habitat types. Ringing sessions lasted from sunrise to noon (CES) or dusk, except on rainy and stormy days when the nets were closed; numbers, locations, types, and lengths of mist nets were held constant (Gyurácz *et al.* 2017). All birds were ringed, sexed and aged according to Svensson (1992). First-year birds that hatched in the year of ringing were defined as juveniles, while all older birds were defined as adults. Thus, in the case of juvenile birds, the sex of each individual could not be determined in the breeding season. We excluded all birds for which there was no sex or age data from the analysis.

Apparent survival and capture analysis

Due to the lack of dispersion data, we could not distinguish between mortality and emigration. Consequently, we used the apparent survival, which underestimated the true survival (Schaub & Royle 2013). It was not possible to distinguish between local breeding birds and non-territory holders. Additionally, the number of "potential transients" (Ryu *et al.* 2016) was very low in the breeding and unknown in migration seasons: therefore, the data for all captured adults were pooled. The survival probabilities of passerines at a particular site are frequently analysed by using capture-recapture models: the Cormack-Jolly-Seber (CJS) formula is used most often (Lebreton *et al.* 1992, Naef-Daenzer *et al.* 2001, Williams *et al.* 2002, Greńo *et al.* 2008, Jones *et al.* 2021). In the CJS model, the probability of encounter (p) is explicitly modelled in order to correct possible biases in survival estimates (Jankowiak *et al.* 2016). In this study, analysis of bird survival and capture probabilities were based on capture-recapture, using the standard CJS model (Barker 1999). The analyses were performed using MARK software (White & Burnham 1999). We ran 22 models for both species to test for the effect of age, sex and time (year of capture) in survival estimates and capture probability for both species. The CJS model enables the calculation of apparent survival φ(i) (the probability that an individual survives from year i to year i + 1 and returns to the sampling area) and the probability of encounter p(i) (the probability that an animal in the sampling area at time i is encountered at time i). The most general model was selected based on the result of the goodness-of-fit (GOF) test performed in UCARE (Choquet *et al.* 2009). Passing all of the tests meant a solely time-dependent CJS model. Failure on test 3.SR (and passing the others) indicated an age-dependent model where survival and encounter probability after the first year (marked as a1 in the models) was different than in the consecutive years (a2). Model adjustments for less-than-optimal fit were performed by changing the ĉ value (ĉ was calculated based on the result of the GOF bootstrapping test in MARK). For the CJS model, model selection was performed using the information-theory approach. The Akaike Information Criterion, corrected for small sample size (QAICc), was used to rank the fit of models to the data. The model with the lowest QAICc was considered to be the best fit. If there were multiple most-probable models (QAICc values differed by less than 2 from the best-fit model), model parameters were calculated by model averaging (weighted average using QAICc weights) (White & Burnham 1999). Differences were considered significant if there were no overlaps between the 95% CI values of p and φ in each age and sex group. Variance due to model variation (MV) was calculated by the built-in routines of the MARK program when we performed parameter averaging. The multivariate linear model was used to determine trends in the annual capture-recapture rate, apparent survival, and capture probability of age and sex groups. The distribution of capture-recapture rates according to age and sex groups of the two species was compared with Fisher's exact test (χ^2). The correlation between annual captures of the two species was checked by Spearman rank correlation. The Past computer program was used for the statistical analysis (Hammer *et al.* 2001).

Results

Annual capture and recapture

A total of 16,355 individuals were ringed: 8,628 Blue Tits and 7,727 Great Tits. A total of 178 (2.06%) Blue Tits and 318 (4.11%) Great Tits were recaptured at the study sites *(Table 1)*. There was significant correlation between the annual captures of Blue Tit and Great Tit ($r_s = 0.82$, $P = 0.001$) *(Figure 1)*, whereas the distributions of annual capture ($\chi^2 = 3.15$, $P = 0.250$) and annual recapture rates ($\chi^2 = 1.23$, $P = 0.611$) of both age categories and sexes showed non-significant differences *(Table 1)*. With the exception of the annual recapture rates of juvenile Blue Tits and Great Tits, the annual capture rate, annual recapture rate, apparent survival and capture probability of both age categories and sexes did not show a significant linear trend from 1998 to 2021 for either species *(Tables 2, 3)*.

Effect of time, age and sex on apparent survival and capture probability

Apparent survival and capture probability were not time-dependent in any of the groups, they were constant during the study period for both species. Based on the result of the goodness-of-fit (GOF) test, for both species an age-dependent model was fitted to the

Table 1. Number of captures and recaptures of juvenile and adult birds at at Tömörd, western Hungary. R% = percentage of birds recaptured

1. táblázat A fiatal és felnőtt madarak fogásának és visszafogásának száma a nyugat-magyarországi Tömördön. R% = a visszafogott madarak százalékos aránya

Species		**juvenile**	**adult male**	**adult female**
Blue Tit *(Cyanistes caeruleus)*	Capture	7455 (86%)	451 (5%)	722 (9%)
	Recapture	151 (85%)	18 (10%)	9 (5%)
	R%	2.03	4.91	1.25
Great Tit *(Parus major)*	Capture	6248 (80%)	899 (12%)	580 (8%)
	Recapture	252 (79%)	39 (12%)	27 (9%)
	R%	4.03	4.34	4.65

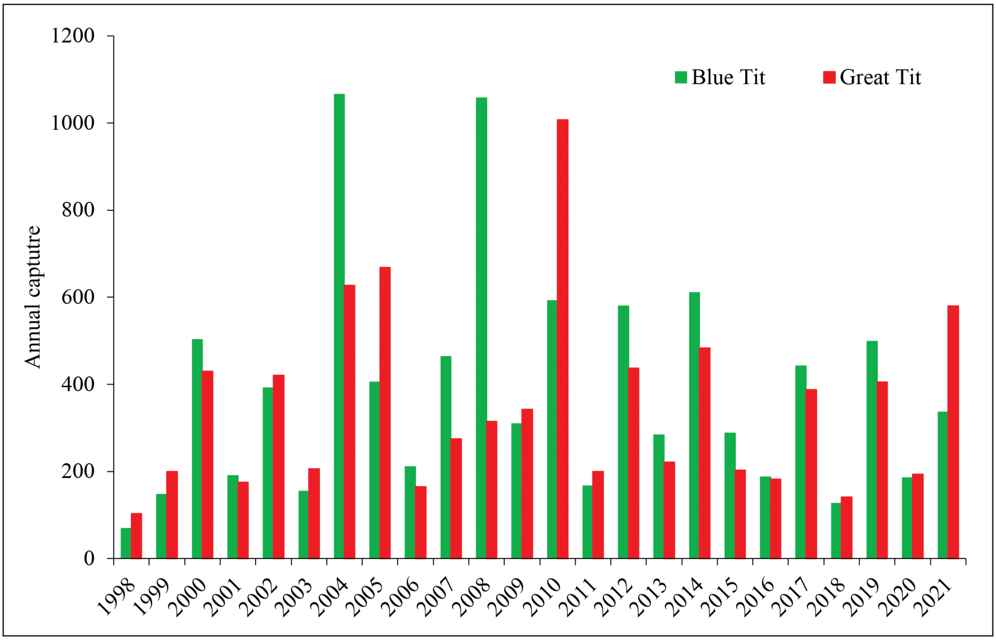

Figure 1. Annual captures of Blue Tit and Great Tit between 1998 and 2021 in Tömörd

1. ábra A kék cinege és a széncinege éves fogásai Tömördön 1998–2021 között

Table 2. Results of the multivariate linear model test of recaptured Blue Tits at Tömörd, western Hungary. Dependent variables: annual capture (C), annual recapture rate (aR%), apparent survival (φ) and capture probability (p). Independent variable: year

2. táblázat A többváltozós lineáris modell vizsgálatának eredményei a nyugat-magyarországi Tömördön visszafogott kék cinegékre vonatkozóan. Függő változók: éves fogási arány (C), éves visszafogási arány (aR%), látszólagos túlélés (φ) és fogási valószínűség (p). Független változó: év

Group	Variable	Slope	Error	Intercept	Error	r	p
Juvenile	C	0.481	7.444	−643.130	14963.000	0.014	0.949
	aR%	0.003	0.001	−5.094	1.609	0.571	**0.004**
	φ	−0.001	0.010	2.148	19.400	−0.022	0.922
	p	0.007	0.013	−14.488	25.237	0.128	0.562
Adult male	C	−0.165	0.478	351.300	960.410	−0.075	0.733
	aR%	0.002	0.002	−3.880	3.944	0.213	0.330
	φ	−0.008	0.009	17.188	17.658	−0.206	0.347
	p	0.008	0.013	−15.023	26.351	0.128	0.561
Adult female	C	0.953	0.715	−1883.300	1437.200	0.279	0.197
	aR%	0.001	0.001	−1.595	1.649	0.208	0.340
	φ	−0.012	0.014	24.611	27.203	−0.191	0.382
	p	0.014	0.011	−28.486	21.797	0.277	0.201

Table 3. Results of the multivariate linear model test of recaptured Great Tits at Tömörd, western Hungary. Dependent variables: annual capture (C), annual recapture rate (aR%), apparent survival (φ) and capture probability (p). Independent variable: year

3. táblázat A többváltozós lineáris modell vizsgálatának eredményei a nyugat-magyarországi Tömördön visszafogott széncinegékre vonatkozóan. Függő változók: éves fogási arány (C), éves visszafogási arány (aR%), látszólagos túlélés (φ) és fogási valószínűség (p). Független változó: év

Group	Variable	Slope	Error	Intercept	Error	r	p
Juvenile	C	1.552	5.557	−2847.100	11165.000	0.061	0.783
	aR%	0.004	0.001	−7.094	2.766	0.491	**0.017**
	φ	−0.011	0.010	23.189	20.025	−0.242	0.266
	p	0.013	0.012	−25.436	23.487	0.233	0.284
Adult male	C	−1.683	0.972	3419.800	1952.500	−0.353	0.098
	aR%	0.004	0.002	−8.712	4.684	0.378	0.075
	φ	−0.002	0.011	3.553	22.271	−0.032	0.883
	p	0.014	0.014	−27.222	27.656	0.214	0.326
Adult female	C	−0.263	0.666	553.270	1338.700	−0.086	0.697
	aR%	0.002	0.002	−3.339	3.321	0.218	0.318
	φ	−0.013	0.009	26.912	17.252	−0.321	0.136
	p	0.024	0.012	−47.968	24.684	0.394	0.062

Table 4. Cormack-Jolly-Seber model selection results examining apparent survival and capture probability of (a) Great Tit and (b) Blue Tit, western Hungary 1998-2021, as a function of age and sex. QAICc = small sample sizes corrected Akaike values; ΔQAICc = difference of models' QAICc values in relation to the best-fit model; QAICc values were calculated using a ĉ (variance inflation factor) of 2.14 for Blue Tit, 2.40 for Great Tit; No. Par. = number of parameters. Only the top models (ΔQAICc<5) are shown

4. táblázat A Cormack-Jolly-Seber-modell szelekciós eredményei, amelyek a) a széncinege és b) a kék cinege látszólagos túlélését és fogási valószínűségét elemezték az életkor és a nem függvényében Nyugat-Magyarországon 1998 és 2021 között. QAICc = kis mintanagysággal korrigált Akaike-értékek; ΔQAICc = a modellek QAICc-értékeinek különbsége a legjobban illeszkedő modellhez képest; a QAICc-értékeket a ĉ (varianciainflációs faktor) 2,14-es értékével számoltuk a kék cinegék esetében, 2,40-es értékével a széncinegék esetében; No. Par. = paraméterek száma. Csak a legjobb modellek (ΔQAICc<5) vannak feltüntetve

Model	QAICc	ΔQAICc	QDeviance	No. Par
Blue Tit *Cyanistes caeruleus*				
φJ(a1)J(a2)AM(.)AF(.) pJ(a1)J(a2)AM(.)AF(.)	847.9	0.00	153.0	8
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AM(.)AF(.)	848.0	0.14	155.2	7
φJ(a1)J(a2)AMAF(.) pJ(a1)JAM(a2)AF(.)	848.0	0.15	157.2	6
φJ(a1)J(a2)AMAF(.) pJ(.)AMAF(.)	849.0	1.14	160.2	5
φJ(a1)JAM(a2)AF(.) pJ(a1)J(a2)AM(.)AF(.)	849.0	1.14	158.2	6
φJ(a1)JAMAF(a2) pJ(a1)J(a2)AMAF(.)	849.2	1.27	160.3	5
φJ(a1)J(a2)AMAF(.) pJ(t)AMAF(.)	850.3	2.37	117.2	27
φJ(a1)J(a2)AM(.)AF(a2) pJ(a1)J(a2)AMAF(.)	850.5	2.58	159.6	6
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AMAF(.)	850.5	2.66	159.7	6
φJ(a1)J(a2)AM(.)AF(.) pJ(a1)J(a2)AMAF(.)	850.9	3.00	158.0	7
Great Tit *Parus major*				
φJ(a1)J(a2)AMAF(.) pJ(.)AMAF(.)	1181.22	0.00	240.8	5
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AMAF(.)	1182.39	1.17	240.0	6
φJ(a1)J(a2)AMAF(.) pJ(a1)JAMAF(a2)	1183.31	2.09	242.9	5
φJ(a1)JAMAF(a2) pJ(a1)J(a2)AMAF(.)	1183.81	2.59	243.4	5
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AM(.)AF(a2)	1184.25	3.03	241.8	6
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AM(.)AF(.)	1184.28	3.06	239.8	7
φJ(a1)J(a2)AM(.)AF(.) pJ(a1)J(a2)AMAF(.)	1184.38	3.16	239.9	7
φJ(a1)J(a2)AMAF(.) pJAMAF(.)	1184.51	3.29	246.1	4
φJ(a1)J(a2)AM(.)AF(a2) pJ(a1)J(a2)AM(.)AF(.)	1185.06	3.84	242.6	6
φJ(a1)J(a2)AMAF(.) pJ(a1)JAM(a2)AF(.)	1185.30	4.08	242.9	6
φJ(a1)JAM(a2)AF(.) pJ(a1)J(a2)AM(.)AF(.)	1185.62	4.40	243.2	6
φJ(a1)J(a2)AM(.)AF(.) pJ(a1)J(a2)AM(.)AF(.)	1186.10	4.88	239.7	8

Table 5. Summary of average values for the different parameters (φ = apparent survival rate, p = capture probability, J = constant parameter for juveniles across study years, AM = constant parameter for adult males across study years, AF = constant parameter for adult females across study years, J(a)1 = juveniles in their first year, J(a)2 = juveniles in their second and following years) for two tit species, according to the best models from the CJS analysis. SE = unconditional standard error, CI = confidence interval, MV = percent of variation attributable to model variation. Significant differences in bold

5. táblázat A különböző paraméterek (φ = látszólagos túlélési ráta, p = fogási valószínűség, J = a fiatal egyedekre vonatkozó konstans paraméter a vizsgálati években, AM = a felnőtt hímekre vonatkozó konstans paraméter a vizsgálati években, AF = a felnőtt tojókra vonatkozó konstans paraméter a vizsgálati években, J(a)1 = a fiatal egyedek az első évben, J(a)2 = a fiatal egyedek a második és az azt követő években) átlagos értékeinek összefoglalása a két cinegefaj esetében, a CJS elemzés legjobb modelljei szerint. SE = feltétel nélküli standard hiba, CI = konfidenciaintervallum, MV = a modellváltozatoknak tulajdonítható eltérés százalékos aránya. A szignifikáns különbségek félkövér betűvel szedve

Parameters	**Weighted averages**	**SE**	**95% CI**		**MV%**
Blue Tit *Cyanistes caeruleus*					
φJa1	0.025	0.007	**0.014**	**0.044**	0.025
φJa2	0.302	0.080	**0.171**	**0.477**	0.302
φAM	0.191	0.115	0.052	0.504	0.191
φAF	0.221	0.142	0.053	0.588	0.221
pJa1	0.612	0.189	0.249	0.882	0.612
pJa2	0.492	0.205	0.162	0.829	0.492
pAM	0.216	0.237	0.017	0.811	0.216
pAF	0.074	0.070	0.011	0.373	0.074
Great Tit *Parus major*					
φJa1	0.051	0.008	**0.036**	**0.070**	5.78
φJa2	0.338	0.065	**0.224**	**0.476**	26.62
φAM	0.176	0.077	0.071	0.376	51.92
φAF	0.177	0.079	0.069	0.383	53.70
pJa1	0.587	0.095	0.398	0.754	9.13
pJa2	0.500	0.124	0.275	0.725	31.58
pAM	0.232	0.129	0.068	0.555	58.83
pAF	0.243	0.139	0.068	0.584	59.68

data the best, which discriminated between first year – J(a1), and consecutive year – J(a2) captures in the case of those birds which were first captured as juveniles *(Table 4)*. In juveniles, apparent survival was significantly lower in the first year than in the second (2-age-group model). The apparent survival rate of first-year birds was very low: only 2.5% of Blue Tits and 5.1% of Great Tits survived and were recaptured in their second year. This means that an unknown proportion of the remaining 94.9–97.5% of birds died and an unknown proportion did not return to the ringing site. The apparent survival probability of second-year birds was significantly higher: 30.2% of Blue Tits and 33.8%

of Great Tits survived the following year. Apparent survivals of males (19.5% of Blue Tits, 17.6% of Great Tits) and females (22.5% of Blue Tits, 17.7% of Great Tits) were similar. Apparent survival in the second year in the juvenile group was not significantly different from apparent survival in the adult male or female groups for both species. Capture probabilities of sexes were similar for both species. Capture probability in the first and second year in the juvenile groups was not significantly higher than capture probability in the adult groups for both species *(Table 5)*.

Discussion

Population dynamics: annual capture-recapture

In Europe, the Blue Tit and Great Tit populations have increased moderately during the recent decades, although there have been regional differences in the changes in both the breeding and overwintering populations, even within Hungary (Gyurácz 2021, Szép *et al.* 2021). Our annual captures also suggest stabile populations in this western Hungarian study site (Tömörd) for both tit species. The results of an earlier study showed that high temperatures in the breeding season was the key determinant of increased annual captures of first-year birds of some short-distance migrants (Gyurácz *et al.* 2016). The increasing and stable populations of forest tit species is most likely due to the expanding forested area of Hungary. In Hungary, the average annual temperature rose by 1.7 °C between 1981 and 2020. The forested area increased by 7.6% in Hungary between 2000 and 2015 (www.ksh.hu), mainly due to acacia and poplar afforestation in areas previously used for farming. Both environmental changes are favourable for tit species. This is also indicated by the significant increasing linear temporal trend in the recapture rates of juvenile Blue Tit and Great Tit between 1998 and 2021 at the study site. However, the annual captures did not show a linear trend between 1998 and 2021, but fluctuated, being very high in a few years (2004 and 2008 for Blue Tit, 2010 for Great Tit). In these invasion years, the most birds were captured primarily in the second half of the autumn migration (Gyurácz *et al.* 2017). The temporal variation of annual captures and the annual capture-recapture proportions of ages and sexes of the closely-related tit species were similar. This indicated that the migration strategies of these two partial migrants did not differ significantly. The partial migration for widely-distributed species like the Blue Tit and Great Tit, involving a mixture of resident and migratory birds in most populations, is associated with general selection for a short migration distance (Nilsson *et al.* 2008). The slightly higher proportions of first-year and adult female Blue Tits indicated that irruptive migration is a little more typical in this species than in the Great Tit. The body-size and the dominance hypothesis can explain the difference in migratory behaviour between species, ages and sexes (Smith & Nilsson 1987, Nyquist 2007). The intensive Blue Tit (2004, 2008) and Great Tit (2010) migration in the study site could be connected with the reduced beech *(Fagus sylvatica)* crop and the large tit populations breeding in the Alps and in the Carpathians as well as further north, e.g. northwest Russia, Poland

and the Baltic region (Heldbjerg & Karlsson 1997). According to our results and the winter-food limitation hypothesis (Perdeck *et al.* 2000), contrary to the conclusion of Nowakowski and Vähätalo (2003), the Great Tits, similarly to the Blue Tits, behave like irruptive partial migrants, with the migration in central Europe also being affected by the population density and beech crop fluctuations.

Apparent survival, capture probabilities across ages and sexes

Apparent survival is one of the most important factors affecting the annual variations in the populations of small passerine species (Peach & Baillie 2004). The average apparent survival probabilities of Blue Tit (ranging 0.025 to 0.302) and Great Tit (ranging 0.051 to 0.338) age and sex groups in western Hungary was lower than in most other European studies, which range from 0.26 to 0.56 (Orell & Ojanen 1979, Horak & Lebreton 2008). Our lower survival probabilities may have been due to the high proportion of "potential transients" during migration seasons. The CJS model selection for the dataset indicated that the time and sex had no effect, but age had an important effect on apparent survival probabilities for both tit species. The first-year birds had a lower apparent survival than individuals in their second year and older male and female adult tits. These age-related differences in survival are found in most bird species, because first-year birds have less experience or hold poorer-quality territories (Martin 1995, Siriwardena *et al.* 1998, Kiss *et al.* 2020). Some studies have given general support to the early-breeding hypothesis for the survival of first-year individuals (Ringsby *et al.* 1998, Yackel *et al.* 2006). However, adult males (AM) and females (AF) also had a lower apparent survival than first-year breeders in their second year J(a2), but J(a2) and AM, AF confidence intervals largely overlapped. In other studies, survival probabilities have also been shown to rapidly decrease with age after two years in the Blue Tit and Great Tit (Bastianelli *et al.* 2021, Bouwhuis *et al.* 2012). Population density had a significant negative impact on adult survival in the less productive habitats, suggesting higher breeding competition (Tremblay *et al.* 2005, Bastianelli *et al.* 2021). Maness and Anderson (2013) reviewed the literature on the predictors of juvenile survival in birds. Factors other than body weight, size and sex can influence juvenile survival, including hatching date, hatching order, brood size and nestling growth rate. Body size and weight predict juvenile survival in many bird species, so sex-biased survival might be expected in species with sexual size dimorphism. However, according to our results, there were no significant differences in survival probability between sexes in both species, although the capture rate of the Blue Tit was female-biased, and the Great Tit was male-biased at the study site. According to our earlier study, the apparent survival is also not sex-related in other passerines in Hungary (Kiss *et al.* 2020). Higher survival of males than females has been reported in most of the earlier studies of Great Tits (Orell & Ojanen 1979), as well as in many other bird species (Breitwisch 1989, Payevsky 1993). However, Clobert *et al.* (1988) found no clear differences between survival of adult male and female Great Tits in Wytham, Oxford. Dhondt *et al.* (1990) found no sex differences in survival in the Blue Tit in Belgium. Female Blue Tits survived slightly better in Corsica, while males survived better in Provence (Blondel *et al.* 1992). Females survived better than males, and the survival probabilities varied over time in Estonia (Horak & Lebreton 2008). These contradictory results suggest that regional environmental conditions (e.g. weather conditions, food supply) could drive survival fluctuations across populations.

Unlike other results (Burton & DeSante 2004, Nur *et al.* 2004), the CJS models in the present study did not reveal an important effect of age and sex on capture probabilities for either tit species. In Hungary, male Eurasian Blackcap *(Sylvia atricapilla)* and Red-backed Shrike *(Lanius collurio)* had significantly higher capture probabilities than females during the breeding season, perhaps due to the sex differences in territorial behaviour and breeding strategy (Amrhein *et al.* 2012, Kiss *et al.* 2020). Similar capture probabilities for ages and sexes of the two tit species in western Hungary may be explained because most of the birds were captured during the autumn migration, when there is less territorial behaviour than in the breeding season, but this needs to be examined directly.

Conclusion

We produce the first robust annual capture-recapture study and estimates of apparent survival and capture probability for Blue Tit and Great Tit in Hungary. We demonstrate annual captures with high year-to-year fluctuation, and low apparent survival probabilities in both tit species. Our results demonstrate that apparent survivals of juveniles and adults are unlikely to drive population trends in these species. Future work should focus on other lifestyle characteristics, such as overwintering survival, stopover strategies and habitat selection, as well as parallel studies of the apparent survival of this species at other sites in Hungary; investigating the annual capture-recapture and apparent survival in other closely-related tit species would also be important for understanding the causes of population dynamics of tits.

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Space use of wintering Eurasian Tree Sparrows *(Passer montanus)* in a semi-urban area: a radiotelemetry-based case study

Attila Fülöp[1,2,3,*], Dóra Lukács[1] & Zoltán Barta[1]

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Abstract Space use, which includes the home range and habitat utilisation pattern of individuals for different activities (e.g. foraging, roosting), is one of the fundamental aspects of a species ecology. Hence, knowledge on the different aspects of space use in general is essential to understand the relationship between species and their habitat. Here, we investigated the home range size (using the minimum convex polygon method; MCP) and roosting site selection, using radiotelemetry, in a sedentary passerine species, the Eurasian Tree Sparrows *(Passer montanus)*. The study was carried out during the non-breeding period (i.e. wintering), in a semi-urban habitat where supplemental feeding was also available. We found that individuals had highly variable home ranges, both in shape and size (mean ± SD of 95% MCP: 6.89 ± 5.73 ha), the location of which was influenced by the presence of bird feeders. Roosting sites of the tracked individuals were largely consistent at an individual level, that is, all birds used the same locations for roosting during the whole tracking period, and the roosting sites of all individuals were located on buildings, except for a few rare occasions. Our results suggest that urbanised habitats can provide multiple benefits for the individuals during the winter in the form of easily accessible resources (e.g. food, roosting place), and individuals readily exploit these resources by adjusting their space use according to their availability.

Keywords: home range, roosting, radiotelemetry, *Passer montanus*

Összefoglalás A fajok ökológiájának egyik legalapvetőbb aspektusa a térhasználat, amely megadja az egyedek mozgásterületét és élőhelyhasználatát különböző tevékenységek (pl. táplálkozás, éjszakázás) közben. Emiatt az egyedek térhasználatának ismerete kulcsfontosságú a fajok és élőhelyek közötti kapcsolatok megértéséhez. Vizsgálatunkban mezei verebek *(Passer montanus)* mozgásterületét (minimum konvex poligon módszerrel; MCP), valamint éjszakázó hely választását vizsgáltuk rádiótelemetriás módszerrel a telelési időszakban, egy urbánushoz közeli élőhelyen. Az egyedek által használt terület mérete és alakja nagymértékű változatosságot mutatott (95%-os MCP, átlag ± szórás: 6.89 ± 5.73 ha), és az egyedi területhasználatot nagy mértékben befolyásolták a vizsgálati területre kihelyezett madáretetők. A nyomon követett egyedek éjszakázó helyei épületeken helyezkedtek el, és használatuk egyedi szinten konzisztens volt, azaz a teljes vizsgálati időszak alatt az összes egyed túlnyomó részt ugyanazt a saját éjszakázó helyet használta. Eredményeink azt mutatják, hogy az urbánushoz közeli élőhelyek a téli időszakban többféle előnnyel is szolgálhatnak az egyedek számára könnyen hasznosítható erőforrások (pl. élelem, éjszakázó hely) formájában, és hogy az egyedek ezeket az erőforrásokat sikeresen ki is aknázzák, módosítva „természetes" területhasználatukat.

Kulcsszavak: mozgásterület, éjszakázás, rádiótelemetria, *Passer montanus*

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[1] *ELKH-DE Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, 4032 Debrecen, Egyetem tér 1. Hungary*
[2] *Evolutionary Ecology Group, Hungarian Department of Biology and Ecology, Babeş-Bolyai University, str. Clinicilor 5–7, RO-400006 Cluj-Napoca, Romania*
[3] *Centre for Systems Biology, Biodiversity and Bioresources (3B), Babeş-Bolyai University, str. Clinicilor 5–7, RO-400006 Cluj-Napoca, Romania*
** corresponding author, e-mail: fulop.attila@science.unideb.hu*

Introduction

Space use is one of the most fundamental aspects of a species ecology and includes the home range and habitat utilisation pattern of individuals. The home range of individuals can be defined as the total area they use for different activities that include, among others, reproduction, foraging, or roosting. Since individuals use parts of their home range for different purposes and with various intensities, mostly avoiding the edges of their home range, habitat utilisation refers to the frequency of usage of the different parts of the home range (Powell & Mitchell 2012). Knowledge on these different aspects of space use in general is therefore essential to understand species-habitat relationships both on individual-, and at species-level.

With the development of modern tracking technologies (e.g. global positioning system; GPS), the amount of information on the space use of numerous bird species has increased exponentially (e.g. Pérez-García *et al*. 2013, Mitchell *et al.* 2016, Gustin *et al.* 2017, Moskát *et al.* 2019, Heggøy *et al.* 2021, Zvidzai *et al.* 2022). Even though modern technology has become increasingly available, some limitations can still constrain their wide-range usage. For instance, for a long period the relatively large weight of the tags (> 5 g) made them unsuitable for small-sized birds (i.e. species with a body mass < 100 g; Barron *et al.* 2010, Bodey *et al.* 2018). Apparently, this issue was recently solved by a new archival GPS-based miniaturised tracking device, weighting only 1 g, and which was successfully deployed even on species with a mass of < 20 g (Hallworth & Marra 2015, see also e.g. Musseau *et al.* 2021). However, as data cannot be downloaded remotely from these miniaturised archival GPS tags, individuals have to be recaptured. Thus, these devices are optimal for species with high site-fidelity, and which can be easily trapped multiple times, but not for others. Also, the financial costs of GPS-based tracking devices are still relatively high. Hence, other tracking methods, as radiotelemetry, still represent a viable and affordable alternative to track the (local) movements of e.g. small passerines (see below).

Numerous studies investigated space use of small-sized birds using radiotelemetry, also attempting to describe the factors influencing individual-level variation in space use. A large proportion of studies focused on the space use of individuals during the reproductive season, when individuals are usually territorial and their movements are restricted around the nest site (e.g. Anich *et al.* 2009, Jirinec *et al.* 2016, Liu *et al.* 2020). During the winter, however, individuals can leave their breeding site and move around more freely to exploit resources from larger areas. Hence, the space use of individuals can be strongly influenced by seasonal effects, and can also be influenced by the type of habitat they use independently of season. For example, individuals of the same species inhabiting natural- or anthropogenic (i.e. urbanised) habitats can have different home range characteristics (reviewed by O'Donnell & del Barco-Trillo 2020). This is not surprising, as urbanisation is a global phenomenon with a strong impact on natural processes (Seress & Liker 2015). Overall, when studying space use of different individuals and/or species it is important to consider multiple factors which can shape the species-habitat relationship.

In this study, we investigated space use using radiotelemetry in Eurasian Tree Sparrows *(Passer montanus)*. Tree Sparrows are small sized passerines (17–25 g), feeding predominantly on seeds and grain during winter, but also on invertebrates during the breeding season (Summers-Smith 1995). At our study area, Tree Sparrows are year-round residents and breed in natural (e.g. trees) or artificial cavities (e.g. nest boxes, buildings). During the winter, Tree Sparrows form large, compact flocks (Mónus & Barta 2010), forage in the open parts of the study area, and they also readily use bird feeders (e.g. Barta *et al.* 2004, Mónus & Barta 2008, 2011, 2016, Mónus *et al.* 2017, Fülöp *et al.* 2019, 2022). Based on our field observations, Tree Sparrows are present in most parts of our study area (see Tree Sparrow Database at http://openbiomaps.org/projects/pasmon/; Bán et al. 2022). However, individual space use has not been investigated yet. Here, we studied home range size and roosting site selection of Tree Sparrows during winter, in a semi-urban study area where supplemental feeding is regularly available. A previous work studying space use in Japanese population of Tree Sparrows found that home range size can vary in the different seasons, being the largest (up to 11.5 ha) during the winter (Sano 1973). This is likely because foraging is one of the main activities of individuals during winter, hence, the spatial distribution of available food sources is expected to strongly influence the space use of individuals in this season (Sano 1973). Similarly, in our study, we expect space use of individuals to be variable on the individual-level, but depending on the habitat characteristics, we also anticipate space use to be influenced to a certain degree by the location of the bird feeders. Regarding the roosting behaviour of Tree Sparrows our knowledge is limited (Summers-Smith 1995). As documented previously, in the summer, Tree Sparrows roost communally in dense vegetation (e.g. trees, bushes, or reed beds), yet during the winter, individuals use mostly holes for roosting and roost in small numbers, usually alone or in pairs (Summers-Smith 1995). In our population, due to the heterogeneity of the habitat *(Figure 1)*, Tree Sparrows have multiple options available to choose from as their roosting site: natural cavities in trees, nest boxes, or building cavities. Whether individuals have a preference for one or another type of cavity, or they use all of these is unknown.

Materials and Methods

General setup

The study was carried out in the Botanical Garden (hereafter 'Garden') and on the Central Campus (hereafter 'Campus') of the University of Debrecen (N 47.55366, E 21.62164; Debrecen, Hungary) between January and March 2017. The study site is a relatively open area with scattered trees and shrubs, also containing some buildings of various sizes forming a heterogeneous semi-urban landscape mosaic (Barta *et al.* 2004, Fülöp *et al.* 2019) *(Figure 1)*.

During the study period we provided *ad libitum* food for the birds, consisting of sunflower seeds, on a daily basis, on five different bird feeders scattered over the study area. The feeders were wooden platforms made of oriented strand board (i.e. "feeding platform"; 120 × 120 cm) that were placed on the ground in the following setup: three in the Garden (*Figure 1*, feeders BG1, BG2 and BG4) and two in the Campus (*Figure 1*, feeders C1 and C2). All feeders were located near at least one larger bush and/or tree which provided shelter for the birds, as Tree Sparrows have a preference for similar feeding habitats (Barta *et al.* 2004).

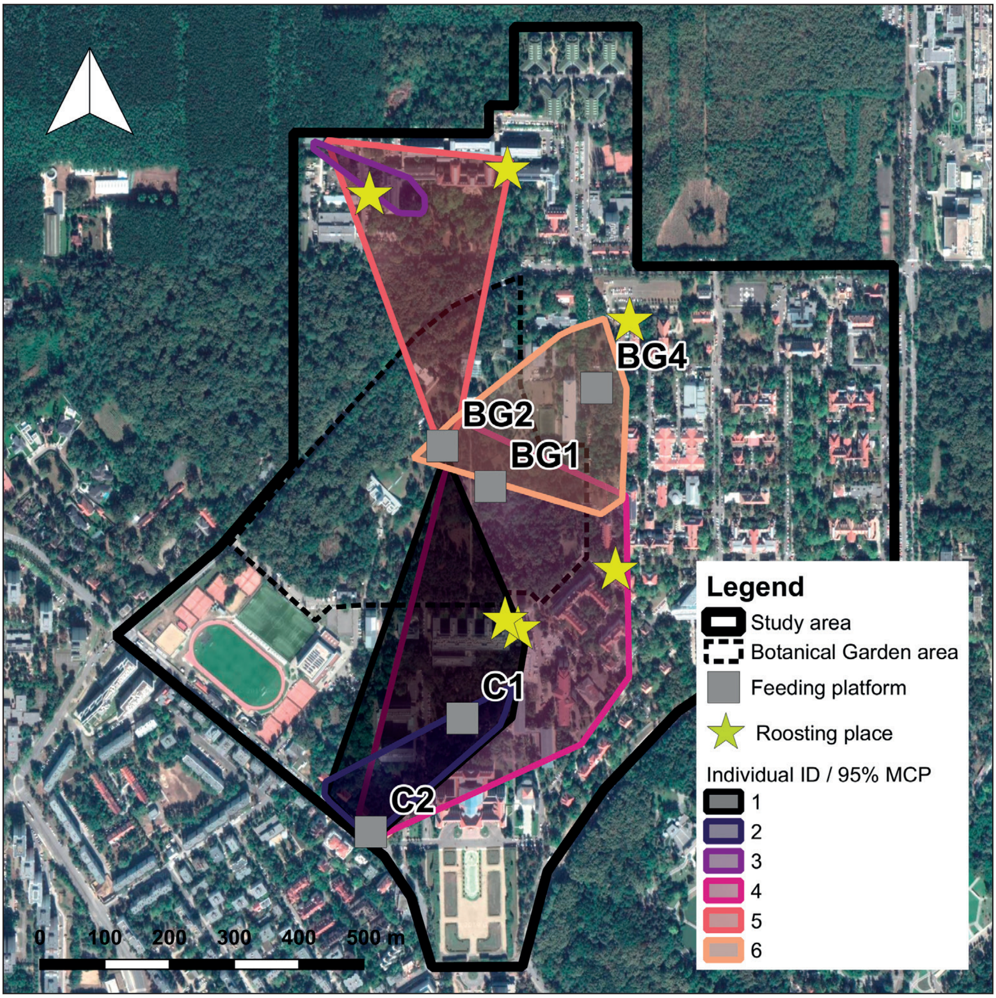

Figure 1. Schematic illustration of the study area covering the Central Campus of the University of Debrecen (black solid line) and the Botanical Garden (black dashed line); and the home ranges and roosting sites of the six radio-tagged Eurasian Tree Sparrows *(Passer montanus)*. The home ranges presented in the figure are based on the 95% minimum convex polygons (MCPs; indicated by the coloured polygons on the figure). The feeders used in the study are also marked (Central Campus: C; Botanical Garden: BG). The arrow on the top map is the direction of North. Background satellite image source: Google Maps

1. ábra A vizsgálati területet bemutató ábra, amely magába foglalja a Debreceni Egyetem Központi kampuszát (fekete folytonos vonal) és Botanikus kertjét (fekete szaggatott vonal), valamint hat rádiójeladóval nyomon követett mezei veréb *(Passer montanus)* mozgásterületét és éjszakázó helyét (sárga csillagok). A mozgásterületek a 95%-os miminum konvex poligon (MCP) alapján lettek megrajzolva. A vizsgálatban használt etetők (C: Központi kampusz, BG: Botanikus kert) elhelyezkedése is látható az ábrán. A terület elhelyezkedését az északi irányhoz képest a sarokban látható nyíl mutatja. Műholdas felvétel forrása: Google Maps

Table 1. Summary data about the radiotelemetry observations in Eurasian Tree Sparrows *(Passer montanus)*. Sex of individuals, trapping site, tracking period, available data quantity and individual home range sizes, expressed as the area of the minimum convex polygons (MCPs) are given

1. táblázat Összefoglaló táblázat a mezei verebek *(Passer montanus)* rádiótelemetrás nyomkövetéséről. A táblázat tartalmazza az egyedek ivara és befogási helye mellett a nyomon követés időszakát, a rögzített helyadatok számát, valamint az egyedek mozgásterületének méretét, a minimum konvex poligon (MCP) módszer alapján becsülve

Bird ID	**Sex**	**Trapping site (feeder)**	**Period tracked**	**No. days tracked**	**No. fixes (total)**	**No. fixes (daytime)**	**No. fixes (roost data)**	**Home range size (100% MCP in ha)**	**Home range size (95% MCP in ha)**	**Home range size (50% MCP in ha)**
1	male	C1	2017/01/25 – 2017/02/19	25	75	52	23	9.496	8.969	2.493
2	male	C1	2017/01/25 – 2017/02/17	23	71	49	22	5.491	2.342	0.146
3	female	BG2	2017/01/30 – 2017/02/21	22	77	55	22	5.150	0.664	0.033
4	female	C1	2017/01/31 – 2017/02/22	22	73	52	21	17.912	16.827	4.363
5	female	BG2	2017/02/03 – 2017/03/02	27	83	63	20	12.211	6.906	0.515
6	male	BG2	2017/02/03 – 2017/02/18	15	55	40	15	6.703	5.658	0.707
Study area total surface										95.20

Bird trapping, measurements and tagging

We captured six Tree Sparrows at two different feeders (details in *Table 1*), with mist nets (Ecotone, Poland), following the protocol described in details by Fülöp *et al.* (2019, 2022). Briefly, at capture, we marked the individuals with a uniquely numbered aluminium ring, issued by the Hungarian Bird Ringing Centre, and with a unique combination of three plastic colour rings to assure individual identification from a distance (see also Fülöp *et al.* 2019, 2022). We measured body mass (± 0.1 g with a Pesola spring balance), tarsus length (± 0.01 mm with a digital calliper), and wing length (± 0.5 mm with a ruler) of individuals, and we photographed their black bib patch (see e.g. Fülöp *et al.* 2021). We also took a blood sample (~50–150 µL) from the brachial vein of each individual to perform molecular sexing (see details in Fülöp *et al.* 2021). The captured birds were subjected to a personality test as well for parallel studies (Fülöp *et al.* 2019, 2021, 2022). Finally, we fitted a radio tag (model PIP3, Biotrack Ltd., UK; weight 0.43 g) on the back of each individual using flexible super glue (Loctite 4860). The weight of the tag represented approx. 2% of the body weight of the tagged individuals (21.58 ± 0.81 g, mean ± SD, N = 6), therefore, we expected negligible (if any) negative effects associated with wearing the tags (Kenward 2000, Barron *et al.* 2010, Bodey *et al.* 2018). After completing all the procedures described above, we released the birds at the site of their capture.

Tree Sparrows were ringed under a licence from the Hungarian Bird Ringing Centre (licence nr. 390 accredited to ZB) and permission for the study was granted by the Hajdú-Bihar County Governmental Office, District Office of Debrecen – Department of Environmental and Nature Protection (permit nr. HB/10-KTF/00487-1/2016).

Radiotelemetry

In order to determine the space use of the radio-tagged individuals, during February and March 2017, we performed regular search sessions (1–3 sessions/day, started at times unspecified beforehand). Search sessions on the same day were separated by a break of at least one hour. During a search session an observer (AF or DL) actively searched for the signal of every tagged individual using a Sika radio tracking receiver and a directional three-element Flex Yagi antenna (both from Biotrack Ltd., UK). When a signal was picked up, the observer determined the position of the tagged individual by following the direction and strength of the radio signals until he/she could accurately locate the tagged bird. After recording, relatively to local landmarks, the position of each tagged individual in the field, we converted these positions into GPS coordinates (WGS1984 projection) by marking them on the Google Maps satellite map (https://maps.google.com/) (see e.g. Farine & Milburn 2013). The spatial heterogeneity of our study area allowed us to record the position of a tagged bird with high accuracy (within an estimated radius of max. 30 m around the recorded position). The tagged individuals were also observed frequently foraging on the feeders, where we could identify them using their unique colour ring combinations, and their exact locations could have been noted. Finally, we also recorded the roosting sites of all birds on multiple days after sunset using a similar methodology as during daytime.

Statistical analyses

All statistical analyses were performed in the R statistical environment version 4.2.1 (R Core Team 2022). To characterise space use of individuals we calculated the home range size of the radio-tagged individuals using the minimum convex polygons (MCPs) method (Mohr 1947). MCP estimates the maximum area an individual uses (i.e. geographical boundaries of its home range). It is a widely used method to estimate home range size and to make comparisons between studies (Seaman *et al.* 1999). We calculated 100% MCPs (i.e. polygons containing all observations, including roosting sites) of individuals using all the radio tracking position data. Besides, since MCP estimates can be influenced by outliers, we also calculated the 95% MCP, and the 50% MCP in order to give a more conservative estimate of the individual's home ranges and the core areas, respectively. Home range analysis was carried out using the R package "adehabitatHR" (Calenge 2006). The map was created using QGIS version 3.18 (QGIS Development Team 2021).

Results

Home range areas of the radio tagged birds varied greatly both in size and in shape *(Table 1, Figure 1)*. Tree Sparrows had a mean home range area of 6.89 ± 5.73 ha (mean ± SD of 95% MCP), with a core area of 1.38 ± 1.71 ha (mean ± SD of 50% MCP). Home range area (95% MCP) was not correlated either with the number of fixes recorded per individual (Spearman's rank correlation test, $r = 0.06$, $N = 6$, $P = 0.913$) or with the number of tracking days (Spearman's rank correlation test, $r = 0.23$, $N = 6$, $P = 0.658$). In general, home ranges of birds from the Campus (bird IDs: 1, 2 and 4) were spatially separated from the home ranges of birds from the Garden (bird IDs: 3, 5 and 6). However, areas of two birds from the Campus overlapped by some extent with the areas of three birds from the Garden on those feeders that were visited by birds from both areas. One individual from the Campus (ID 2) was fully separated spatially from one bird from the Garden (ID 3).

Roosting sites of the tracked individuals were largely consistent at an individual level: all birds used the same locations for roosting during the whole tracking period. Interestingly, even if some of the tracked individuals shared the same feeders during the day, roosting sites were located in different locations *(Figure 1)*. Although the tracked individuals could not be directly observed in the dark, due to the configuration of the habitat, we could determine with a good confidence the locations of the roosting sites. All of the birds were regularly using buildings for roosting, except for a few cases when some of the birds roosted on trees.

Discussion

In this study we explored space use of wintering European Tree Sparrows in a semi-urban area. We found that Tree Sparrows had home ranges of varying sizes and shapes, and the spatial distribution of home ranges was largely influenced by the location of the feeders.

The tracked individuals spent most of their time in the vicinity of the feeders. The roosting sites of the tracked individuals were stable over the period of the tracking and were located predominantly on buildings situated in different parts of the study area.

A previous study investigating home range size of Tree Sparrows found that individuals' home ranges are the largest during winter, when individuals are not constrained to use only the areas around their nest (Sano 1973). The size of the home ranges from our study are comparable in absolute values to previous findings. For instance, Sano (1973) reported 11.5 ha home range for Tree Sparrows in Japan. Also, we have found that individuals apparently limit their daily movements opportunistically around the feeders and hence, tend to spend most of their time around the food source. Consequently, individuals are presumably moving much less around, as compared to when supplemental food is not provided. A similar adaptation was observed in Japanese Tree Sparrows, where individuals stayed mostly in the vicinity of an abundant food source (i.e. rice field) during winter (Sano 1973). Therefore, although our home range estimates are similar to Sano (1973), we are aware that they are influenced to some extent by the presence of bird feeders. This phenomenon is interesting and should be taken into account when the effect of human practices (e.g. bird feeding) on wildlife is investigated. Bird feeding during the winter is a standard procedure aiming to increase the survival of individuals when environmental conditions are harsh. However, our results indicate that artificial bird feeding can influence the behaviour of individuals, shaping for instance their habitat usage.

We found that individuals captured in the Campus and in the Garden, respectively, had home ranges with only a moderate overlap, and the home range of one individual from the Campus had no overlap at all with the home range of individuals from the Garden. This spatial segregation of individuals hints for the existence of multiple social communities, which are separated in space, and perhaps they also form separated social units.

Interestingly, we have found that individuals had different roosting places despite that they shared the same feeders during the day and being members of the same foraging group. As documented in other populations, during the winter Tree Sparrows roost most frequently either alone or pairs (Summers-Smith 1995). On rare occasions, when the temperature drops below freezing, small groups of up to 5 individuals can roost together (Summers-Smith 1995). Our observations on the roosting habits of Tree Sparrows from our population suggests that individuals exhibit a similar behaviour as described by earlier studies, more specifically, that larger foraging groups split at the end of the day and individuals roost alone, or in smaller groups.

All of the tracked individuals were using buildings for roosting. Buildings can have parts and/or cavities that are inaccessible for predators hunting during the night (e.g. cats, owls). Also, some building cavities (e.g. holes in the insulation of the buildings) can assure a warmer microclimate then e.g. tree cavities or artificial nest boxes. Therefore, roosting in/on buildings can confer a higher safety against predators and individuals can also gain thermal benefits from it.

To conclude, our study widens our knowledge about the space use of Tree Sparrows during the winter. We show that individuals have highly variable home ranges, which are partly influenced by the presence of bird feeders. Besides, we show that individuals have a strong preference for certain places where they roost and use the roosting sites consistently during the winter. Although the Tree Sparrow is a species inhabiting primarily rural areas (e.g. farmlands) in Europe, our results indicate that this species can successfully adapt to urbanised areas as well, exploiting the resources and niches provided by these human-modified habitats.

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Urbanisation of the Common Wood Pigeon *(Columba palumbus)* in Southeast Hungary and its impact on the population of Eurasian Collared Dove *(Streptopelia decaocto)*

András István Csathó[1] & László Bozó[2]*

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Abstract The Common Wood Pigeon (*Columba palumbus* Linnaeus, 1758) has very large populations in the European cities. However, the urbanisation of the species in the Maros–Körös köze region (Maros–Körös Interfluve) is recent and is happening before our eyes. In our study, we summarized our observations on the urbanised populations of the species in the region. Populations of the species in populated areas are currently spreading rapidly in the Maros–Körös köze region. In the past, it was a breeding species in the landscape of suburban areas far from populated areas. In recent years, it has appeared in towns and villages. It did not gradually arrive from the outer area of the settlements towards the interior of populated areas, but it was precisely in the park areas of the centres of settlements that the first pairs in these areas appeared and spread outwards. During the study, we also surveyed the nesting populations of the Eurasian Collared Dove (*Streptopelia decaocto* [Frivaldszky, 1838]) in the sampling areas, using the same methodology, so that we could also examine the proportion of both urbanised species. The population of that species was decreasing during the study period. The pairs of Common Wood Pigeons were more common in the central, more parked parts of the settlements, while the Eurasian Collared Dove was mainly found in peripheral areas. The increase in the population of the Common Wood Pigeons will cause major problems for agriculture, for which there is no solution at present.

Keywords: Columbiformes, Columbidae, tawns, settlements, urban fauna, Tiszántúl region, Great Hungarian Plain

Összefoglalás Az örvös galamb (*Columba palumbus* Linnaeus, 1758) igen jelentős városiasodott populációkkal rendelkezik Európában. A faj urbanizálódása a Maros–Körös közén viszont újkeletű, napjainkban, a szemünk előtt zajlik. Tanulmányunkban az örvös galamb a régióban kialakult lakott területen fészkelő populációira vonatkozó megfigyeléseinket foglaltuk össze. A faj lakott területeken élő állományai jelenleg gyors terjedésben vannak a Maros–Körös közén. A tájban korábban a lakott területektől távoli külterületi részek fészkelő faja volt. Az utóbbi években jelent meg a belterületeken, a városokban, falvakban. Nem a külterületek felől fokozatosan érkezett a lakott területek belseje felé, hanem pont a települések központjainak parkos részein jelentek meg az első urbanizálódott párok, és onnan terjednek kifelé. A vizsgálat során a mintavételi területeken a balkáni gerle (*Streptopelia decaocto* [Frivaldszky, 1838]) fészkelő-állományát is felmértük, azonos módszerrel, így a két faj arányát is vizsgálni tudtuk. Eredményeink szerint ennek a fajnak csökkent az állománya a vizsgálati periódus során. Az örvösgalamb-párok inkább a települések központi, parkosított részein voltak jellemzőek, míg a balkáni gerle elsősorban a perifériás részeken volt gyakori. Úgy tűnik, hogy a nagyobb termetű örvös galamb a belterületeken egyre inkább ki fogja szorítani a most még általánosan gyakori balkáni gerlét.

Kulcsszavak: galambalakúak, galambfélék, városok, falvak, városi fauna, Tiszántúl, Alföld

[1] *Independent researcher, H-5830 Battonya, Somogyi Béla utca 42/A, Hungary*
[2] *Eötvös Loránd University, Department of Systematic Zoology and Ecology, Pázmány Péter sétány 1/C., H-1117 Budapest, Hungary*
* *corresponding author, e-mail: bozolaszlo91@gmail.com*

Introduction

The urbanisation of birds and their adaptation to inhabited areas has probably proceeded in parallel with industrialisation (Marzluff *et al.* 2001, Evans *et al.* 2010) and is still continuing today. Nesting in cities and villages has several advantages over natural habitats. Cities have a more stable microclimate, food sources are more constant and predictable, adult birds are often under less predation pressure, and there is no possibility to control otherwise huntable species within the city (Bedő & Heltai 2003, Vuorisalo *et al.* 2003, Kövér *et al.* 2015). These advantages have led to the emergence and spread of a number of species of human-avoidant birds that used to nest in open spaces. However, the process has not occurred simultaneously for different bird species.

While, for example, the Common Blackbird *(Turdus merula)* had breeding populations in the cities already at the beginning of the 20th century (Haraszthy 2019a), this was the case for the Hooded Crow *(Corvus cornix)* only in the 1970s (Tapfer 1974, Fintha 1994), while for the Eurasian Magpie *(Pica pica)* it was only from the 1990s onwards (Haraszthy 2019c). For some species, the process started decades or even centuries ago (e.g. Western Jackdaw *Coloeus monedula*, Benmazouz *et al.* 2021), but has only intensified in recent years. These species include, among others, the Common Wood Pigeon *(Columba palumbus)*.

The Common Wood Pigeon is a polytypic species with four subspecies living today. Its range is concentrated in Europe, where it is a widespread breeder in all but the northernmost and highest areas. It also breeds in western Siberia and the Middle East, while the other three subspecies nest in the Azores, Iran and its region, and Central Asia (Baptista *et al.* 2020). Its European range has not changed significantly over the last two decades. Its global population is estimated at 26–36, while its European population is estimated at 20.45–29 million pairs, and is a least concern species. The population still increasing in most parts of Europe (Birdlife International 2022). It occurs in both natural and human-modified habitats, except in treeless landscapes, but prefers landscapes mosaic with patches of woodland and areas with tree-lines.

In Hungary, it used to be a forest-dwelling bird, but now nests in the busiest urban areas. It also colonises closed forests, but prefers forest edges (Haraszthy 2019a). Between 2014 and 2018, its nesting population was estimated at 151–166,000 pairs, almost four times the number estimated in the early 1990s (Magyar *et al.* 1998) and about one and a half to two times the number estimated between 1999 and 2002 (Hadarics & Zalai 2008). According to the most recent data, populations are three to five times denser in built-up, anthropogenic habitats than in the Kiskunság and Nyírség regions, where, incidentally, the most significant suburban populations are found at the national level (Czirák 2021a).

In Europe, it is a partial migrant. Populations in Western and Northern Europe winter in NW France, Southern Iberian Peninsula and North Africa, and nesting populations in Central and Northeastern Europe also migrate west to northwest. The Mediterranean populations are resident (Bea *et al.* 2003, Sruoga *et al.* 2005, Faragó 2009, Baptista *et al.* 2020). The Hungarian population is also migrating in a southwestern direction (Faragó 2000, Bankovics 2001). It is typically present in the Carpathian Basin between early March and late October, but its migration is influenced by the weather (Molnár 1979, Főnyedi 1981, Dénes 1982, Varga 1982, Anonymus 1993, Kárpáti 2003, Bozó & Csörgő 2020). During mild weather in spring, large flocks can be seen as early as late January – early February, while in autumn migrating Common Wood Pigeons can be seen even in early November (Faragó 2009, Czirák 2021a, Magyar Madártani és Természetvédelmi Egyesület 2022). The migration peak in spring is in March and April (Faragó 2009). The size of migrating flocks can be several hundred individuals in spring and autumn. Due to the moderating weather conditions, some individuals are now regularly attempting to overwinter, but the extent of overwintering is still very small (Czirák 2021a, Magyar Madártani és Természetvédelmi Egyesület 2022).

Like other pigeon species, such as the Eurasian Collared Dove *(Streptopelia decaocto)*, it is a highly successful species, due to a number of factors. Already in the first decades of the 20th century, it was demonstrated that Common Wood Pigeons are opportunistic, able to adapt to the feeding conditions of a given area and season (Collinge 1924–27, Colquhoun 1951, Murton *et al.* 1963, 1964, Murton 1965). Unlike most seed-eating birds, they also consume fruits and berries, such as the seeds of ivy *(Hedera helix)*, which are poisonous to other species (Snow & Snow 1988). However, these studies were largely conducted before the high intensification of agriculture, and the situation is nevertheless similar today (Ó hUallachain & Dunne 2013). Changes in agricultural practices have also benefited the species (Negrier *et al.* 2021), for example the expansion of rapeseed *(Brassica napus)* in Britain, which has contributed significantly to the species' population growth (Kenward & Sibly 1977, Lane 1984, Inglis *et al.* 1997, Gill *et al.* 1998). This has also resulted in the species posing a serious economic risk in agriculture (Tayleur 2008). In Hungary, damage by Pigeons, including the Common Wood Pigeon, was already observed in the 1970s and 1980s in agriculture, mainly on sunflower fields (Csernavölgyi 1975, Rékási 1982). This is likely to become a more serious problem in the future, as the size of migrating flocks increases with the population (Czirák 2021a). Another possible reason for the extraordinary population increase could be the breeding biology of the species, as it can settle in highly diverse habitats (Haraszthy 2019a). Climate change is also having a significant impact on the population of the species, through changes in migration behaviour (Dolenec & Dolenec 2010), which may lead to an increase in the proportion of overwinterers in the population. Birds returning earlier and leaving later, and thus an increase in the number of breeding birds annually can be observed.

It is a highly urbanising species. In some cities in Western and Central Europe, this process was already underway at the beginning of the 19th century (Glutz von Blotzheim *et al.* 1980), while in Northern Europe it only started or became intense at the beginning of the 20th century (Denmark) and in the middle of the century (Sweden). In Finland, it only became established in large cities in the 1990s (Fey *et al.* 2015). In Hungary, breeding pairs appeared in inhabited areas in the first half of the 20th century. In Kaposvár, it was already nesting in 1929 (Greschik 1929), but its significant urbanisation took place decades later, when it typically nested in floodplains and forests far from people (e.g. Jánossy & Zlinszky 1979, Mag 1980, Erős 1982, Molnár 1991). In the early 1980s, it was common along Lake Balaton. In 1981, a pair bred near a fishing hut at Balatonederics (Nagy 1981). In the same period, in Budapest, it bred only on Margit Island and in Népliget (Rékási 2000), but already then it was nesting in large numbers in the wooded areas around the city

(Ébert 1980, Kalivoda 1986, 1990). It only became more urbanised in the 1990s: in Vác in 1990 (Drexler 1995), in Kömlő in 1993 (Ambrus 1996), in Foktő in 1994 (Sipos 1995), and by the 2010s it was nesting in all inhabited areas, including the busiest areas of Budapest (Haraszthy 2019a). However, this phenomenon was not common, as in the mid-1990s it did not bred in Debrecen (Fintha & Szabó 1995) or in the cemeteries of Szeged (Lovászi 1994). Schmidt (1994) published a call for the documentation of the urbanisation of the species, and also pointed out that the behaviour of "wild" and "urban" birds differs significantly. While forest-dwelling individuals are extremely shy and avoid humans, individuals breeding in the cities have become extremely trusting.

In Békés County, according to the literature, at the turn of the 19th and 20th centuries and until the 1930s, it did not breed in the area of Szarvas or Békéscsaba (Tarján 1930, Molnár 1942), while according to Csath (1938), a few pairs bred undisturbed in the forests of Doboz, Póstelek, Gyulavári and Gyomaendrőd. Spring migration also occurred during this period, with the first returning birds being seen in Békéscsaba on 15 March 1907 (Schenk 1908), 27 March 1919 (Schenk 1920), 8 April 1923 (Warga 1924), and in Csorvás on 20 March 1909 (Greschik 1910). Since the 1940s, nesting has been reported throughout the county, typically in arboretums and floodplain forests, but no published data are available on when urbanisation started (Bozó 2022).

A similar process took place decades ago with the Eurasian Collared Dove in Hungary, but this species is not native to Hungary, unlike the Common Wood Pigeon. The species arrived to the Carpathian Basin from the Balkan Peninsula in the 1930s. After several alleged sightings, the first breeding was observed in Berettyóújfalu in 1932. In 1934, it was found in Székesfehérvár, in 1935 in Derecske and Bicske, in 1936 in the vicinity of Budapest, Lake Balaton and Komárom, and in 1937 it became common in these areas. Continuing its expansion towards the northeast, it slowly spread throughout the country (Keve-Kleiner 1944, Keve 1947). However, even in the early 1950s, there were still a few settlements in the country where it did not bred (Keve 1962). Its urbanisation started in the mid-1940s and proceeded at a rapid pace (Keve 1947, Tomasz 1955). Today it nests mainly in populated areas (Czirák 2021b), but in some large cities the population has declined in the city centre for various reasons (Varga & Juhász 2020).

In the last few years we have observed that the nesting population of the Common Wood Pigeon has increased spectacularly in the southern part of Békés County. Given that we have recorded the date of the first pairs breeding in the inhabited areas in several settlements of the region, we thought to survey the population of the Common Wood Pigeon in the central part of some settlements in 2022. In our work, we were mainly interested in the extent to which the population had increased in recent years. We also examined whether the population increase of this species has affected the population of the Eurasian Collared Dove, which occurs in similar habitats. This is an interesting question, because during the urbanisation of the Eurasian Collared Dove in the early period, it was found to share habitats with the Turtle Dove *(Streptopelia turtur)*, and the nesting areas of the two species were well separated (Keve 1947). Hunting data were also used, as they provide an excellent indication of the direction of population change. In addition to these data, we also report data on the migration of the species, as no detailed study has been carried out on this issue in Hungary.

Material and Methods

We chose three settlements (Mezőhegyes, Battonya, Kevermes) in the Közép-Tiszántúl, Maros–Körös köze region (Maros–Körös Interfluve) (SE Hungary) as the location of our research. In each of the three municipalities, an area of roughly the same size – approximately 31–37 hectares – was selected for the survey as follows. In Mezőhegyes, Vörösmarty street and Kiskatonák square, Kossuth street, the railway track and Posta street (31.2 hectares), in Battonya, Puskin street, Táncsics Mihály street, Állomás street and Hunyadi János street (36.9 hectares), while in Kevermes the area delimited by Battonyai street, Jókai street, Toldi street, Kossuth street, Felszabadulás street and the sports field (36.9 hectares).

Given that both species are easily recognisable by both vocal and visual observation, the survey was carried out using simple field observations. We considered birds as nesting pairs that were moving, singing or perching in a well-defined area. Maps were created of the nesting pairs found during the surveys. Surveys were conducted on 8 and 9 April in all three settlements in sunny, calm weather. In Mezőhegyes, we surveyed the area late in the afternoon on 8 April, in Battonya from dawn to mid-morning and late afternoon on 8 April, and in Kevermes late in the afternoon on 8 April and early morning on 9 April.

Since data on the dates of the appearance of the Common Wood Pigeon as a nesting species were available for the respective sites, we also reported them.

We have also collected hunting data from the period between 1999 and 2020, because the annual shooting statistics in Békés County can also be an indicator of possible population changes. For this purpose, we used the annual reports of the National Hunting Data Repository (www.ova.hu).

The migration pattern of the Common Wood Pigeon has also changed over the last century, so it was important to process local migration data as well, so that they could serve as a basis for future country-wide studies. These data are available in Kevermes from 2005, but as standard sampling was only carried out in the area from 2012 onwards, we were only able to describe the migration (medians, start and end dates) from that time onwards. For the calculation of the median dates, the Past 3.14 program was used (Hammer *et al.* 2001).The spring migration period was considered to be from 1 February to 1 April, while the autumn migration period was considered to be from 1 August to 30 November.

Results

The first urbanised individuals of the Common Wood Pigeon

The first pair breeding in the city was recorded in Mezőhegyes on 3 May 2016 (but urbanised birds probably appeared some years earlier in this settlement), and in 2020 it was already common (A. I. Csathó).

In Battonya, the first urbanised Common Wood Pigeon was recorded on 2 May 2015 in the area of the Thermal Baths (A. I. Csathó & Eszter Csathó). In 2019, it was already more widespread (A. I. Csathó), while in 2020 the population in the city continued to increase, with approximately 10 pairs breeding here (A. I. Csathó).

In Kevermes, the first, probably urbanised bird was observed in the village centre on 26 July 2014, and a bird was also observed in the same place on 10 May 2015. On 17 May 2016, an individual was seen again at a garden pond in the village centre.

On the other settlements of Maros–Körös köze region our first data of urbanised Common Wood Pigeons: Lőkösháza (22 April 2015) (L. Bozó), Szarvas (25 March 2014) (A. I. Csathó), Tótkomlós (15 April 2016) (A. I. Csathó). In 2020 the Common Wood Pigeon was already frequent in downtown area of Orosháza, the number of nesting urbanised pairs in this settlement was estimated by an order of hundreds pairs (A. I. Csathó).

Point counts

The results of the population survey by species (number of pairs and population density per settlement) are presented in *Table 1*, while the results of the point counts are presented in *Figures 1–3*. The largest nesting population and population density of the Common Wood Pigeon was in Mezőhegyes and the smallest in Kevermes. For the Eurasian Collared Dove, the same was found in Battonya and Mezőhegyes.

Table 1. Results of the population survey of Common Wood Pigeons and Eurasian Collared Doves in the three settlements in Békés County

1. táblázat Az örvös galamb és a balkáni gerle állományfelmérésének eredményei a három vizsgált Békés megyei településen

		Mezőhegyes	**Battonya**	**Kevermes**
Area of the sampling unit surveyed (hectare)		31.2	36.9	36.9
Common Wood Pigeon	Number of nesting pairs	35	16	7
	Population density (number of nesting pairs/hectare)	1.12	0.43	0.19
Eurasian Collared Dove	Number of nesting pairs	6	48	30
	Population density (number of nesting pairs/hectare)	0.19	1.3	0.81

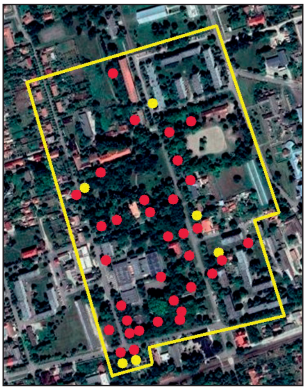

Figure 1. The results of the point counts in Mezőhegyes. Yellow line indicates the study area, red dots the mapped nesting pairs of Common Wood Pigeons, and yellow dots the mapped pairs of Eurasian Collared Doves

1. ábra A pontszámlálás eredményei Mezőhegyesen. A sárga vonal a vizsgálati területet, a piros pontok felmért fészkelő örvösgalamb-, a sárga pontok pedig a balkánigerle-párokat jelölik

Figure 2. The results of the point counts in Battonya. Yellow line indicates the study area, red dots the mapped nesting pairs of Common Wood Pigeons, and yellow dots the mapped pairs of Eurasian Collared Doves

2. ábra A pontszámlálás eredményei Battonyán. A sárga vonal a vizsgálati területet, a piros pontok felmért fészkelő örvösgalamb-, a sárga pontok pedig a balkáni-gerle-párokat jelölik

Figure 3. The results of the point counts in Kevermes. Yellow line indicates the study area, red dots the mapped nesting pairs of Common Wood Pigeons, and yellow dots the mapped pairs of Eurasian Collared Doves

3. ábra A pontszámlálás eredményei Kevermesen. A sárga vonal a vizsgálati területet, a piros pontok felmért fészkelő örvösgalamb-, a sárga pontok pedig a balkáni-gerle-párokat jelölik

It can be concluded that the nesting population of Common Wood Pigeon showed an aggregated distribution in the sampling areas. More pairs were breeding in the central, more parked areas of the settlements. The Eurasian Collared Dove was clearly more abundant in the non-central, less parked parts of the settlements. During the field survey, it appeared that for the latter species, pairs preferred common spruce *(Picea abies)* and Colorado spruce *(Picea pungens)* trees for nesting.

Hunting data

The shooting data for Békés County between 1999 and 2020 are shown in *Figures 4–5*. The number of birds shooted increased significantly over time for the Common Wood Pigeon (R = 0.81, P < 0.0001), while the number of birds shooted for the Eurasian Collared Dove did not change significantly over time (R = 0.0305, P = 0.44). When the same is calculated for the period 2011–2020, there is a similar significant increase for the Common Wood Pigeon (R = 0.82, P = 0.003), but a significant decrease for the Eurasian Collared Dove (R = -0.87, P = 0.001).

Migration data of Common Wood Pigeon

For the area of Kevermes and Lőkösháza, we have observation data for a total of 1,148 different days between 1 January 2005 and 12 May 2022. Statistics describing spring and

Figure 4. Hunting data of the Common Wood Pigeon for the period 1999–2020 in Békés County
4. ábra Az örvös galamb vadászati statisztikákban szereplő terítékadatai 1999 és 2020 között Békés megyében

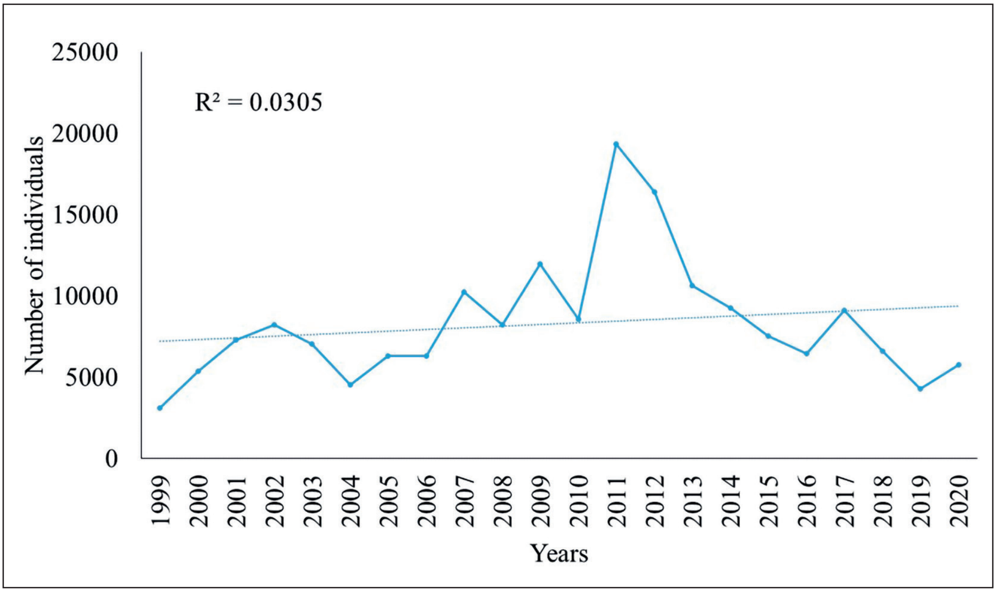

Figure 5. Hunting data of the Eurasian Collared Dove for the period 1999–2020 in Békés County
5. ábra A balkáni gerle vadászati statisztikákban szereplő terítékadatai 1999 és 2020 között Békés megyében

autumn migration between 2012 and 2022 are presented in *Table 2*. On average, the spring migration started on 24 February (SD = 9.4 days), ended on 5 April (SD = 2.1 days) and had a length of 40 ± 8.8 days. Autumn migration started on average on 16 September (SD = 12.8 days), ended on 8 November (SD = 10.9 days) and had a length of 52.6 ± 17 days. It is not clearly possible to determine the exact end of spring migration and the beginning of autumn migration due to the presence of nesting birds. These dates coincide with the appearance of the last flocks in spring and the first flocks in autumn. Migration peaks could not be determined in either period, but the highest numbers migrated in the area between the end of March and the first week of April in spring and the first half of October in autumn.

Taking data from 2005 to 2022, the earliest spring occurrence is from 14 February 2014, while the latest autumn occurrence is from 22 November 2014.

In spring, they typically migrated in small groups of 10–15 individuals, but groups of several hundred individuals were also common. Groups larger than 200 individuals (200–400, possibly 1,000–1,500 individuals) were recorded in seven cases, all during late March. The largest flock of about 1,500 was seen on 20 March 2017 at the former pheasant farm in Kevermes. In autumn, flocks of only a few dozen individuals were typically seen in September (occasionally as early as August), but flocks of 100 individuals or more were only seen in October. On 13 occasions, we observed groups larger than 200 individuals. The highest total number of individuals observed in one day was about 2,000 on 7 October 2017 in the vicinity of the Tábornok Forest in Kevermes.

During both migration periods, the flocks preferred quiet, undisturbed patches of woodland and woodland edges, where the only threat was the Northern Goshawk *(Accipiter gentilis)* (based on several killed Common Wood Pigeons). In these places they sometimes stayed for several days (up to a week or two in autumn).

Table 2. Migration data of Common Wood Pigeon from Kevermes and Lőkösháza between 2012 and 2022

2. táblázat Az örvös galamb vonulási adata Kevermesről és Lőkösházáról 2012 és 2022 között

Year	Period	First data	Last data	Length of migration period (day)
2012	spring	2 Mar	6 Apr	35
	autumn	15 Sep	26 Oct	41
2013	spring	5 Mar	8 Apr	34
	autumn	2 Oct	2 Nov	31
2014	spring	10 Febr	6 Apr	55
	autumn	12 Sep	22 Nov	71
2015	spring	7 Mar	6 Apr	30
	autumn	28 Aug	10 Nov	74
2016	spring	11 Feb	5 Apr	53
	autumn	7 Sep	25 Oct	48
2017	spring	26 Feb	7 Apr	40
	autumn	25 Sep	26 Oct	31
2018	spring	9 Mar	7 Apr	29
	autumn	1 Oct	17 Nov	47
2019	spring	15 Feb	2 Apr	46
	autumn	2 Sep	17 Nov	76
2020	spring	28 Feb	3 Apr	35
	autumn	2 Oct	16 Nov	45
2021	spring	23 Feb	2 Apr	38
	autumn	16 Sep	17 Nov	62
2022	spring	20 Feb	6 Apr	45
	autumn	–	–	

A total of 10 sightings were made during the winter period from 1 December to 31 January, seven of which occurred in December and three in January. Six individuals were sighted on 13 January 2016, otherwise all were solitary birds.

Observation data from the breeding period

The spring migration period overlaps almost completely with the breeding period of the local population, as the first spring individuals are often observed singing in the territories. At the time of the surveys in 2022, on 8–9 April, most birds were already on the nest. In one case in Mezőhegyes, the distance between two occupied nests was only 20 m. In the second half of August, we observed several nesting or singing birds in Kevermes. Urbanised birds nesting in the area are much more familiar than those nesting in the woodlands outside. Few birds regularly visit garden ponds to drink.

It is also worth noting that flocks of 20–50 individuals are now regularly found during the breeding season. This is most noticeable in late April and the first half of May, when the seeded sunflowers have hatched but the plants have not yet become strengthened. At this time, the Pigeons snip off the fresh shoots, causing damage similar to that of the European Hares *(Lepus europaeus)*. This is why the Bréda Hunting Company of Lőkösháza has already carried out a diversionary feeding in May 2022, spreading maize on the sunflower fields (István Elek – personal communication).

Discussion

Based on our data, we can conclude that urbanised populations of the Common Wood Pigon are spreading rapidely in the Maros–Körös köze region. This is so great that it is probably one of the fastest population changes of any bird species in the area.

It has bred in the area in the past, when it was a nesting species in suburban areas far from populated areas. In the 2000s and 2010s, it was ubiquitous in planted forests and woodlands in the outer area of the settlements, and was particularly found in oleaster forests (Bozó 2017). A population survey was conducted in 2000 in the outer area of Battonya, covering the entire administrative boundary (14,577 hectares). The breeding population was estimated at 32 pairs, all mapped pairs nested in the outer area of the settlement (Csathó & Csathó 2009). According to our observations, the species appeared as a breeding species in the mid-2010s in the interior, in towns and villages. The year of the first breeding of the first urbanised pair in a given locality is probably imprecise, but it is still important to document it as soon as possible, because the later we try to estimate it, the more imprecise it becomes. Our data are more accurate for Battonya and Kevermes because the avifauna of these settlements has been monitored continuously over the last decades. However, it is a fact that the first breeding pairs in the study area appeared much later than the urbanisation pattern of the species in Hungary. In the nearest large cities, such as Szeged, Békéscsaba and Orosháza, we have observed earlier appearances, but abundant breeding is now taking place in these settlements. The reason why it appears later in our area is probably due to the lower population size of the municipalities in the region and the smaller size of the park areas.

The highest population density was recorded in the largest municipality with the most parkland, Mezőhegyes, while the lowest density was recorded in the smallest and least parkland municipality, Kevermes. One of the drivers of urbanisation is predator avoidance, which may also be the case for the species. However, it is possible that the low number of (or lack of) birds of prey has led to the late appearance of the first pairs in populated areas in this region. As the area is one of the best small game areas in the country, there is very high year-round hunting pressure on predators, so there is no evidence of nesting Northern Goshawks in the area, for example.

It is very important to underline that the first urbanised pairs did not gradually arrive from the outer area of the settlements towards the interior of populated areas (i.e. not in a centripetal direction), but rather appeared in the park areas of the centres of the settlements and spread outwards from there. Thus, the rapid spread of the species in recent years is even more striking.

The rapid population growth of the species in the cities, in addition to its extraordinary adaptability in terms of both breeding and feeding biology, is certainly helped by the fact that it can be hunted between 15 August and 31 January (www.omvk.hu). However, this cannot take place inside inhabited areas, so settlements provide protection for the birds. For the time being, this may be a less important driver of urbanisation, as it rarely appears in inhabited areas beyond the breeding season, but in the longer term it may be an important factor in the process.

The impact of climate change on the migration of the Common Wood Pigeon has already been demonstrated in the region (Bozó & Csörgő 2020), and this is likely to contribute not only to the earlier spring arrival of the species, but also to its urbanisation. Overwintering has not yet been observed in the region, but some mid-winter data may already predict future overwintering.

Our observations suggest that the species' population in the outer area of the settlements is stable rather than increasing. These birds are still much more shy than birds in the cities and villages and will take off immediately when approaching a nest or a feeding individual. The increasing damage in agricultural areas is therefore more in line with the exponential increase in the population in inhabited areas than with the stability of the population in the outer area of the settlements. Damage in agriculture was already occurring, but the increase in biomass in recent years has created increasingly tense situations. This will most certainly become even more problematic in the future, and it is a good question whether the early summer damage on sunflower fields, for example, can be contained within the legal framework.

At the time of the survey, it was clear that the Common Wood Pigeon was competing with the also urbanised and large populations of the Eurasian Collared Dove, and that the populations of the smaller dove would decline, if not in the near future. We do not have precise figures on how many pairs of Eurasian Collared Dove were breeding in the inhabited areas of the region even a decade ago, but it is very likely that many more than the number of pairs counted now. In Battonya and Kevermes, the two less parkland settlements, the

Eurasian Collared Dove still nests in greater numbers than the Common Wood Pigeon, but in the centre of Mezőhegyes the larger species has clearly dominated. It is clear that the Eurasian Collared Dove is being displaced from the central, parked areas to the garden streets of villages and towns, and is now also becoming more common in the open outer areas of the settlements, on the edges of forest patches and in tree-lines (Bozó 2017). A decline in the population of the species in the city centre and a parallel displacement to peripheral areas were also observed in Debrecen. Here, a density of 94.5 pairs/10 ha was recorded in the 1980s, but between 2016 and 2020 this figure was less than halved to 37.45 pairs/10 ha, while the density of breeding population in peripheral areas doubled. The reason for this change was that the food supply of the species decreased due to the bankruptcy of mills in the city (Varga & Juhász 2020).

The process seems to be taking place between the two species as between the Eurasian Collared Dove and the European Turtle Dove in the mid-20th century. At that time, the rapid spread of the Eurasian Collared Dove triggered a division of territory between the two species: the European Turtle Dove was confined to the outer area of the settlements and parks, while the other species became the “bird of the gardens”. In the places where they bred side by side, there were often conflicts between the two species, with one or the other emerging victorious (Keve 1947). However, the difference in body size between the two species is not nearly as great as between the Common Wood Pigeon and the Eurasian Collared Dove, so it is understandable that the latter’s distribution is dictated by its spread.

In Hungary, the Eurasian Collared Dove can nest in a wide variety of habitats, but it builds its nest mostly in the cover of evergreens (Haraszthy 2019b). We observed this, as in most cases we saw singing individuals in places where there was some kind of evergreen tree.

It should be noted that in Battonya, and especially in Kevermes, the European Turtle Dove has also become urbanised in recent years. In Kevermes, for example, they are already breeding in the centre of the village (L. Bozó pers. obs.). However, the reason for this is clearly the increasing number of unoccupied houses and empty plots of land, which are growing year by year due to the unfavourable demographic conditions, creating an excellent habitat for the species. Even in the first half of the 20th century, nesting in the cities was not unprecedented for the European Turtle Dove (Dorning 1928, Balassa 1930).

The increase in the population of the Common Wood Pigeon since the mid-2010s is paralleled by hunting data. This trend has been visible since the late 1990s. In the case of the Eurasian Collared Dove, however, the distribution data from 1999 to 2020 and from 2011 to 2020 show a different trend. Until the 21-year period, there was no change in the number of birds shot annually, while in the last 10 years have seen a significant decrease. Both the stability and the decline are interesting, as the most recent national data show that the population of the species in Hungary has been increasing steadily, and this has become even more intense in the last period (Czirák 2021b). The decline could be related to the spread of the Common Wood Pigeon, but it cannot be excluded that some local, unknown effect is behind it.

In relation to the migration data, it is worth noting that there have been no multi-year studies at regional level from the other parts of the country, so our own results can only be compared with the national data. However, the timing of the migration is similar to the national average (Faragó 2009, Czirák 2021a). Groups of several hundred, sometimes thousands of individuals are not unprecedented in Hungary (Orbán & Kovács 1985, Hadarics 1997, Hadarics 1998a, 1998b), so the observed flocks of this size in the region are not exceptional. The question is whether they will become common in the future.

In conclusion, the explosive urbanisation of the Common Wood Pigeon has only just begun in the study area, so further population increases are expected in the coming years. At the same time, the Eurasian Collared Dove is expected to become increasingly displaced to the periphery of settlements. One reason for displacement could be that they have similar lifestyles, but the Common Wood Pigeon is stronger, larger and therefore a stronger competitor. It is already apparent that the Common Wood Pigeon will cause significant damage to agriculture, but we do not yet know what the solution to this problem will be. It will also be worth keeping an eye on the populations in the outer area of the settlements, as it is an interesting question whether their size will change over time.

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The population dynamics of the Red-footed Falcon *(Falco vespertinus)* on the southwestern limit of its breeding range

Jenő J. Purger[1*] & Sándor Lukács[2]†

†This article is dedicated to the memory of Sándor Lukács (1948–2019).

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Abstract The western boundary of the Palearctic range of the Red-footed Falcon *(Falco vespertinus)* is located in the Carpathian Basin, with significant breeding areas in the northern part of Serbia, Voivodina Province. The size of the breeding population has been estimated and surveyed several times since the middle of the last century. The number of breeding pairs showed considerable variation, while estimates suggested a declining trend in the population size, though the dynamics of the Red-footed Falcon population was less known. This motivated us to perform censuses every year from 2000 until 2009. During that period, the number of confirmed breeding pairs varied from 61 to 179. We found that the number of breeding pairs decreased significantly (> 40%) after a 3-4 year of increase. The number of breeding sites and the extent of the distribution area changed in proportion to the increase or decrease of the population size. However, the change in population size was unrelated to the general proportion of pairs breeding in colonies (87–96%) and those breeding solitarily (4–13%).

Keywords: census, estimation, fluctuation, nesting strategies, Serbia, Voivodina

Összefoglalás A kék vércse palearktikus elterjedési területének délnyugati határa Észak-Szerbiában, Vajdaság tartományban van. A múlt század közepétől többször megbecsülték és felmérték a költőállomány nagyságát. A költő párok száma változó volt, a becslések a populáció csökkenő tendenciájára utaltak, azonban a populáció dinamikája kevésbé volt ismert. Emiatt 2000-től 2009-ig évente census felméréseket végeztünk. A vizsgált időszakban a bizonyítottan költő párok száma 61 és 179 között változott. Megállapítottuk, hogy a költő párok száma 3–4 éves növekedést követően jelentősen (> 40%) visszaesett. Az állomány növekedésével, illetve csökkenésével arányosan változott a költőhelyek száma és az elterjedési terület kiterjedése. A populáció nagyságának változásaival a telepekben (87–96%), illetve magányosan (4–13%) költő párok aránya viszont nem változott lényegesen.

Kulcsszavak: állományfelmérés, becslés, fluktuáció, fészkelési stratégiák, Szerbia, Vajdaság

[1] *Department of Ecology, Institute of Biology, Faculty of Sciences, University of Pécs, 7624 Pécs, Hungary*
[2] *Nature Photographers Group Egretta, 21000 Novi Sad, Serbia*
* *corresponding author, e-mail: purger@gamma.ttk.pte.hu*

Introduction

The western border of the Palearctic range of the Red-footed Falcon *(Falco vespertinus)* is located in the Carpathian Basin, with significant breeding areas in the eastern parts of Hungary and in the northern parts of Serbia, Voivodina Province (Cramp & Simmons 1980, Barna 2015, Kotymán *et al.* 2015). The Red-footed Falcon does not build a nest, but breeds in colonies or solitarily in abandoned nests of corvids (Cramp & Simmons 1980). Thus, their populations are also affected by the number of available nests of the Rook *(Corvus frugilegus)*, Hooded Crow *(Corvus cornix)* and Magpie *(Pica pica)*. Pairs of Red-footed Falcons nesting in Rook colonies usually occupy less than 10-20% of available nests (e.g. Horváth 1955, 1963, Végvári *et al.* 2002). The reason for this is that at the time of their nest occupancy the nesting of Rooks is still ongoing, other bird species also compete for these nests, and very often there is a lack of open grasslands nearby with potential food sources (Fehérvári *et al.* 2009, Palatitz *et al.* 2011). The population in Hungary decreased from 2500 to 600 pairs between 1950s and 2006 (Keve & Szijj 1957, Palatitz *et al.* 2022). The drastic decrease was mainly caused by the lack of nesting sites due to organized extermination of Rooks (Fehérvári *et al.* 2009, 2012). Thus, only 30–40% of the breeding pairs of Red-footed Falcons in Hungary had bred in Rook colonies (Tóth & Marik 1999, Végvári *et al.* 2002), which is also a disadvantage, as the breeding success of solitary pairs is significantly lower than that of pairs breeding in colonies (e.g. Haraszthy & Bagyura 1993, Tóth 1994). In order to stop the unfavourable process, artificial colonies of nest-boxes have been established in the appropriate habitats since 1989 (Molnár 2000, Vilagosi 2005, Kotymán *et al.* 2015), but the population has started to increase gradually only since 2007 (Fehérvári *et al.* 2009, Palatitz *et al.* 2022). The population of the Red-footed Falcon in Voivodina was estimated to be 80–150 pairs in the second half of the last century (e.g. Ham 1977, Vasić *et al.* 1985, Vasić 1996), but the first census performed in 1990 showed that the number of breeding pairs exceeded 300 (Purger 1996). Estimates conducted in later years (e.g. Ham & Rašajski 2000, Puzović *et al.* 2003, 2009) and several censuses (Purger 2008) indicated significant fluctuations and a declining trend in population size. However, there were no monitoring surveys, so our knowledge about the extent, dynamics and influencing factors of fluctuations was incomplete.

The aim of our work was to perform a population survey in several consecutive years using the same method in order to 1) reveal the temporal and spatial changes in the size of the Red-footed Falcon population in Voivodina, 2) to determine whether there is relationship between breeding pairs and number of breeding sites, 3) whether there is a difference in the proportion of colonial and solitary breeding pairs in each year.

Materials and Methods

Voivodina Province is a region in Northern Serbia located in the south-eastern part of the Carpathian (Pannonian) Basin, encompassing the confluence area of the Danube, Sava and Tisa rivers covering a total area of 21,506 km^2. The largest part of Voivodina (about 95%) is characterized by low altitudes ranging from 68 m to 120 m, while the southeast area stands out with low mountainous forms Fruška Gora (538 m) and Vršačke Planine (639 m). Sandy areas (Deliblato Sands and Subotica-Horgoš Sand), lower terrains, and alluvial plains are also situated in the Voivodina region. Forests comprise only about 7% of Voivodina and mainly occur in the mountains and terrains along the rivers, while agricultural lands occupy about 84% (Grujić *et al.* 2021). The climate of Voivodina is moderate continental, with

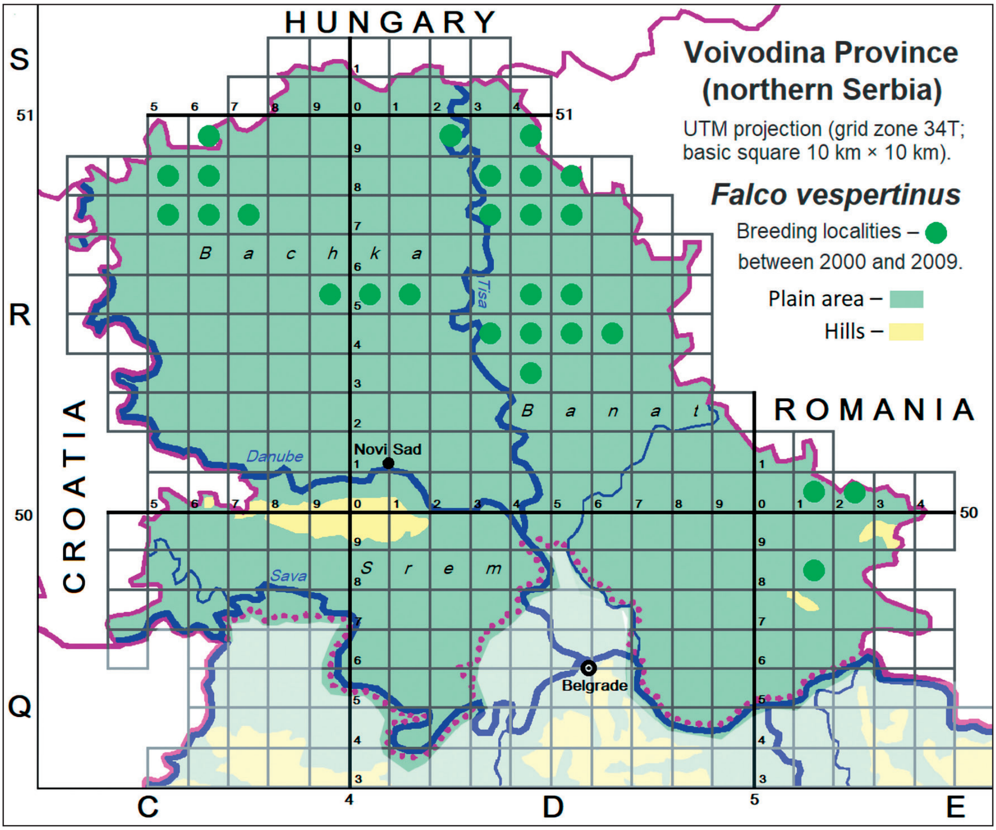

Figure 1. Breeding distribution of the Red-footed Falcon in Voivodina between 2002 and 2009 based on the bird census data

1. ábra A kék vércsék fészkelőterületei Vajdaságban a 2002 és 2009 között végzett állományfelmérések alapján

cold winters, and hot, humid summers, with huge range of extreme temperatures and a very irregular distribution of rainfall per month. The mean annual air temperature was 11.1 °C and annual amount of precipitation was 606 mm between 1949 and 2006 (Tošić *et al.* 2014).

Our survey of the distribution and population size of Red-footed Falcons covers the breeding period from 2002 to 2009 following the same routes in 1990 and 1991 (Purger 1996) and 2000 and 2001 (Purger 2008). Involving one or two observers, we drove all main roads and a lot of dirt roads, usually ca. 300–400 km per day. The census was carried out covering the entire territory of Voivodina, but focused on the known breeding sites of the Red-footed Falcon (Ham & Rašajski 2000, Barna 2015). The squares in which breeding was registered within the study period were highlighted on the 10 × 10 km UTM *(Figure 1)*. We followed the suggestion of Postupalsky (1974) who proposed at least two checks of each occupied nest per breeding season. The census was done every year between 20–30 June and 5–15 July in about 10–15 days. One or two days were spent in Srem (3,838 km^2 area between the Danube and the Sava and the Croatian state border), where breeding is probable in some years. Three-four days were spent in Bachka = Bačka, which region is an 8,956 km^2

wide plain bordered by the Danube, the Tisa and the Hungarian state border, where nesting sites are mostly isolated. Seven-nine days were spent in Banat (8,886 km^2 area bordered by the Tisa, the Danube and the Romanian state border), because the main breeding sites are located in the northern and central parts of Banat (Purger 1996, 2008, Ham & Rašajski 2000). In earlier studies (Purger 1996, 2008) birds nesting in Rook colonies were considered "colony nesters" irrespective of the number of pairs, whereas those occupying Magpie or Hooded Crow nests were regarded as "solitary nesters". In this study, we considered solitary nesting if only one pair bred in a Rook colony. The number of the Red-footed Falcon pairs was determined during the first field trip on the basis of the birds sitting in and flying out of the nest. During the repeated fieldwork, we did not only search for a new nesting sites, but also refined the results of the previous survey, so each year we only considered the number of pairs that really breed. In the second survey, the nestlings were already sitting in the nests, but when we did not see them, nest checking was done using a mirror (Parker 1972).

For the analysis of the relationships between the number of breeding sites of the Red-footed Falcon and the number of breeding pairs in the colonies and solitarily, we used the PAST 3.17 software (linear bivariate model, ordinary least squares regression) (Hammer *et al.* 2001).

Results and Discussion

The Red-footed Falcon bred in Voivodina in 2000 and 2001 (Purger 2008) and between 2002 and 2009 in the area between the Danube and the Tisa rivers in Bachka *(Table 1)* and east of the Tisa river in Banat *(Table 2, Figure 1)*, similar to previous decades (e.g. Purger & Mužinić 1997, Ham & Rašajski 2000). Based on our results of the monitoring, their population fluctuated between 61 and 179 pairs *(Table 3)*. We found that the number of breeding pairs decreased significantly (> 40%) after a 3–4 year increase *(Table 3)*. Such population declines occurred in 2001 (61 pairs) and 2006 (83 pairs), and then in 2010 (60 pairs) in the year following our study (Solt *et al.* 2010). Between 2000 and 2009, the Red-footed Falcon population in the study area was estimated to 100–150 pairs (Puzović *et al.* 2009), which is consistent with the results of our census. However, our monitoring was ended in 2009, as the placement of nesting boxes began in Voivodina from that year onwards and until 2014 the population surveys were carried out according to the Hungarian protocol (Fehérvári *et al.* 2012). The results of our monitoring of the Red-footed Falcon population in the period between 2000 and 2009 allowed to accurately describe the dynamics of fluctuations. The importance of precisely defined and performed census is shown by the example of the very different population size in 2009 as a result of simultaneous surveys conducted by different methods. That year, we proved the breeding of 179 pairs of Red-footed Falcon at 45 sites *(Table 3)*. Ružić *et al.* (2009) reported the breeding of 164–171 pairs at 22 sites, but they did not provide details of the method of their survey. Solt *et al.* (2010) in the same year found 150 breeding pairs at 20 locations, but Barna (2015) suggested that the number of breeding pairs exceeded 200. The different results suggested that the same survey method should always be used for long-term surveys. According to

Table 1. Number of breeding pairs of Red-footed Falcon in Bachka between 2002 and 2009 (1 – Breeding in Hooded Crow or Magpie nest)

1. táblázat Bácskában költő kék vércse párok száma 2002 és 2009 között (1 – költés dolmányos varjú vagy szarka fészekben)

UTM	Locality	2002	2003	2004	2005	2006	2007	2008	2009
CR57	Obzir		3	3	2	1	1		1
CR58	South-west part of Stanišić	4	7	4	5	5	10	1	5
	North-east part of Stanišić		3						1
	1 km east of Stanišić			1	1				
	1.5 km east of Stanišić				1				
	Stanišić			1	1				1
CR67	North-west part of Svetozar Miletić				1			1	2
CR68	4km north-east of Svetozar Miletić						1		
	2 km south-west of Aleksa Šantić			1					1
CR69	3 km north-east of Stanišić		1	1				1	
	4 km north-east of Stanišić				1			1	
CR77	2.5 km west of Gornja Rogatica	4	5	4	3	4	3	2	1
CR95	3 km south of Feketić	1	2	1	3				
	4 km south-east of Feketić				3	1	3	1	1
DR05	4 km east of Feketić	4	7	8	4		2		
	4 km east of Feketić	1							
DR15	12 km north-west of Bečej				2				1
	14 km north-west of Bečej						1		
DR29	2.5 km north-west of Zimonjić	6	2	2		1			
	2 km west of Zimonjić	1		1					1
	3 km south-west of Mali Pesak		24	9	26	2	7	9	12
	Total	21	54	36	53	14	28	16	27

Barna (2015), the number of breeding pairs following a decline in 2010 increased until 2012, then declined again in 2013 and 2014. For the 2008–2013 period, the number of Red-footed Falcons in Voivodina was estimated at 262–335 pairs (Puzović *et al.* 2015). The Red-footed Falcon population in Hungary has been monitored since 2003 and we can conclude that until the drastic decrease of the population in 2010, the number of pairs breeding in the territory of the two countries changed similarly from year to year (Palatitz *et al.* 2015). After that, the population in Hungary steadily increased until 2014, then declined again in 2015, but the decrease in the number of breeding pairs was smaller than in previous years, which can be explained by the positive effect of the nesting boxes. The Red-footed Falcon population in Hungary increased further and in 2019–2020 the estimated number of breeding pairs was 1,200–1,300, which is considered to be stable due to the usage of nest boxes (Palatitz *et al.* 2022). The fluctuation of the population depends on outbreaks of small mammal populations and weather conditions in spring (Fehérvári *et al.* 2011).

Table 2. Number of breeding pairs of Red-footed Falcon in Banat between 2002 and 2009 (1 – Breeding in Hooded Crow or Magpie nest)

2. táblázat Bánátban költő kék vércse párok száma 2002 és 2009 között (1 – költés dolmányos varjú vagy szarka fészekben)

UTM	Locality	2002	2003	2004	2005	2006	2007	2008	2009
DR34	2 km north-west of Kumane							1	2
DR37	2 km east of Padej		1						2
	4 km east of Padej			1					
	1 km north of Padej			1				1	1
	2 km north-east of Padej						1		2
	2.5 km north-east of Padej								2
	3 km north-east of Padej							3	9
DR38	Ostojićevo (south part)	1							1
	1 km south of Ostojićevo				1				1
	1.5 km south of Ostojićevo								1
DR43	Okanj, 3 km south-west of Melenci		10	12	7	4		1	1
	5 km south-east of Melenci			1					
	Elemir (north part)			1					2
	1.5 km north of Elemir							3	1
DR44	3 km north-east of Melenci				9	8	5	4	
	Rusanda (north-west part of Melenci)				1	1	2	4	7
DR45	10 km east of Novi Bečej		13	15	34	12	12	7	10
DR47	1 km north-east of Sajan	1							
DR48	2 km south-east of Jazovo	28	3	11	13	22	40	46	43
	Jazovo (north part)		1				1		1
	4 km east of Jazovo						1	2	5
	5 km east of Jazovo							2	4
	1 km south-west of Banatski Monoštor			1	1				2
	5 km south of Crna Bara			1					
	6 km west of Mokrin				2				4
DR49	2 km south-west of Vrbica	3	12	17	10	11	22	20	9
	1 km east of Banatski Monoštor		1						
	5km north-west of Crna Bara								1
DR54	Torda (south-east part)	15	13	7	4	3	4	6	6
	2 km south of Torda	2	1	2	3				
	3 km west of Banatski Dvor						6	14	15
	4 km north-west of Banatski Dvor							1	
	7 km south-west of Bašaid								2

UTM	Locality	2002	2003	2004	2005	2006	2007	2008	2009
DR55	1 km south-east of Bašaid	1	2		5	3	3	6	7
	4 km north of Bašaid			5	3	3	3		1
	3.5 km south-east of Bašaid						1		
	1 km south of Bašaid							1	
	1 km south-west of Bašaid								1
	2 km south-west of Bašaid								1
DR57	Kikinda (west part)								1
	3 km west of Kikinda							1	1
DR58	Mokrin (Vašarište)	22	15	2					
	1 km north-west of Mokrin	4							
	4 km west of Mokrin			1					4
DR64	1.5 km north-west of Banatski Dvor	1		1		1			1
EQ18	Potporanj		2						
ER10	Margita				1				
ER20	3 km east of Vatin					1			1
	Total	78	74	79	94	69	101	123	152

Table 3. The distribution of Red-footed Falcon colonial and solitary breeding pairs and nesting sites in Voivodina according to the census survey conducted by using the same method

3. táblázat Telepekben, illetve magányosan költő kék vércse párok és a fészkelőhelyek számának megoszlása a Vajdaságban az azonos módszerrel végzett állományfelmérések alapján

Year	Colonial	Solitary	Total	Nesting sites	Source
2000	108 (93%)	8 (7%)	116	17	Purger 2008
2001	57 (93%)	4 (7%)	61	11	Purger 2008
2002	92 (93%)	7 (7%)	99	17	this study
2003	123 (96%)	5 (4%)	128	21	this study
2004	102 (89%)	13 (11%)	115	28	this study
2005	139 (95%)	8 (5%)	147	27	this study
2006	77 (93%)	6 (7%)	83	17	this study
2007	122 (95%)	7 (5%)	129	21	this study
2008	128 (92%)	11 (8%)	139	25	this study
2009	156 (87%)	23 (13%)	179	45	this study

The number of breeding sites changed in proportion to the increase or decrease in the number of Red-footed Falcon pairs nesting in Voivodina (linear regression, $n = 10$, $B = 0.245$, $t = 5.123$, $P < 0.001$) *(Figure 2, Table 3)*. This means that in the years when Red-footed Falcons breed in greater numbers and in more places than e.g. in 2005 or 2009 *(Table 3)*, nesting sites are also scattered over a larger area. In this case, the boundary of the distribution area shifts to the west and south, as our previous survey results have already pointed out (Purger 1996, 2008). One of the most important factors influencing the

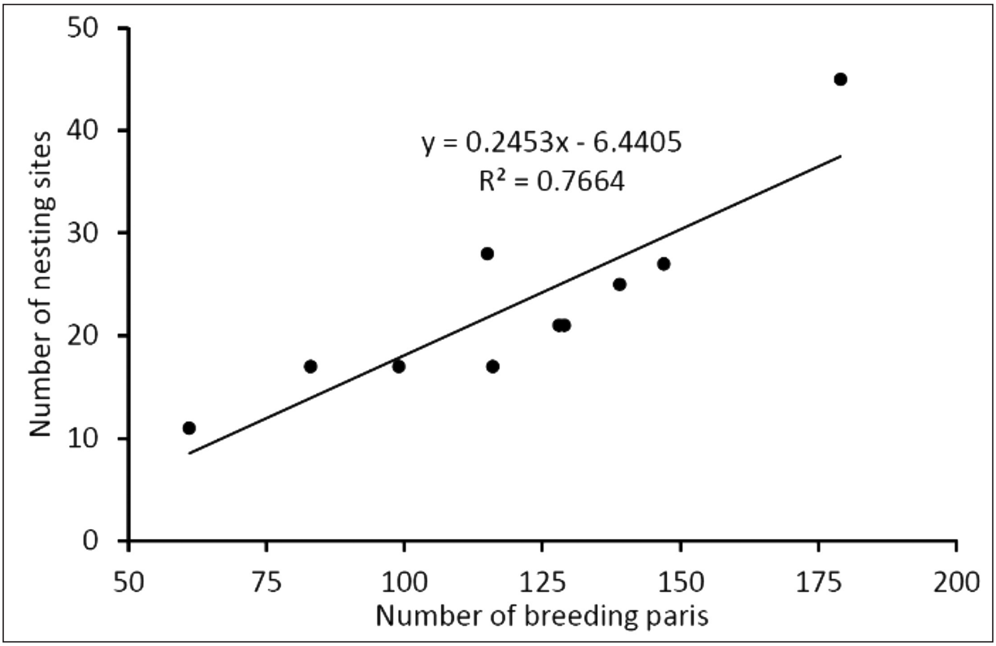

Figure 2. Relationship between the number of breeding pairs of Red-footed Falcon and the number of nesting sites

2. ábra A kék vércse költő párok és költőhelyeik száma közötti kapcsolat

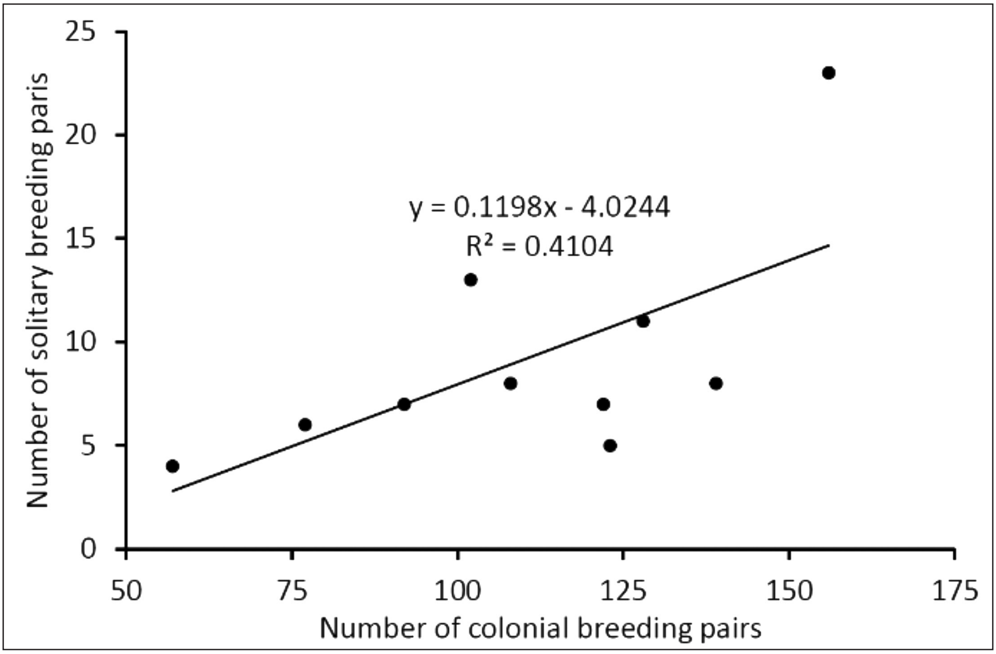

Figure 3. Trends of sympatric solitary and colonial breeding pairs of Red-footed Falcon in Voivodina

3. ábra A telepekben, illetve magányosan költő kék vércse párok számának alakulása a Vajdaságban development of the population and the size of the occupied areas in Hungary was the lack of rookeries (Palatitz *et al.* 2022). According to our previous surveys in Voivodina, more than 90% of Red-footed Falcons used abandoned nests in Rook colonies for breeding (Purger 1996, 2008), suggesting that there was no shortage of suitable breeding sites here. This is supported by the fact that during our field trips we observed several abandoned rookeries in the previously known breeding sites of Red-footed Falcon. Nesting in colonies results in higher breeding success, therefore the proportion of birds breeding in colonies or solitarily may be important. In Voivodina, we could not find different trends in the number of solitary and colonial nesting pairs in the study period (linear regression, n = 10, B = 0.119, t = 2.359, P = 0.046) *(Figure 3)*. The change in population size was unrelated to the proportion of pairs breeding in the colonies (87–96%) and solitarily (4–13%) did not change *(Table 3)*. Our results did not support the previous assumption (Purger 2008) that in years when the number of breeding pairs is lower, the proportion of birds breeding in colonies increase to achieve higher breeding success. In Voivodina, the number of Rook nests in the 1970s exceeded 80,000 (Garovnikov 1976), but this halved by the end of the century (Puzović *et al.* 2003). A survey conducted in Bachka in 2009 (Tucakov *et al.* 2010) suggested a significant decline in Rook population (Tucakov *et al.* 2010). The population estimate for the period between 2008 and 2013 indicated a further decline (Puzović *et al.* 2015), but it was nevertheless concluded that the Rook population after 2000 remained stable (Puzović *et al.* 2015). The depletion of Rook affects the areas along the Danube and the Tisa rivers rather than the areas preferred by the Red-footed Falcon. The fluctuation of the Red-footed Falcon population is influenced by the number of nests suitable for breeding, and also by weather conditions and the proximity and richness of feeding sites (Fehérvári *et al.* 2011). Their clutch size and fledging success are affected by the nesting strategy (colonial or solitary) and also by the weather in early spring, which affects the birds' food availability, as well as the timing of nest occupying and beginning of breeding (Fehérvári *et al.* 2011, Palatitz *et al.* 2015).

In Voivodina, about 70% of the Red-footed Falcons were breeding in the IBA (Important Bird Area) during the period of our survey (Puzović *et al.* 2009), but there is still a lack of grasslands which provide food, as well as around steppe forest patches and bushes with suitable nesting place (Barna 2018). The effect of the amount and distribution of precipitation on the size of Red-footed Falcon population could be detected in Voivodina in 2001 and 2010, when precipitation was much higher than average (Popov & Svetozarevich 2021) and the number of breeding pairs reached its minimum (Purger 2008, Solt *et al.* 2010).

The results of our survey showed that between 2000 and 2009 Red-footed Falcon bred only in Bachka and Banat, mostly within their previously known nesting areas in Voivodina. Despite changes in the number and spatial distribution of breeding pairs, more than 90% of the birds nested in Rook colonies. The extent of fluctuations in the number of breeding pairs was not influenced by the limited availability of Rook nests, but rather by the rainy weather and limited food supply. The number of breeding pairs in Voivodina (N Serbia) from year to year developed similar to Hungary, despite that the nesting strategies (the proportion of colonial and solitary nesters) differ significantly in the two countries.

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Presentation of so far undetermined bird remains from the Upper Miocene (MN13) of Polgárdi 4 and 5 (Fejér county, West Hungary)

Jenő (Eugen) KESSLER[1] & Ida HORVÁTH[2]*

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Abstract The authors have identified the mostly very fragmentary bird fossils from the uncatalogued material of the Hungarian Institute of Geology and Geophysics to the level that the condition of the bones allows. Almost half of the 102 bone pieces (42 fragments) could be completely or partially identified, while the rest (60 fragments represented either by bone fragments or by toe phalanges, claws, mandibles, etc.) could not be identified. The material identified includes taxa previously published and known from the site, but a good number of these are represented by other bones or parts of bones, as in previous publications (*Palaeortyx phasianoides* Milne-Edwards, 1869, *Palaeocryptonix hungaricus* Jánossy, 1991, *Porzana † kretzoii* Kessler, 2009, *Glaucidium † baranensis* Kessler, 2010, *Apus † baranensis* Jánossy, 1977, *Lullula † minor* Kessler, 2013, *Delichon † polgardiensis* Kessler, 2013, *Riparia † major* Kessler, 2013, *Sitta † gracilis* Kessler, 2013). The taxa identified at order, family or genus level are listed in the main text and complemented by one figure, as well as a rich bibliographic material.

Keywords: Hungary, Polgárdi, Upper Miocene, bird fauna

Összefoglalás A szerzők azonosították az előző vizsgálatokból fennmaradt (a Magyar Geofizikai és Földtani Intézetek nem leltározott anyagából származó), javarészt igen töredékes madárfosszíliákat, olyan szintig, amit a csontok állapota megengedett. A 102 csonttöredék majdnem felét (42 darab) sikerült részben vagy teljesen azonosítani, míg a többit (amely 60 darab csonttöredék vagy lábujjpercek, karmok, mandibulák stb.) nem lehetett meghatározni. Az azonosított anyagban a lelőhelyről előzőleg már közölt és ismert taxonokat találunk, de ezek jórésze más csontokkal, illetve azok más részeivel is vannak képviselve, mint az előző publikációkban (*Palaeortyx phasianoides* Milne-Edwards, 1869, *Palaeocryptonix hungaricus* Jánossy, 1991, *Porzana † kretzoii* Kessler, 2009, *Glaucidium † baranensis* Kessler, 2010, *Apus † baranensis* Jánossy, 1977, *Lullula † minor* Kessler, 2013, *Delichon † polgardiensis* Kessler, 2013, *Riparia † major* Kessler, 2013, *Sitta † gracilis* Kessler, 2013). A csak rend, család, genus szintig azonosítottakat nem soroljuk itt fel, ezek megtalálhatóak a szövegben. A cikk szövegét egy táblakép, valamint gazdag szakirodalmi anyag egészíti ki.

Kulcsszavak: Magyarország, Polgárdi, késő-miocén, madárfauna

[1] *Department of Paleontology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c, Hungary*
[2] *University of Sopron, Faculty of Forestry, Institute of Wildlife Management and Biology, 9400 Sopron, Bajcsy-Zsilinszky utca 4., Hungary*
** corresponding author, e-mail: idahorvath03@gmail.com*

Introduction

Polgárdi is located in the western part of Hungary, in Fejér County. In the boundary of the village, there are quarries on the Somlyó and Kőszár hills at an altitude of 226 m above sea level. Tivadar Kormos published the fossil remains of sites 1 and 2 as early as 1911, while the bird material was published by Kálmán Lambrecht in 1912 and 1933 (Lambrecht 1912, 1933). In 1952, Miklós Kretzoi summarised the knowledge gained up to that time. In 1971 and 1984–85, sites 3 and 4 were discovered, and their material was described by Mathias Freudenthal and László Kordos in 1989. Finally, in 1988, site 5 became known.

Polgárdi 4 was discovered in 1984–1985 (Kordos 1991). This locality yielded a rich mammal and bird assemblage, of which both the mammal (Freudenthal & Kordos 1989) and bird fauna were published (Jánossy 1991). Polgárdi 5 was discovered in the NE part of the quarry system in 1988 (Kordos 1991) and the bird fauna was published by Dénes Jánossy in 1991 (Jánossy 1991). Previously, Jánossy reidentified from Locality 2 the carpometacarpus of *Gallus* sp.? as *Gallus aesculapi* Gaudry, 1862 (Jánossy 1976) and the complete *carpometacarpusus* of *Mergus* sp. ? as *Anas albae* Jánossy, 1979 (Jánossy 1979). The list of the bird fauna from Polgárdi 4 and Polgárdi 5 (Jánossy 1991, 1995) includes the following taxa: *Palaeocryptonix hungaricus* Jánossy, 1991; *Pavo aesculapi phasianoides* Jánossy, 1991; *Porzana estramosi veterior* Jánossy, 1991; *Rallicrex polgardiensis* Jánossy, 1991; *Otis* aff. *khosiatzkyi* Bochenski *et* Kurochkin, 1987; *Capella* sp. ? *Cursorius* sp., *Tringa* sp., *Tyto campiterrae* Jánossy, 1991; *Chaetura* aff. *baconica* Jánossy, 1977; *Motacilla* sp., *Acrocephalus* sp. I. (*'arundinaceus'*), *Acrocephalus* sp. II., *Cettia* sp., *Sylvia* sp., *Turdus* sp. ('*iliacus*'), *Luscinia* sp., Fringillidarum gen. *et* sp. indet., *Corvus* sp. (Jánossy 1991, 1995).

From the unidentified material, the author identified and published the following taxa in 2009 and 2010: *Egretta polgardiensis* Kessler, 2009 (P4); *Anas. clypeata* L. 1758 (P4, 5), Anatidae indet. (P4, 5), *Buteo* sp. (P4), *Falco* cf. *cherrug* Gray, 1834 (P4), *Falco tinnunculus atavus* Jánossy, 1972 (P5), *Palaeortyx gallica* Milne-Edwards, 1869 (P4, 5), *Palaeortyx brevipes* Milne-Edwards, 1869 (P4, 5); *Palaeortyx phasianoides* Milne-Edwards, 1869 (from *Pavo aesculapi phasianoides*) (P4, 5); Galliformes indet. (P4, 5), *Porzana estramosi* Jánossy, 1979 (P4, 5); *Porzana kretzoii* Kessler, 2009 (P4); *Rallicrex polgardensis* Kessler, 2009 (P4, 5); *Otis kalmani* Jánossy, 1972 (P4); *Calidris janossyi* Kessler, 2009 (P5); *Gallinago veterior* Jánossy, 1979 (P4); *Charadrius lambrechti* Kessler, 2009 (P4); *Limosa* sp. (P5), *Tringa* sp. (P4), *Tyto campiterrea* Jánossy, 1991 (P4); *Athene noctua veta* Jánossy, 1992 (P4); *Surnia robusta* Jánossy, 1977 (P4, 5); *Cuculus pannonicus* Kessler, 2010 (P4); *Apus baranensis* Jánossy, 1977 (P4); *Chaetura baconica* Jánossy, 1977 (P4); *Anthus* sp. (P4), *Motacilla* sp. (P5), *Parus* sp. 1, 2 (P4), *Muscicapidae* gen. *et* sp. indet. (P5), *Luscinia* sp. (P4), *Turdus* sp. (P4, 5), *Bombycilla* sp. (P4, 5), *Acrocephalus* sp. (P4), *Prunella* sp. (P4), *Troglodytes* sp. (P4), *Certhia* sp., (P4), *Sitta* sp. (P5), *Lanius* sp. 1, 2 (P5), *Corvus pliocaenus* (P5), *Corvus* sp. indet. (P4), *Miocorvus larteti*, Milne-Edwards, 1871 (P4); *Sturnus* sp. (P4), *Fringillidae* sp. (P5), *Emberizidae* sp. indet. (P5), Passeriformes indet. (P4), Aves indet. (P4, 5) (Kessler 2009a, 2009b, 2010).

From this material, the following extinct new species have been identified and are described by Eugen Kessler (Kessler 2013a, 2013b): *Alauda tivadari* 2013; *Lullula minor* 2013;

Calandrella gali 2013; *Hirundo gracilis* 2013; *Delichon polgardiensis* 2013; *Riparia minor* 2013; *Aegithalos gaspariki* 2013; *Sitta gracilis* 2013; *Tichodroma capeki* 2013; *Muscicapa miklosi* 2013; *Luscinia denesi* 2013; *Saxicola lambrechti* 2013; *Oenanthe kormosi* 2013; *Turdicus pannonicus* 2013; *Turdus miocaenicus* 2013; *Turdus polgardiensis* 2013; *Cettia janossyi* 2013; *Acrocephalus major* 2013; *Acrocephalus minor* 2013; *Hippolais veterior* 2013; *Sylvia intermedia* 2013; *Locustella kordosi* 2013; *Phylloscopus venczeli* 2013; *Anthus híri* 2013; *Motacilla intermedia* 2013; *Bombycilla brevia* 2013; *Troglodytes robustus* 2013; *Cinclus gaspariki* 2013; *Prunella freudenthali* 2013; *Lanius capeki* 2013; *Sturnus brevis* 2013; *Passer híri* 2013; *Carduelis kretzoii* 2013; *Carduelis lambrechti* 2013; *Pyrrhula gali* 2013; *Fringilla kormosi* 2013; *Emberiza pannonica* 2013; *Emberiza polgardiensis* 2013; *Plectrophenax veterior* 2013.

The species lists are complementary and suggest a very diverse and complex environment. In addition to the numerous open water species, wading birds, coastal sand, gravel but also shingle habitats, extensive grassland and woodland are indicated. A significant proportion of the new songbird species lived in wooded environments.

The as yet undetermined and uncatalogued, mostly very small and fragmentary bones located in the Hungarian Institute of Geology and Geophysics (HIGG) collection, have been identified by the authors and are published in this paper. As most of the material is highly fragmentary and not previously identified by J. (E). Kessler (Kessler 2013a, 2013b), the present study was also only able to identify a few bones or bone fragments to species level, the rest could only be identified to order, family or genus level. They can be compared with the characters and sizes of species already reported from the sites and their affiliations can be assumed.

Abrevations: HIGG – Hungarian Institute of Geology and Geophysics; † – fossil species; Q1-Q2 – Lower Pleistocene.

Anatomical terminology: after Lambrecht (1933), Baumel *et al.* (1979), Gilbert *et al.* (1981), Kessler (2013a).

Method of measurement: (after: von den Driesch 1976, Kessler 2013a). A=TL – total length; B=PL – partial length; C=Bp – breadth of the proximal end; C1=partial breadth of the proximal end; D=partial length of the proximal end; E=Sc – breadth of the corpus; E1=partial breadth of the corpus; F=Bd – breadth of the distal end; G=thickness of the distal end; H=height of the distal end.

Systematic

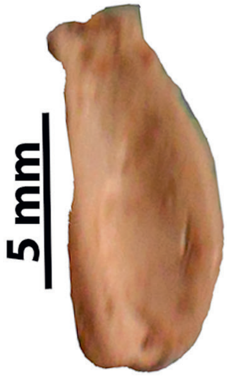
Ord. Galliformes (Temminck), 1820

Fam. Phasianidae (Vigors, 1825)

†Palaeortyx phasianoides **Milne-Edwards, 1869** / *†Palaeoperdix longipes* Milne-Edwards, 1869 / *Coturnix † longipes* Mlíkovskỳ, 2002 *(Figure 1/1)*

Site and era: Polgárdi 4 and 5, Upper Miocene (MN13)

1



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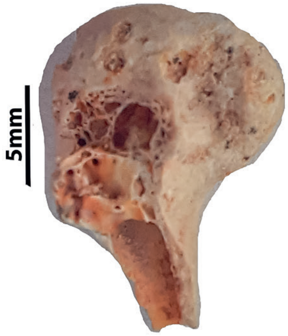

5

6

7

8

9

Material: complete juvenile *humerus* (P4); *phalanx proximalis digiti majoris* and 3 distal fragment of *tibiotarsus* (P5)

Dimensions (in mm): *humerus* A-30.82 mm; B-7.49 mm; C-7.25 mm; E-2.29 mm; F-4.44 mm; *phalanx ungularis* A-10.10 mm; C-2.64 mm; E-4.62 mm; F-3.29 mm; *tibiotarsus* (3) 3.54–4.18 mm; F-6.71–7.48 mm; G-7.23–8.84 mm. (HIGG)

Typical pheasant-like, Grey Partridge-sized bones. The *humerus* is from an underdeveloped juvenile specimen. There are no data in the literature for the wing fingertip, but its characters and dimensions are consistent with the species indicated.

Based on size, it is considered to be the largest *Palaeortyx* species (Göhlich & Mourer-Chauviré 2005).

It has been reported from numerous sites from the Late Oligocene (MP28) Desse in France, through Germany and the Czech Republic, to the Late Miocene of the Carpathian Basin. It is also known from the Late Miocene of Spain, from the Early Miocene of Litke 2 (MN5) (Kessler & Hír 2012a) and from the Late Miocene of Rudabánya (MN9) (Kessler 2009b).

***†Palaeocryptonix* (Depéret 1892)**

***†Palaeocryptonix hungaricus* Jánossy, 1991** *(Figure 1/2)*

Site and era: Polgárdi 5, Upper Miocene (MN13)

Material: 3 fragments of *coracoideum*, 3 *radius* and 2 *tibiotarsus*

Dimensions (in mm): *coracoideum* A-ap. 24.00 mm; C-3.11 mm; D-3.25 mm; E (3) -1.77–2.37 mm; F-5.12 mm; *radius* E-1.73–190 mm; F-2.93–3.39 mm; G-1.95–2.01 mm; *tibiotarsus* E-2.02 mm; F-3.02–3.19 mm; G-3.05–3.19 mm

The quail-sized endemic fossil species is known only from the Carpathian Basin: Rátka, Upper Miocene (MN12/13) (Kessler 2009b); Polgárdi 4, 5, Upper Miocene (MN13)

Figure 1. 1. *Palaeortyx phasianoides* (Milne-Edwards, 1871) – Polgárdi 5, *phalanx proximalis digit majoris* (right side, dorsal surface); 2. *Palaeocryptonix hungaricus* Jánossy, 1991 – Polgárdi 5, *coracoideum* (left side, medial aspect); 3. *Porzana kretzoii* (Kessler, 2009) – Polgárdi 5, *humerus* (fragment distal, right side, cranial aspect); 4. *Glaucidium baranensis* (Kessler, 2009) – Polgárdi 5, *humerus* (fragment proximal, left side, caudal surface); 5. *Apus baranensis* (Jánossy, 1977) – Polgárdi 5, *femur* (fragment distal, left side, caudal aspect); 6. *Lullula minor* (Kessler, 2013) – Polgárdi 5, *humerus* (distal fragment, left side, cranial aspect); 7. *Delichon polgardiensis* (Kessler, 2013) – Polgárdi 5, *ulna* (fragment proximal, left side, ventral aspect); 8. *Riparia major* (Kessler, 2013) – Polgárdi 5, *tibiotarsus* (fragment distal, left side, cranial aspect); 9. *Sitta gracilis (*Kessler, 2013) – Polgárdi 5, *tarsometatarsus* (fragment distal, left side, plantar aspect)

1. ábra 1. *Palaeortyx phasianoides* (Milne-Edwards, 1871) – Polgárdi 5, szárny ujjperc (jobboldali, dorzális nézet); 2. *Palaeocryptonix hungaricus* Jánossy, 1991 – Polgárdi 5, hollócsőrcsont (baloldali, mediális nézet); 3. *Porzana kretzoii* (Kessler, 2009) – Polgárdi 5, felkarcsont (jobboldali, disztális töredék, craniális nézet); 4. *Glaucidium baranensis* (Kessler, 2009) – Polgárdi 5, felkarcsont (baloldali, proximális töredék, caudális nézet); 5. *Apus baranensis* (Jánossy, 1977) – Polgárdi 5, combcsont (baloldali, disztális töredék, caudális nézet); 6. *Lullula minor* (Kessler, 2013) – Polgárdi 5, felkarcsont (baloldali, disztális töredék, craniális nézet); 7. *Delichon polgardiensis* (Kessler, 2013) – Polgárdi 5, *singcsont* (baloldali, proximális töredék, ventrális nézet); 8. *Riparia major* (Kessler, 2013) – Polgárdi 5, lábszárcsont (baloldali, disztális töredék, craniális nézet); 9. *Sitta gracilis* (Kessler, 2013) – Polgárdi 5, csüd (baloldali, disztális töredék, plantáris nézet)

(Jánossy 1991, 1995); Beremend 26, Lower Pliocene (MN15) (Kessler 2009b), Beremend 17, 18; Lower Pleistocene (Q1) (Jánossy 1992, 1996).

J. Mlíkovskỳ (2002) places it in the taxon *Alectoris † donnezani* (Deperet, 1892), while Zelenkov places it in the new taxon *† Eurobambusicola turolicus* (Zelenkov 2016), but we doubt this. No records from other localities than those mentioned above.

Ord. Ralliformes (Reichenbach, 1852)
Family. Rallidae (Vigors, 1825)
***Porzana † kretzoii* Kessler, 2009** *(Figure 1/3)*
Site and era: Polgárdi 4 and 5, Upper Miocene (MN13)
Material: fragments of *humerus* (P5), *femur* (P5), 2 *tibiotarsus* (P4 and P5)
Dimensions (in mm): *humerus* E-2.33 mm; F-3.80 mm; G-2.26 mm; *femur* E-1.83 mm; F-3.93 mm; G-3.17; *tibiotarsus* E-1.68–1.96 mm; F-3.34–3.53 mm; G-2.97–3.03 mm

Smaller than the smallest extant species. It was already indicated from other skeletal parts in Polgárdi 4 and 5, from where it was described (Kessler 2009b). Two other fossil species are known from the Carpathian Basin: *Porzana † estramosi* Jánossy, 1979 [Mátraszőlős 1, Middle Miocene (MN7/8) (Gál *et al.* 1998–1999); Polgárdi 4, 5, Late Miocene (MN13) (Jánossy 1991, Kessler 2009b); Osztramos 9, Early Pliocene (MN15) (Jánossy 1979a, 1979b)] and *Porzana † matraensis* Kessler, 2009 [described from the Middle Miocene of Mátraszőlős 1 (Kessler 2009b)].

The three extinct species are known only from the Carpathian Basin. Crakes are rare in Neogene fossils. Their most recent records (*Porzana porzana* Linneaus, 1758, and *Porzana* sp.) are known outside the Carpathian Basin from the Pliocene-Pleistocene boundary (MN17/18) at Mallorca in Spain (Sondaar *et al.* 1995), Vǎršec in Bulgaria (Boev 1996), Voigstedt in Austria (Jánossy 1965) and Stránská skála (Q2) in the Early Pleistocene of the Czech Republic (Jánossy 1972, Mlíkovskỳ 1995).

Ord. Charadriiformes (Huxley, 1867)
Fam. Charadriidae (Bonaparte, 1831)
Charadriidae gen. *et* sp. indet.
Site and era: Polgárdi 4, Upper Miocene (MN13)
Material: distal fragment of *carpometacarpus*
Dimensions (in mm): E-2.52 mm; E1-1.61 mm; F-2.04 mm

This extremely distinctive distal fragment allows identification only to the family level, but its dimensions are most suggestive of the *Charadrius* genus. From the Late Miocene of Polgárdi 4 (MN13), a nearly intact right *coracoid* bone has been described (Kessler 2009b) as *Charadrius lambrechti* Kessler, 2009. Presumably, the present remains may belong to this fossil species, but this cannot be stated with certainty.

The *Charadrius* genus was known only from the Late Pliocene (MN16) onwards. The species *Charadrius morinellus* extant is mentioned by Jánossy from Rebielice, Poland (Jánossy 1974) and from Stránská skála (Q2) in the Early Pleistocene of the Czech Republic (Jánossy 1972), while *Charadrius* sp. from Beremend 15 (MN16) (Jánossy 1987), the latter possibly belonging to the extinct species.

Ord. Columbiformes (Latham, 1790)
Columbidae (Illiger, 1811)
Columbidae gen. *et* sp. indet.
Site and era: Polgárdi 5, Upper Miocene (MN13)
Material: distal fragment of *tibiotarsus*
Dimensions (in mm): E-2.14mm; F-3.01 mm; G-3.19 mm

A fragment of the size of the extant *Streptopelia turtur* species size can only be identified to family level.

Representatives of the family are known only from the Early Pliocene throughout Europe. The oldest are *Columba omnisanctorum* Ballmann 1976 and *C. pisana* (Portis, 1889) from the Early and Middle Pliocene of Italy (MN14/15, MN15/16) (Portis 1889, Ballmann 1976).

Ord. Strigiformes (Wagler, 1830)
Fam. Strigidae (Leach, 1820)
***Glaucidium* Boie, 1826**
***Glaucidium † baranensis* Kessler, 2010** *(Figure 1/4)*
Site and era: Polgárdi 5, Upper Miocene (MN13)
Material: proximal fragment of *humerus*
Dimensions (in mm): C-8.47 mm; D-8.40 mm

The fossil species has been described from the Early Pliocene (MN15) of Csarnóta 2 and Beremend 26 (Kessler 2009b), including a proximal epiphysis of *humerus*.

It is a species of owl largely matching the size and character of the extant Pygmy Owl *(Glaucidium passerinum)*, which may have been the ancestor of the recens species in Europe and thus, also in the Carpathian Basin. On the proximal epiphysis of the *humerus*, the *crista bicipitalis* is more articulated, the *crus dorsale fossae* is more elongated and the *tuberculum ventrale* is blurred.

From outside the Carpathian Basin, Jánossy (1974) reports another *Glaucidium* sp. from the Late Pliocene of Rebielice (Poland (MN16)), otherwise only the extant species is known in fossil material from the Early Pleistocene onwards. The genus is known from only one Late Pliocene site in Florida (USA) (Inglis, Cytrus County, Florida) with one described species: *G. explorator* Emslie, 1998, with numerous skeletal parts, but only a fragmentary *proximal humerus*, corresponding to the size of the extant *G. brasilianum*. A *tibiotarsus* from the same material, with dimensions similar to those of extant *G. minutissimum* is also reported but only defined to genus level (Emslie 1998). An extinct species described from the Pleistocene of the Bahamas as *G. dickinsoni* Brodkorb, 1959, an extinct species of *tibiotarsus*, was subsequently (Olson 1985) synonymized with the recurrent species *Speotyto cunicularia* (Mollina, 1782). The ancestor of the Pygmy Owl was already present in the Eocene. It has been described from the Middle Eocene of Geiseltal in Germany from several *humerus* specimens under the name *Eoglaucidium pallas* Fischer, 1987 and is also indicated from the Middle Eocene of Messel, also in Germany (Fischer 1987, Mayr & Peters 1998, Mlíkovskỳ 2002).

Ord. Apodiformes (Peters, 1940)
Fam. Apodidae (Olphe – Galliard, 1887)

***Apus* Scopoli, 1777**

***Apus † baranensis* Jánossy, 1977 /? *Apus † wetmorei* Ballmann, 1976** *(Figure 1/5)*

Site and era: Polgárdi 5, Upper Miocene (MN13)

Material: distal fragment of *femur*

Dimensions (in mm): E-1.74 mm; F-4.29 mm; G-2.00 mm

Fossil species from Polgárdi 4, Upper Miocene (MN13) (Kessler 2010); Csarnóta 2, Lower Pliocene (MN15) (Kessler 2010); Beremend 5 (Jánossy 1977); Osztramos 20 (Kessler 2010); Upper Pliocene (MN16).

Typical swift-shaped, but smaller fossil species than the extant species. Mlíkovskỳ (2002) assigns it to the species *Apus wetmorei* Ballmann 1976 described from the Late Pliocene in Italy (Chiro 24, MN14/15) on the basis of its size. The bones subsequently identified from Csarnóta 2 (MN15), but mainly from Polgardi (MN13), suggest a species even smaller than the Italian one and even earlier in age. In our opinion, they are not identical species.

The genus is known from Europe only from the Middle Miocene of France (*Apus gaillardi* Ennouchi, 1930 – Grive-Saint-Alban, MN7/8). The extant species are known only from the Early Pleistocene (Czech Republic-Stránská skála, Q2).

Ord. Passeriformes (Linnaeus, 1758)

Family. Alaudidae (Vigors, 1825)

***Lullula † minor* Kessler, 2013** *(Figure 1/6)*

Site and era: Polgárdi 5, Upper Miocene (MN13)

Material: distal fragment of *humerus*

Dimensions (in mm): E-1.41 mm; F-3.51 mm; G-1.91 mm

The fossil species is also described from Polgárdi 4 and 5 (whole *ulna*, distal *humerus* and *tarsometatarsus* fragment) and corresponds in size with *Lullula minor* (Kessler 2013a, 2013b).

Three other fossil *Lullula* species have been described from the Carpathian Basin. *Lullula † neogradensis* Kessler *et* Hír, 2012 – from the Middle Miocene of Mátraszőlős 1 (MN7/8), *Lullula † parva* Kessler, 2013 – from the Early Pliocene of Csarnóta 2 and Beremend 26 (MN15), and – *Lullula † minuscula* Kessler, 2013 from the Early Pliocene of Beremend 26 (MN15). The first is much older, the second is larger and the third is smaller in size (Kessler 2013a, 2013b).

The genus is known from areas outside the Carpathian Basin through *Lullula* sp. from the Late Miocene (Boev 1996), the Late Pliocene (MN17) of Văršec and Slivnica (Boev 2000), also in Bulgaria as *Lullula slivnicensis* Boev, 2012 and *L. balcanica* Boev, 2012 (Boev 2012). An extant species has been reported from the island of Mallorca, Spain, from Late Pliocene – Early Pleistocene (MN18) material (Sondaar *et al*. 1995).

Alaudidae sp. indet.

Site and era: Polgárdi 4 and 5, Upper Miocene (MN13)

Material: 2 proximal and 2 distal fragments of *humerus* (P5), and distal fragment of *tibiotarsus* (P4)

Dimensions (in mm): *humerus* C-4.38–5.51 mm; D-5.03 mm; F-3.65–4.48 mm; G-2.23–2.37 mm; *tibiotarsus* E-1.44 mm; F-2.46–2.42 mm

Fragments could only be identified up to family level.

Fam. Hirundinidae (Vigors, 1825)

Delichon (Moore, 1854)

Delichon † polgardiensis Kessler, 2013 *(Figure 1/7)*

Site and era: Polgárdi 5, Upper Miocene (MN13)
Material: proximal fragment of *ulna*
Dimensions (in mm): C-2.32 mm; D-2.46 mm; E-1.48 mm

Species also described from Polgárdi 5 but from distal fragment of *ulna* and complete *coracoideum*.

Two other fossil species are known from the Carpathian Basin: *Delichon † pusillus* Kessler, 2013 from the Early Pliocene of Csarnóta 2 (MN15) and *Delichon † major* Kessler, 2013 from the Early Pliocene of Beremend 26 (MN15) (Kessler 2013a, 2013b).

The genus is known from areas outside the Carpathian Basin only from the Early Pleistocene (Q1), from sites in Quibas, Spain (Montoya *et al.* 1999) and Stránská skála, Czech Republic (Mlíkovskỳ 1995).

Riparia (Forster, 1817)

Riparia † major Kessler, 2013 *(Figure 1/8)*

Site and era: Polgárdi 5, Upper Miocene (MN13)
Material: distal fragment of *tibiotarsus* (5)
Dimensions (in mm): E-0.91–1.09 mm; F-1.96–2.21 mm; G-2.03–2.27 mm

The fossil species was determined from Polgárdi 4, but from other skeletal parts. The dimensions of the present material are larger than those of the extant species.

The genus is known with the extant species only from the Early Pleistocene (Q1), in the Romanian Betfia 9 (Gál 2002) and from Stránská skála (Mlíkovskỳ 1995) in the Czech Republic.

Fam. Sittidae (Bonaparte, 1831)

Sitta Linnaeus, 1758

Sitta † gracilis Kessler, 2013 *(Figure 1/9)*

Site and era: Polgárdi 5, Upper Miocene (MN13)
Material: distal fragment of *tarsometatarsus*
Dimensions (in mm): E-1.59 mm

The fossil species was described from Polgárdi 4, but from a proximal fragment of a *metacarpal* bone (Kessler 2013a, 2013b).

The extremely small fragment is broken off in *trochlea* II, so the anatomically deep incision on *trochlea* III, the shape of *trochlea* IV and the location and shape of the tubercle on the dorsal aspect of the margo above helped to determine the definition.

Sitta † pusilla Kessler, 2013 (Csarnóta 2) and *Sitta † villanyensis* Kessler, 2013 (Beremend 26) are also known from the Early Pliocene of the Carpathian Basin (MN15).

The genus is known from areas outside the Carpathian Basin from the Late Pliocene I of Rebielice Królowskie, Poland (Jánossy 1974). From the Late Miocene of Senigallia in Italy (MN13), described in *Sitta senigalliensis* Portis 1887, an extinct species, is placed by Mlíkovskỳ (2002) in the ‚Family incertae sedis'.

Fam. Muscicapidae (Vigors, 1825)

***Erithacus* (Cuvier, 1801)**

***Erithacus* sp. indet.**

Site and era: Polgárdi 5, Upper Miocene (MN13)

Material: distal fragment of *ulna*

Dimensions (in mm): E-1.33 mm; F-2.55 mm; G-1.88 mm

Characteristics and dimensions allowed identification only up to genus level. The known extinct species from the Carpathian Basin differ in age and are described from different types of skeletal parts. These are *Erithacus † horusitskyi* Kessler *et* Hír, 2012 – Mátraszőlős 1, Middle Miocene (MN7/8) and *Erithacus † minor* Kessler, 2013 – Beremend 26, Lower Pliocene (MN15) (Kessler & Hír 2012, Kessler 2013a, 2013b).

The genus recens has been annotated with the recens species from the Early Pleistocene of Spain and the Middle Pleistocene of France, Israel, the United Kingdom and Italy (Tyrberg 1998).

Muscicapidae gen. *et* sp. indet.

Site and era: Polgárdi 5, Upper Miocene (MN13)

Material: distal fragment of *tarsometatarsus*

Dimensions (in mm): F-2.78 mm; G-2.20 mm

The condition of the fragment only allows identification down to the family level.

Fam. Turdidae (Rafinesque, 1815)

***Turdus* (Linnaeus, 1758)**

***Turdus* sp. indet.**

Site and era: Polgárdi 5, Upper Miocene (MN13)

Material: distal fragment of *femur*

Dimensions (in mm): E-2.15 mm; F-3.80 mm; G-3.16 mm

The dimensions of the bone fragment suggest the smallest species of thrush, but as there are no *femur* remains in many Carpathian Basin fossil species, it was not possible to identify the find to species level.

The following fossil thrush species are known from the Carpathian Basin: *Turdus † miocaenicus* Kessler, 2013 and *Turdus † polgardiensis* Kessler, 2013 – from the Later Miocene of Polgárdi 5 (MN13); *Turdus † major* Kessler, 2013, *Turdus † medius* Kessler, 2012 and *Turdus † minor* Kessler, 2013 – from the Early Pliocene of Csarnóta 2 and Beremend 26 (MN15).

The earliest known indication of the genus is from the Middle Miocene of Credinta, Romania (MN8), under the name *Turdus* sp. (Gál & Kessler 2006), while from the Late Pliocene it is from the sites Rebielice Królowskie I in Poland (Jánossy 1974), Vǎršec in Bulgaria (Boev 2000), Sandalja I in Croatia (V. Malez-Bačić 1979). From the Early Pleistocene onwards, the number of known sites multiplies throughout Europe (Austria, Bulgaria, Czech Republic, France, Germany, Romania, Spain, etc.) (Tyrberg 1998).

Fam. Sylviidae (Vigors, 1825)
Sylviidae gen. *et* sp. indet.
Site and age: Polgárdi 5, Upper Miocene (MN13)
Material: distal fragment of *femur*
Dimensions (in mm): E-1.44 mm; F-3.14 mm; G-2.01 mm

The condition of the fragment only allows identification down to the family level.

Fam. Fringillidae (Leach, 1820)
Fringillidae gen. *et* sp. indet
Site and era: Polgárdi 5, late Miocene (MN13)
Material: 4 distal fragments of *tibiotarsus*
Dimensions (in mm): E-0.89–2.22 mm; F-1.88–2.72 mm; G-1.59–2.23 mm

With few exceptions, the songbirds' beaks are not particularly suitable for genus and species identification. The specimens in the present material also vary considerably in size but morphologically show no particular differences. Thus, the condition of the fragments allows only identification down to the family level.

Conclusions

The examination of bones and bone fragments has resulted in the identification of about half of the remains to at least the level of order, in accordance with the nature of the fossil material. The two sites in question are close to each other both in age and geographic location. The vast majority of the bones are white, in keeping with the medium, but there are also some almost black specimens. There are few completely intact skeletal remains, and most of these are found in the remains of waterfowl.

The faunal assemblage corresponds to that reported in previous studies from a palaeoecological point of view. The bird fauna of both wetlands, open and wooded areas and rock faces is represented in the fossil material.

As the majority of species are of small size, only the small-medium sized patridges are represented, indicating the size of the predators. The Pygmy Owl also represents these birds of prey. Diurnal raptors are not included in the faunistics list of the new material.

In conclusion, the finds from the Upper Miocene of Polgárdi are a good representation of the former bird life in the western part of the Carpathian Basin.

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Drone monitoring improves nest detection of Squacco Herons *Ardeola ralloides*, but fails to assess its productivity

Roberto G. Valle[1*], Alejandro Corregidor-Castro[2], Emiliano Verza[3] & Francesco Scarton[4]

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Abstract In the last decade, the use of drones has proven to be the major innovation for studying various aspects of waterbird breeding biology, overcoming the environmental obstacles inherent in monitoring their breeding sites. The Squacco Heron *(Ardeola ralloides)* represents an example of the aforementioned difficulties, since it nests in impenetrable reed beds and nearby bushes, trees and shrubs. The present work reports the results of drone assessment of nest counting and reproductive success of the Squacco Heron in a colony in the Po Delta (NE Italy). At the beginning of the breeding season, far more nests (46) were found using drones than by eye from the nearest embankment (12). After four weeks (estimated hatching period), only ten nests were relocated by drone, due to vegetation overgrowth. All relocated nests were placed directly either within reed beds or on lower branches of shrubs, but always without higher branches obstructing the view from above. Finally, in the fledging period, no nest was relocated on drone imagery, due to further vegetation growth. Only 27 juveniles were found by drone, mostly perching on the canopy, without any evidence of nest failure, suggesting a critical underestimation. In conclusion, drone use improves accuracy of counting nesting Squacco Herons, but fails to assess productivity.

Keywords: counting, disturbance, drone monitoring, productivity, Squacco Heron

Összefoglalás Az elmúlt évtizedben a drónok használata bizonyult a fő innovációnak a vízimadarak költésbiológiája különböző aspektusainak tanulmányozásában, leküzdve a fészkelőhelyeik megfigyelésében rejlő környezeti akadályokat. A selyemgém *(Ardeola ralloides)* a fent említett nehézségek egyik példája, mivel áthatolhatatlan nádasokban és az azokban levő bokrokon, fákon fészkel. Jelen munka a Pó-deltában (Észak-Olaszország) található kolóniában a selyemgém fészekszámlálása és szaporodási sikere drónvizsgálatának eredményeiről számol be. A költési időszak elején jóval több fészket (46) találtak drónok segítségével, mint a legközelebbi töltésről megfigyelve (12). Négy hét (becsült kelési időszak) után csak tíz fészek volt azonosítható a drónok által a növényzet túlburjánzása miatt. Valamennyi újra megtalált fészek közvetlenül a nádasban vagy a cserjék alacsonyabb ágain helyezkedett el, mindig anélkül, hogy a magasabb ágak akadályoznák a rálátást felülről. Végül a kirepülési időszakban a drónfelvételeken egyetlen fészket sem került azonosítani a növényzet további növekedése miatt. Csak 27 fiatal madarat találtak drónnal, többnyire a lombkoronában állva, anélkül, hogy a fészek meghibásodására utaló bizonyítékot észleltek volna, ami jelentős alulbecslésre utal. Összefoglalva, a drónok használata javítja a fészkelő selyemgémek számlálásának pontosságát, de nem tudja felmérni a költési sikert.

Kulcsszavak: számlálás, zavarás, drón megfigyelés, termékenység, selyemgém

[1] *Rialto 571, San Polo, I-30125 Venice, Italy*
[2] *Department of Biology, University of Padova, Via U. Bassi 58/B, I-35131 Padova, Italy*
[3] *Via Cairoli 38, I-45100 Rovigo, Italy*
[4] *Via Franchetti 192, I-31022 Preganziol (TV), Italy*
** corresponding author, e-mail: robertovalle@libero.it*

Introduction

Long-term monitoring of breeding birds is fundamental to understand the health status of the ecosystem they thrive in (Şekercioğlu *et al.* 2004). Aerial surveys have long been used for studying breeding waterbirds, which frequently nest in areas characterized by scarce accessibility and/or huge extension, both in the past using fixed-wing aircraft (Henny *et al*. 1972) and in recent times with drones (Mulero-Pázmány *et al*. 2017). Drones overcome the limitations of traditional fixed-wing aircraft surveys, which are expensive and often impractical, thus being restricted to professional ornithologists or academic researchers and even dangerous (Sasse 2003).

Growing evidence is showing the extraordinary capabilities of drones in the study of reproductive biology and in particular various aspects of breeding success of birds (Junda *et al.* 2015, Weissensteiner *et al.* 2015, Gallego & Sarasola 2021). This is particularly true for waterbirds, as drones have proven to be as (and in some cases even more) accurate as traditional ground-based approaches (Dundas *et al.* 2021, Valle & Scarton 2021), while reducing the disturbance caused in the breeding grounds (Brisson-Curadeau *et al.* 2017, Sardà-Palomera *et al.* 2017, Valle & Scarton 2019a).

In addition, one issue that drones have shown to solve is related to the accessibility of the monitoring areas. One of the main inherent obstacles in monitoring waterbirds is the presence of nests in environmental settings that make traditional land or boat access difficult, if not impossible (Scarton & Valle 2020). Several studies have shown the possibilities of monitoring in inaccessible areas (Afán *et al.* 2018, Scarton & Valle 2020, Dundas *et al.* 2021, Dunn *et al.* 2021). However, the enthusiasm for the results obtained with the use of drones can overshadow the limitations of the method, which have been highlighted by some recent works (Afán *et al.* 2018, Valle & Scarton 2020), in particular when vegetation cover is high (McKellar *et al.* 2021). It is therefore fundamental to test the drone approach on as many species and environmental contexts as possible, in order to assess methodological constraints.

The Squacco Heron *(Ardeola ralloides)* is a marsh dwelling waterbird found in fresh water habitat with abundant marsh vegetation, mainly reed beds and nearby bushes, trees and shrubs. Because their nests are typically built in dense thickets of trees or shrubs frequently placed less than two meters above water level (AWL) within single- or mixed-species colonies (del Hoyo *et al.* 1992, Kushlan & Hancock 2005), it represents an optimal example of species breeding in a difficult monitoring area. In Europe, the Squacco Heron is present with about 15,000–25,900 nesting pairs (BirdLife International 2022). In Italy, where the species presents a conservation status of near threatened (BirdLife International 2022), the breeding population is concentrated in the inner and coastal Po Plain, mainly in the western part (Brichetti & Fracasso 2018), with the most recent estimates giving a figure of 314–461 pairs (Ercole *et al.* 2021). In the eastern Po Plain, the species is scarce; for instance, in the Veneto region only 27–29 pairs were censused in 2020 (Verza *et al.* 2021).

In 2021, the establishment of a fair-sized colony of Squacco Heron in a floodplain of the northern Po Delta (NE Italy) offered the opportunity to test the possibility of studying the breeding biology of the species using drones. The present work reports the results of drone assessment of nest counting and reproductive success measurement of the Squacco Heron, quantifying disturbance to breeders as a secondary endpoint.

Materials and Methods

Study Site

Fieldwork was conducted during the 2021 breeding season, in a heronry of the Po Delta along the northern Adriatic coastline within the framework of a broader project aimed at monitoring the breeding species of herons (Verza *et al.* 2021). We counted nests of Squacco Heron in a mixed colony of Ardeidae (Cattle Egret *Bubulcus ibis*, Little Egret *Egretta garzetta*, Night Heron *Nycticorax nycticorax*, Purple Heron *Ardea purpurea*) and Pygmy Cormorant *(Microcarbo pygmaeus)* for overall 591 nests located on a 0.14 ha muddy islet on a floodplain of the Po di Maistra river (44°58’34.21” N, 12°20’18.19”E). The islet was covered with small trees of false indigo-bush *Amorpha fruticosa* with a maximum height of 3.5 m, surrounded by a strip of common reed *Phragmites australis*. It laid 60 m from the western river embankment, thus being clearly visible from the latter *(Figure 1)*. The islet was virtually inaccessible: it was a few centimeters above the water level and made of soft mud, being surrounded by a large, shallow (<10 cm) waterbody with very soft bottom.

Field procedures

In total, we conducted eight weekly surveys. In order to compare accuracy between traditional (i.e. by eye) and drone methods, we conducted paired surveys from the nearest embankment on the first two visits in mid May, when surveys were conducted alternating the order of the methods to avoid observer-bias or other influences in disturbance. We considered drone counts as ground truth due to its high accuracy in nest detection, as previously shown in several studies (Chabot *et al.* 2015, Hodgson *et al.* 2016, Pöysä *et al.* 2018, Valle & Scarton 2022). Nests were mapped on a drone image of the colony *(Figure 1)* to be checked at subsequent visits. Then, nests were checked weekly from early May to late June and then on mid-July exclusively using drones in order to assess hatching and fledging success respectively. We used a small off the shelf drone (DJI Mini2), with the following parameters: weight 249 g, maximum speed 35 mph (56 km/h), flight time 31 min, sensor 1/2.3″, lens 24 m, f/2.8, 4K camera. No ground surveys within the colony were conducted in order to avoid disturbance to the incubating birds that could ultimately lead to abandonment or even colony failure. Nests were searched and monitored flying at elevations of 15 m above ground level (AGL), which have been shown to be higher than the agitation distance (i.e. adults opening wings to cover eggs and/or newly hatched chicks in response drone intrusions) for the species (Valle & Scarton 2018). According to current recommendations (Hodgson & Koh 2016, Valle & Scarton 2018), the drone was launched at least at 150 m

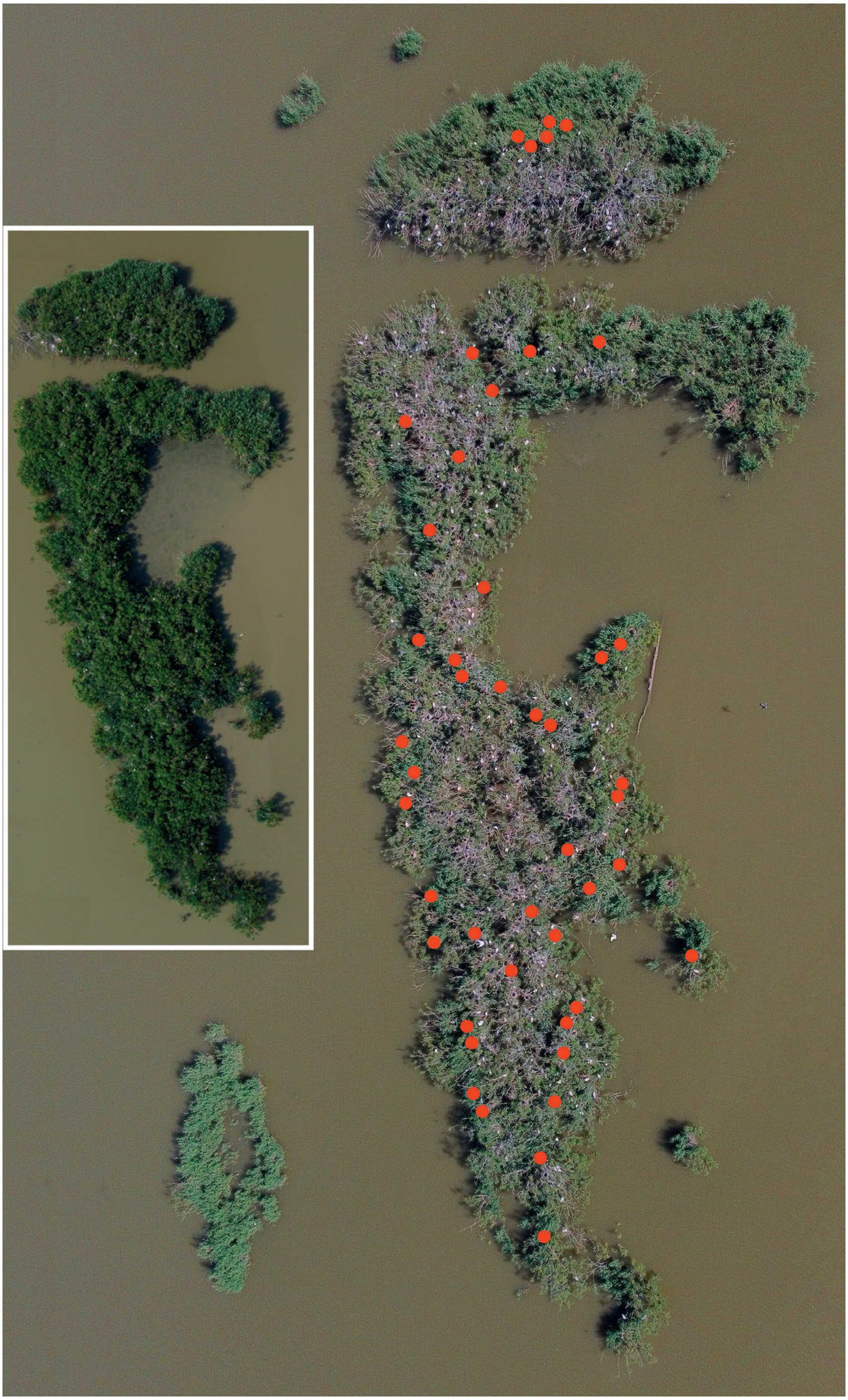

Figure 1. Study site (Po Delta – NE Italy, breeding season 2021). Orange circles indicates nests of Squacco Heron. A clear preference for placing nests in reed beds, rather than in shrubs, is evident. Left inset shows vegetation overgrowth in mid-June

1. ábra Vizsgálati hely (Pó-delta – ÉK Olaszország, költési szezon 2021). A narancssárga körök a selyemgémek fészkeit jelzik. Nyilvánvaló, hogy a fészket inkább a nádasba építik, nem a bokrokra. A bal oldali bevágás a növényzet túlnövekedését mutatja június közepén

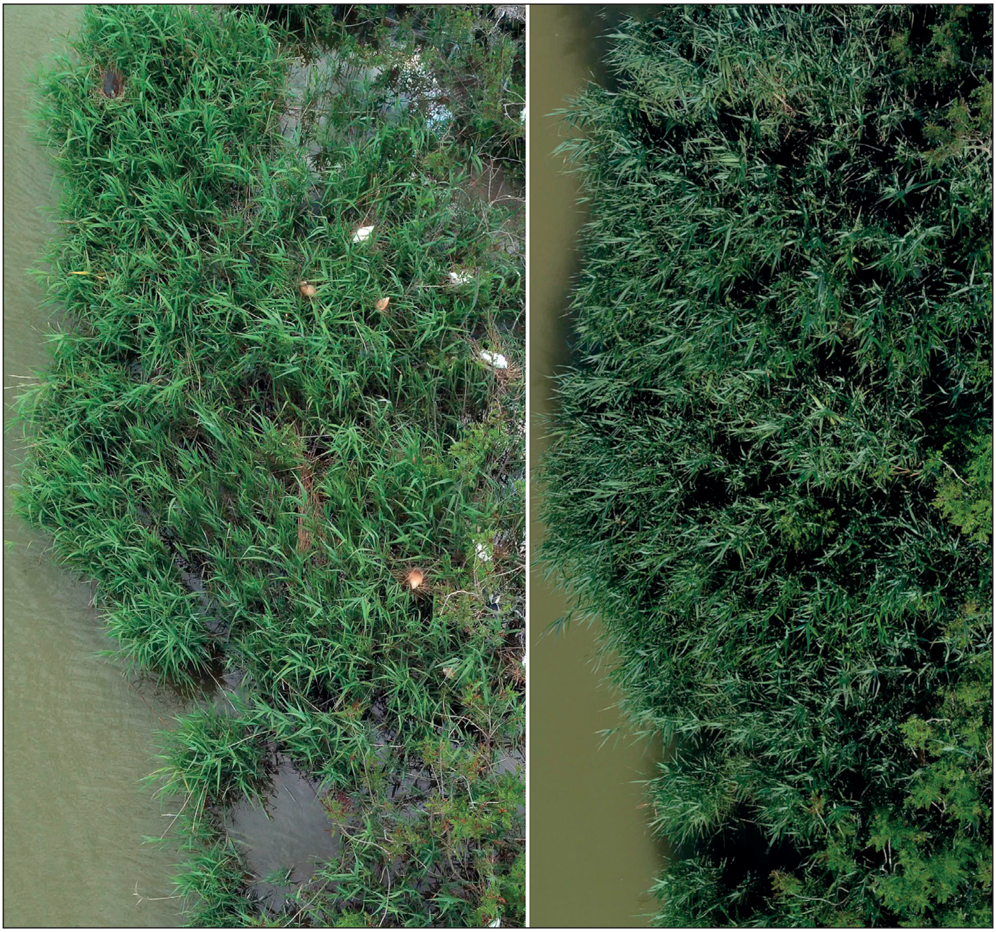

Figure 2. Comparison between mid-May (laying period; left panel) and mid-June 2021 (hatching period; right panel) of a subset of a colony of Squacco Herons, showing the impossibility of relocating nests due to vegetation overgrowth on drone imagery

2. ábra A selyemgém kolónia egy részének május közepén (a tojásrakás időszaka; bal oldali panel) és június közepén (kelési időszak; jobb oldali panel) végzett összehasonlítása azt mutatja, hogy a drónok képén a növényzet túlnövekedése miatt nem lehet azonosítani a fészkeket

from the colony, in order to minimize disturbance to birds. The drone reached the vertical point of the colony (where nest attendance was registered) following a lawn-mower flight pattern, flying 70 m AGL. Then, the drone was slowly driven to an altitude of 15 m AGL, allowing for incubating birds to be clearly detected upon post-processing *(Figure 2)* and it slowly flew over the colony at a speed of 2–5 km/h. During each drone flight, an assistant researcher observed the colony from afar to exclude possible predation of unattended clutches and/or chicks by possible predators.

Disturbance was calculated as a function of the number of incubating birds flew away during the surveys because of census activities (i.e. birds moving/flying away after showing alert behavior) (Valle & Scarton 2022).

Figure 3. Nests of Squacco Heron in a mixed-species heronry (Po Delta, NE Italy in 2021)
3. ábra A selyemgém fészkek egy vegyes fajösszetételű gémtelepen a Pó-deltában (Észak-Olaszország) 2021-ben

Image Processing

In the post-processing phase, individual nests were assigned a number and counts were performed by two observers on a personal computer using DotDotGoose's count tool v. 1.3.0 (https://biodiversityinformatics.amnh.org/open_source/dotdotgoose/) on images directly

Figure 4. Drone view of a juvenile Squacco Heron perching on a shrub in a mixed-species heronry (Po Delta, NE Italy in late June 2021.)

4. ábra Drónos felvétel egy vegyes fajösszetételű gémtelepen bokron álló fiatal selyemgémről (Pó-delta, Észak-Olaszország 2021 június vége)

shot in the field or selected frames obtained from videos automatically stitched together using ICE (Microsoft's Image Composite Editor, release 2.0; www.microsoft. com); a grid was overlaid on all images and we performed a systematic counts of nests, grid cell-by-grid cell (Valle 2022).

Statistics

Categorical data are presented as percentages. Whereas we calculated the agreement between counts of nests by eye from embankments and on drone imagery, using the latter as ground truth, we did not try to compare the two methods for assessing either hatching or fledging success, due to problems of vegetation overgrowth (Valle & Scarton 2018).

Results

At the beginning of the breeding season, 46 and 12 nests were detected using drone and by eye from the embankment, respectively *(Figures 1, 2)*. These findings allow to ascribe a poor detection rate (agreement: 26%) to traditional counts of the species. Counts by eye found only the shrub nests located over the higher edge of reeds, whereas the remaining were concealed by dense vegetation that precluded their identification by observers.

Early in the season, both “high” (on shrub branches) and “low” (within reeds) nests are visible in the drone image *(Figure 2)*.

After four weeks (estimated hatching period, Heron Conservation 2022), only ten nests were relocated (among which in one case two chicks were visible), due to vegetation overgrowth *(Figure 2, 3)*. All relocated nests were placed directly either within the reed bed or on lower branches of shrubs, but always without higher branches obstructing the view from above.

Finally, in the fledging period, no nest was relocated due to further vegetation growth (sensitivity was 0%), but 27 juveniles were found, most perching on the canopy, except for two which were seen among reeds *(Figure 4)*.

As an aside, we mention that among the five more Ardeidae species, which bred in the study area, colony detectability markedly decreased across the breeding period for all the species, though at a variable extent among species, except for Purple Herons, which kept being easily detectable.

Disturbance due to drone surveys was negligible, birds being apparently unaffected by the overflying drone, though latent effects cannot be excluded. Nonetheless, no birds flew away during close-up drone inspections.

Discussion

The main result of our work is that drone monitoring allows accurate nest counts of an elusive species such as the Squacco Heron. Accuracy of counts is critical for population studies, since excess estimates may delay needed conservation actions, while in contrast, underestimation may divert resources from other truly endangered species (Thompson 2002). In the present study, drone use provided reliable counts of nesting Squacco Heron, showing a severe underestimation provided by eye counts from the nearest embankment. On the contrary, drone surveys failed to accurately assess both hatching and fledging success of Squacco Herons due to vegetation overgrowth.

Derived accurate counts of nests in our colony allowed to adjust the population estimate to more than triple the number of pairs previously thought to be present in the whole Po Delta in 2021: from 14–19 pairs (estimated using traditional methods) to 50–57 pairs (this work). This is in accordance with previous studies reporting an increase of similar magnitude in the breeding population of Purple Herons using drone rather than ground surveys (Verza *et al.* 2021, Valle & Scarton 2022).

The fact that almost four times (46 vs. 12) more nests were detected when conducting our drone surveys clearly indicates a strong underestimation due to byeye monitoring from vantage points. This finding is in agreement with those of Barbraud *et al.* (2004), who showed that a relevant underestimation (from 33 to 50%) can occur if only one observer counts nests, without taking into account the detection probability, which could be due to a number of factors: i) the low nest detection probability for this species (Barbraud *et al.* 2004), which is worsened by its asynchronous nesting period (Hafner 1978, Delord *et al.* 2003); ii) the necessity to limit the disturbance in the nesting areas, which are frequently difficult to access; and iii) the habit of the species to build small nests at little height from the ground or from the water in thickly vegetated areas. These factors make the accurate assessment of the nesting population of Squacco Heron in a colony complex, leading to nest miscount and a consequent population underestimation (Hafner 1978). Nevertheless, serial measurement of a species' breeding population is an inescapable tool for understanding its trend, which in turn is a prerequisite for implementing conservation measures, if and when needed (Carter *et al.* 2000, Thompson 2002). Drone surveys can overcome this problem. The introduction of low cost drones in the market equipped with good quality optics of small size allows entering the colonies with minimal disturbance, if any (Sardà-Palomera *et al.* 2017, Valle & Scarton 2022). A drone with these characteristics, even in low altitude surveys aimed to increase individual detectability (Corregidor-Castro *et al.* 2021), flying at low pace (10 km/h), without stopping and hovering at a precise point is often tolerated without obvious reactions from Squacco Herons, but also from the coexisting species.

In recent years, evidence on the superiority of drone monitoring in terms of accuracy and precision for counting breeding waterbirds has been numerous and nearly unequivocal. Gulls, terns, flamingos, and grebes were reported to have been counted faster and frequently better in term of accuracy and precision using drones in comparison to traditional ground counts (Hodgson *et al.* 2018, Lachman *et al.* 2020, McKellar *et al.* 2021, Valle 2022.). More controversial is the question when considering sites where vegetation occludes nests causing low detection probabilities on UAV (unoccupied aerial vehicles)-derived photographic surveys (but also on by eye monitoring). This particularly applies to herons, and more generally to Pelecaniformes, in relation to the frequent high vegetation cover of the sites usually selected by these species for nesting. Our data showed that drones are inaccurate for counting heron nests in highly vegetated habitat even when vegetation overgrowth occurs after nest location early in the season, due to obstruction of the view from above. These findings add weight to previous research, which showed that vegetation overgrowth impairs an effective use of drones in the study of the breeding biology of waterbirds (Barr *et al.* 2018). Recently, detection rates for Purple Herons nesting on reed beds using drones were reported decreasing (even if slightly) across the season, due to vegetation overgrowth, which prevents nest from being visualized (Valle & Scarton 2018).

Disturbance to breeders in response to drone intruding in colonies is a highly debated topic (Burger & Gochfeld 2009, Mulero-Pàzmàny *et al.* 2017). Colonial waterbirds were reported to abandon colonies under high disturbance pressures. In particular, a catastrophic, massive nest desertion has reported for a large (1,500 pairs) colony of Elegant Terns *(Thalasseus elegans)* after a drone crash in the colony area (www.audubon.org). In addition, in other breeding area a scarce tolerance to drone surveys was reported for Great White Egrets (Collins *et al.* 2019). At the best of our knowledge, there are no data on tolerance of Squacco Heron to drone intrusion in the colony. The absence of obvious signs of disturbance to breeders in the present study is congruent with what was previously found in our area for drones flying at elevations above ground level larger than flight initiation distances known for many species of herons (Valle & Scarton 2018). In particular, we found that many species of Pelecaniformes are highly tolerant to drone surveys in the wetland complex Lagoon of Venice – Po Delta, including herons *(Ardea cinerea, Ardea alba, Ardea purpurea, Bubulcus* *ibis, Egretta garzetta)*, Eurasian Spoonbill *(Platalea leucorodia)*, and ibises *(Plegadis falcinellus, Threskiornis aethiopicus)* (Valle & Scarton 2018, Valle & Scarton 2019b, Valle *et al.* 2021).

Our study declares a number of limitations. The main limitation is the lack of a ground inspection of the study colony to be used as ground truth. Nevertheless, we chose to restrict surveys to drones in order to avoid disturbance in a large, crowded heronry, where ground intrusions would have caused unbearable disturbance. This also explains a second limitation, residing in the impossibility of excluding settlement of late nesters as well as nest abandonment by identified breeders, when vegetation overgrowth obstructed the view from above, late in the season.

In conclusion, a drone-based monitoring greatly improves counting accuracy of breeding Squacco Herons, but fails to assess productivity, due to later vegetation overgrowth. What matters most is the possibility of collecting accurate count data early in the season using drones, without apparent disturbance to the breeders.

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Spectrum of animal and plant in the diet of Woodcock (*Scolopax rusticola* L.) based on literature data

Attila Bende* & Richárd László

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Abstract Based on the results of dietary surveys of the Woodcock (*Scolopax rusticola* L.) in 11 countries (Great Britain, Scotland, France, Italy, Croatia, Germany, Hungary, Poland, Ukraine, Russia, and Romania), 63 taxa (42 animal and 21 plant) were detected in Woodcock gizzard contents, of which the predominant dietary components were of animal origin. The composition of the dietary components varies only within a narrow spectrum, adapting to seasonal changes in the insect fauna and the supply of the area. Earthworms (*Lumbricus* spp.) represent the dominant proportion, also with larvae of Dermaptera, Myriapoda, Coleoptera taxa, and Diplopoda and Araneidae species being present in significant numbers. The mass fraction of plant components (mainly weed seeds) is low, with occasional occurrence of vegetative plant parts. The narrow species range of animal taxa recorded and the low proportion of plant dietary components clearly indicate that the Woodcock is a specialist species, and the availability of a few major dietary component taxa groups are a limiting factor in case of the Woodcock. Therefore, it is a major determinant of the diurnal, seasonal and annual movement patterns.

Keywords: Woodcock, *Scolopax rusticola* L., nutritional spectrum, percentage of prey

Összefoglalás Az erdei szalonka (*Scolopax rusticola* L.) elterjedési területén 11 országban (Nagy-Britannia, Skócia, Franciaország, Olaszország, Horvátország, Németország, Lengyelország, Ukrajna, Oroszország, Románia, Magyarország) végzett táplálék vizsgálatok eredményei alapján 63 taxont (42 állati és 21 növényi) mutattak ki szalonka begytartalmakban, amiből a meghatározó hányadot az állati eredetű táplálékalkotók képezték. A táplálékkomponensek összetétele csak szűk spektrumban változik, igazodva a rovarvilág évszakos változásához és az adott terület kínálatához. A meghatározó hányadot a földigiliszták (*Lumbricus* spp.) képviselik, mellettük a Dermaptera, Myriapoda, Coleoptera taxonok lárvái és a Diplopoda valamint az Araneida fajok mennyisége volt számottevő. A növényi komponensek tömegaránya (főként gyommagvak) alacsony, a vegetatív növényi részek előfordulása eseti. A felvett állati eredetű taxonok szűk fajspektruma, valamint a növényi eredetű táplálékkomponensek alacsony aránya alapján az erdei szalonka egyértelműen specialista fajnak tekinthető, tehát a meghatározó néhány fő táplálékalkotó taxoncsoport rendelkezésre állása limitáló tényező a szalonka esetében, ezen keresztül pedig a napszakos, a szezonális és az éves mozgásmintázat egyik meghatározó befolyásoló tényezője.

Kulcsszavak: erdei szalonka, *Scolopax rusticola* L., táplálkozási spektrum, zsákmányállat-taxonok

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

Introduction

The Woodcock is a game species in many European countries. However, probably due to the difficulty of detecting its dietary components, few dietary biology studies have been published in the ornithological literature in relation to its importance for hunting and the annual size of the bags. A few major monographs (e.g. Gyementyev & Gladkov 1951, Glutz *et al*. 1973, Cramp & Simons 1983) and a few authors (Ferrand *et al*. 1979, Hirons 1982, Kiss 1973, Koubek 1986, Kiss *et al*. 1990, Fadat 1995, etc.) provide data on the unique features of dietary biology, but in many cases only the major taxon groups are given, and precise data on the mass ratios are rarely available. Based on the results of recent bromatological studies (Hoodless & Hiorons 2007, Aradis *et al*. 2019), our knowledge has been expanded over the last decades. Based on them and previous literature, we would like to provide a comprehensive picture of the dietary spectrum of the Woodcock.

Results and Discussion

Based on the results of dietary biological studies carried out in eleven countries of the Woodcock's range (Great Britain: Seebohm 1885, Borrer 1891, Campbell 1936, Gordon 1915, Sperry 1940, Hirons 1978, Hoodless & Hirons, 2007, France: Garavini 1962, Shorten 1974, Fadat *et al*. 1979, Ferrand *et al*. 1979, Lebeurier 1982, Granval 1987, Fadat 1995, Italy: Lo Valvo 1988, Spanò & Borgo 1993, Aradis *et al*. 2019, Croatia: Cvitanić & Novak 1968, Germany: Bettmann 1975, Glutz von Blotzheim 1986, Poland: Steinfatt 1938, Ukraine: Kistyakivski 1957, Grekov *et al*. 1973, Russia: Buturlin 1902, Aradis *et al*. 2019, Romania: Kiss & Sterbetz 1973, Kiss *et al*. 1990, 1999, Hungary: Bod 1901), 21 plant and 42 animal taxa (63 in total) were detected in the gizzard content. The dominant part is made up of dietary components of animal origin, which are summarised in *Table 1* included in the study.

Plant dietary components are considered insignificant by some authors (Steinfatt 1938, Kiss & Sterbetz 1979, Hoodless & Hirons 2007), but in other studies they represent a significant proportion up to 21% (Shorten 1974, Koubek 1986, Fadat 1995).

The plant parts in the gizzard content were mainly made up of weed seeds and a small number of other seeds (buttercups *Ranunculus* spp., orache *Atriplex* spp., knotweed *Polygonum* spp., sorrel *Rumex* spp., spurge *Euphorbia* spp., sedge *Carex* spp., cottongrass *Eriophorum* sp., rush *Juncus* sp., bur-reed *Sparganium* sp.). In addition, seeds of cultivated plants (pea *Pisum* sp., oat *Avena* sp., maize *Zea mays*), as well as fruits (blueberry *Vaccinium* spp., elderberry *Sambucus* sp., whitebeam *Sorbus* spp., berry *Rubus* spp.) and juniper pine nuts *Juniperus* sp. were found in the tested gizzard contents. Among the vegetative plant parts, Norway spruce *Picea abies* needles and in several cases root fragments were found. In addition to these, inorganic components (pebble, sand) were also present in small quantities in the gizzard content.

The results of most dietary biology studies (Seebohm 1885, Sperry 1940, Buturlin 1902, Hirons 1982, Granval 1987, Kiss *et al*. 1990, 1999, Duriez *et al*. 2005, Hoodless & Hirons 2007) are in agreement with Hoffmann's observations (1867), who found that earthworms

Table 1. Nutritional spectrum of the Woodcock (*Scolopax rusticola* L.) from animal sources based on gizzard content analyses from 1885 to 2019

1. táblázat Az erdei szalonka (*Scolopax rusticola* L.) állati eredetű táplálékspektruma 1885–2019-es évek között végzett begytartalom-vizsgálatok alapján

Taxonomy						
Phylum	**Class/Subclass**	**Order/Suborder**		**Family**	**Genus**	**Species**
Nemertea	–	–		–	–	–
Annelida	Clitellata / Oligochaeta	Opisthopora / Lumbricina		Lumbricidae	Lumbricus	***Lumbricus* spp.**
	Clitellata / **Hirudinea**	–		–	–	–
Mollusca	Gastropoda / Orthogastro-poda	**Pulmonata / Stylommatophora, Basommatophora**		–	–	–
	Bivalvia	Mytiloida		**Mytilidae**		
Arthropoda	Chilopoda	Scolopendromorpha		**Scolopendridae**	–	–
		Lithobiomorpha		**Lithobius**		
	Diplopoda	Glomerida		**Glomeridae**	–	–
		Julida		**Julidae**		
	Malacostraca / Eumalacostraca	Isopoda / Oniscidea		Oniscidae	Oniscus	***Oniscus* spp.**
	Branchiopoda	Laevicaudata / Cladocera		Leptodoridae	Leptodora	***Leptodora kindtii***
	Araneae	Araneae / Labidognatha		**Araneidae**	–	
	Insecta / Pterygota	Dermaptera / Forficulina		Forficulidae	**Forficula**	–
	Insecta	Hemiptera / Heteroptera		Nabidae, Pentatomidae	**Eurydema** **Notonecta**	–
		Orthoptera		**Gryllidae**	–	
		Hymenoptera		Formicidae	**Forficula**	–
		Diptera	Nematocera	**Tipulidae** **Limoniidae** **Chironomidae** **Bibionidae**	–	–
			Brachycera	**Tabanidae** **Asilidae** **Therevidae** **Calliphoridae** **Tephritidae**	–	–
		Coleoptera	Adephaga	**Cicindelinae** **Carabidae** **Dytiscidae** **Histeridae**	–	–
			Polyphaga	**Silphidae** **Staphylinidae** **Elateridae** **Tenebrionidae** **Curculionidae** **Hydrophilidae** **Geotrupidae** **Scarabaeidae** **Heteroceridae**	–	–

The taxa in bold were described during gizzard content analysis.

(*Lumbricus* spp.) represent the dominant part of the diet – in terms of abundance and dry weight (up to 85%) (Granval 1987, Duriez *et al*. 2005). According to Gordon (1915), *"…it consumes an extraordinary number of worms, almost equal to its own weight in a single day."* In the samples (n = 42) collected in Ukraine during the migration and reported by Kistyakivski (1957), the proportion of earthworms was 2% in total, with spiders (34%), Diplopoda species (34%), and Julidae and other Myriapoda (29%) taxa predominating. This matches well with the results of samples collected in Italy and Sicily during the winter period by Aradis *et al*. (2019). All this points to the fact that insects and centipedes may be the main dietary source in different zones and in the absence of earthworms in the autumn-winter period.

Little is known in the literature about the diet spectrum of chicks, but the available studies suggest that there is no significant variation in the diet spectrum, at best only during the first few days (Hoodless & Hirons 2007). Birds hatched in captivity will pick up small earthworms independently after a few hours, provided they are moving. Woodcock broods are not able to search in the topsoil during the first days, so during this period they feed with the help of the hen. The mother bird turns over the soil and uses her beak to "offer" her chicks food of animal origin; the broods typically eat small insects found on the soil surface or in the forest litter cover (Bettmann 1975).

The composition of the dietary components varies over a narrow spectrum, adapting to seasonal changes in insect life and supply of the area (Aradis *et al*. 2019). The number of larvae of Dermaptera, Myriapoda, Coleoptera taxa and of Diplopoda and Araneida species in the diet increases with the activation of soil life, as indicated by the gizzard content collected in spring. During this period, the proportion of earthworms (Lumbricidae) is still low because the soil is still too cold for them and their activity is therefore low (Kistyakivski 1957, Glutz von Blotzheim 1986, Aradis *et al*. 2019). However, from late spring to autumn *Lumbricus* species become dominant in the consumed diet (Glutz von Blotzheim 1986). During wintering, the diet spectrum varies from area to area (Aradis *et al*. 2019). Fadat (1995) found no statistically significant difference in the dietary composition of hens and cocks in his studies.

The number of taxa recognized as diet is high, but due to the dominant *Lumbriscus*, Coleoptera and Diplopoda mass ratios, the Woodcock is considered a specialist species, so it only finds the required quantity and quality of diet in periods and areas with optimal conditions for the main dietary component taxa.

Through the special dietary strategy of the Woodcock, the daily, seasonal and annual variation in the abundance of the main dietary component taxa – mainly Lumbricidae – has a profound influence on the occurrence and habitat use of this bird species in a given area. The abundance and activity of Lumbricidae species – typically *Lumbricus terrestris* – is influenced mainly by the physical properties of the soil, its chemistry, compactness, temperature and moisture content, and last but not least, its dietary content (Lee 1985, Binet *et al*. 1987, Edwards & Bohlen 1996, Curry 2004). Earthworms typically come to feed near the soil surface only under optimal moisture and temperature conditions – usually at night – and during the day they typically stay in the safety of their burrows, which extend down to depths of several metres (Binet *et al*. 1987, Binet 1993). This, therefore, is the most optimal time for the Woodcock to feed, but it is known that Woodcock feeding is not exclusively restricted to the night. The choice of night feeding sites is dominated by open areas, especially low-grassed cattle pastures (Burton 1974, Niçaise 1996, Aradis *et al*. 2019), where the main food sources, *Lumbricus* species and insect larvae developing in dung, are abundant. Agricultural fields are far inferior to the dietary supply of pastures, with studies by Binet *et al*. (1997) showing that earthworm abundance was only one-tenth in maize fields, compared to pastures. The population decline in the UK in the 1960s was partly explained by Lewis and Roberts (1993) as a result of pasture ploughing. Numerous studies have shown that the Woodcock may cease to change habitat diurnally during periods of excessive drought as the dietary supply becomes more limited (Hirons & Jonhson 1987, Duriez *et al*. 2005, Hoodless & Hirons 2007, Braña *et al*. 2010), so changes in the abundance and availability of dietary components determine daily and seasonal movement patterns as well as habitat selection.

The dietary spectrum compiled based on literature data – given the species' specialist dietary strategy – is likely to include the taxa groups to be regarded as food for the Woodcocks migrating through our country or nesting in small numbers in Hungary. However, the literature reviewed in this study shows that soil condition, through the availability of food of animal origins, has a fundamental influence on the choice of wintering sites, migration intensity, and reproductive success of the Woodcock.

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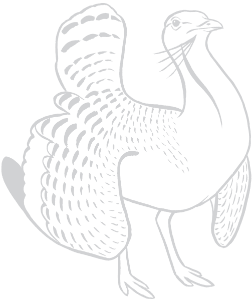

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A new species for Algeria, White-throated Bee-eater *(Merops albicollis)*, observations of probably escaped individuals of Cut-throat Finch *(Amadina fasciata)* and Village Indigobird *(Vidua chalybeata)* and a checklist of southern Sahara birds

Belkacem Aimene Boulaouad[1,2*], Bachir Harzallah[2], Khaled Ayyach[2], Karim Attouche[2], Walid Soukkou[2], Djamel Hadj Aissa[2], Hamza Faidi[2] & Mohamed Missoum[2]

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Abstract In this paper we present a report about the birds of the southern part of the Algerian Sahara. A total of 62 species were recorded with direct observations in nine different localities of two regions (from Tamanrasset city to In Guezzam city), belonging to 29 families and 12 orders in 2021. Three species were recorded for the first time in Algeria, White-throated Bee-eater *(Merops albicollis),* Cut-throat Finch *(Amadina fasciata)* and Village Indigobird *(Vidua chalybeata)*. The latter two were probably escaped from captivity. The House Sparrow *(Passer domesticus)* were observed for the first time in this region.

Keywords: Algeria, bird species diversity, *Merops albicollis, Amadina fasciata, Vidua chalybeata,* North Africa, Palearctic Region, new records

Összefoglalás A szerzők a Szahara dél-algériai részéről közölnek madártani adatokat. Kilenc területen – Tamanrassettől In Guezzamig – 12 rendbe, 29 családba tartozó 62 madárfajt figyeltek meg 2021-ben, amelyek közül egy – fehértorkú gyurgyalag *(Merops albicollis)* – a területre új volt. A megfigyelt fajok között volt két olyan is, amelyeket korábban szintén nem láttak még a területen, viszont ezek – szalagpinty *(Amadina fasciata),* piroslábú vidapinty *(Vidua chalybeata)* – nagy valószínűséggel fogságból szökött példányok voltak. Egy új területen kimutatták a házi verebet *(Passer domesticus)* is.

Kulcsszavak: Algéria, madárfajok diverzitása, fehértorkú gyurgyalag, szalagpinty, piroslábú vidapinty, Észak-Afrika, Palearktikum, új megfigyelés

[1] *Department of Agronomy, SNV-TU Faculty, Mohamed El Bachir El Ibrahimi Bordj Bou Arreridj University, Algeria*
[2] *Algerian Wildlife Watchers Association*
** corresponding author, e-mail: belkacemaimene.boulaouad@univ-bba.dz*

Introduction

Given its vast area in Africa with more than 2 million km^2 and considered as the largest country in the Mediterranean basin, Algeria has an ecosystem unit classified biogeographically among the richest and most diverse countries of the Palearctic region. The Sahara is located in the south of the country and covers almost 90% of its area.

Several studies were carried out focusing on the diversity of birds in the Algerian Sahara, mostly in the northern part, such as in Ziban region (Farhi & Belhamra 2012) in Ghardaia (Chedad *et al.* 2020a, 2020b) and in three oases of the Northern Algerian Sahara (Biskra, Oued Souf and Ouargla, Guezoul *et al.* 2013).

A few studies were conducted on the diversity of the southern part of the Algerian Sahara. This part is the boundary between two biogeographic regions Palearctic and Afrotropical. In the last decades, the newest records of species were observed in the southern part such as the Moltoni's Warbler *(Curruca subalpina)* in El Borma (Viechec & Haddad 2019), Rüppell's Warbler *(Curruca rupelli)* in Djanet (Haddad & Afoutni 2019), Jacobin Cuckoo *(Clamator jacobinus)* in Tamanrasset (Haddad & Afoutni 2020a), African Crake *(Crecopsis egregia)* at Kerzaz (Haddad *et al.* 2021b), White-rumped Seedeater *(Crithagra leucopygia)* in Tamanrasset (Boulaouad *et al.* 2021), Blue-naped Mousebird *(Urocolius macrourus)* in Tinzaouten (Haddad & Bekkouche 2021), Dunn's Lark *(Eremalauda dunni)* in Djanet (Harzallah *et al.* 2021) and African Grey Woodpecker *(Dendropicos goertae)* in municipality of Tin Zaouatine, region of In Guezzam (Haddad & Afoutni 2022).

The objectives of the present work are to enrich the bibliography of the birds of the southern part of the Algerian Sahara and to describe the new observations of the White-throated Bee-eater *(Merops albicollis),* and the probably escaped Cut-throat Finch *(Amadina fasciata)* and Village Indigobird *(Vidua chalybeata)* for the birds of Algeria.

Material and Methods

Study area

This study was conducted in the region of Tamanrasset, located in the south of Algeria, at about 2,000 km southeast from Algiers *(Figure 1)*. The region is characterized by a Saharan climate with mild winter (Chenoune 2005). It is located at 1,400 m above the sea level and has a super-dry climate with temperature ranging between 12 °C and 40 °C (Hamdi 2013).

A field survey was conducted during the last week of December 2021 to collect data about the diversity of birds in nine localities from the region of Tamanrasset to the region of In Guezzam for about 400 km. Localities were chosen with dependence on vegetal cover, four in Tamanrasset and five in In Guezzam. Birds were surveyed in each locality all the day by a group of naturalists from Algerian Wildlife Watchers Association (AWWA).

The line transect method has been used in this study. This technique consists of walk in the study locality, a well-defined route several times, while advancing at a steady speed (1 to 2 km/h), marking a stop every 20 meters, and noting and photographing all birds seen and

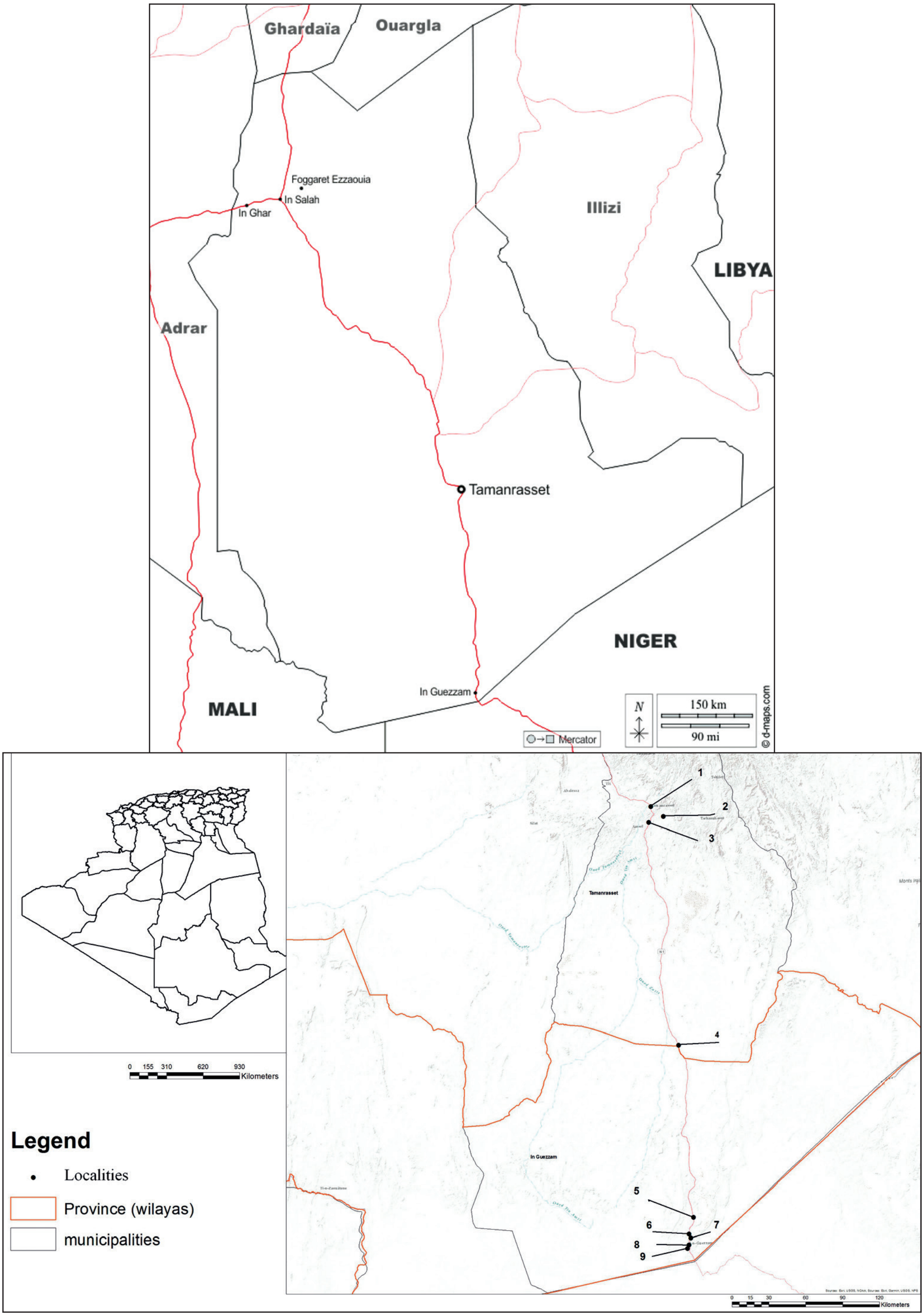

Figure 1. Geographical location of the study area (d-maps.com)
1. ábra A vizsgálati helyek földrajzi elhelyezkedése

heard by locating them in the course. Bird species were identified using standard field guides (Heinzel *et al.* 2004, Svensson 2012). We were using information from Isenmann and Moali (2000), for the geographical distribution of birds of Algeria.

The list of areas contains the name of locality, coordinates, short descriptions of the habitat, altitude

1. Tamanrasset: Tamanrasset city (22°46'56"N 5°31'47"E), with approx. 37 km^2, is the most visited place in this locality, gardens and green space, 1,370 m.
2. Tamanrasset: Agricultural zone (22°42'33"N 5°37'38"E) is located 20 km in the east of Tamanrasset with about 0.13 km^2, this locality is consisted of orchards and characterized by palm and citrus and vineyards, 1,340 m.
3. Tamanrasset: Agricultural zone in Amsel with about 0.4 km^2 (22°40'03"N 5°30'33"E) is located 20 km in the south of Tamanrasset city and is characterized by palm, citrus and grapes and a line of *Acacia* sp., 1,240 m.
4. Tamanrasset: Base of life (21°01'37" N 5°42'53"E) is located 200 km in the south of Tamanrasset and characterized by small construction and some ornamental trees, 620 m.
5. In Guezzam: Agricultural zone (19°45'37"N 5°48'31"E) is located about 40 km north of Ain Guezzam, this area occupies 1.1 km^2 which contains olive trees, palm trees and cereal farming, and the surround with common reed, 410 m.
6. In Guezzam: *Acacia* trees (19°38'20"N 5°46'23"E) is located 10 km north of In Guezzam city, this locality is an orchards, characterized by *Acacia* sp. trees, 405 m.
7. In Guezzam: Agricultural zone (19°36'38"N 5°47'06"E) located on the north of In Guezzam city. It is characterized by palm trees, olive trees and mango trees with 0.8 km^2, 410 m.
8. In Guezzam: In Guezzam city (19°33'31"N 5°46'13"E), with a surface of about 12 km^2 where we visited green space and trees in the village, 400 m.
9. In Guezzam: Sewage treatment station (19°31'57.9"N 5°45'29.4"E) is located 2.8 km southwest of In Guezzam city and it is characterized by common reed and some grace, 410 m.

Results

A total of 62 bird species belonging to 29 families and 12 orders were recorded in the southern part of the Algerian Sahara *(Table 1)*. The richest order in species was Passeriformes with 37 species, followed by Charadriiformes and Pelecaniformes with six species, Columbiformes with three species and Bucerotiformes and Falconiformes with two species. The rest of the orders were represented by one species.

The number of species observed at different localities are varied between 5 and 34, as follows *(Figure 2)*: a total of 34 species were observed in the agricultural area near In Guezzam city, 30 species were observed in wetland, 29 were observed in Amsel region, 21 species in the 5. locality which is an agricultural area, 14 species were observed in the 2. and 8. localities, 13 species were recorded in Tamanrasset city, 12 species were observed in Acacia trees and the lowest richness was observed in the 4. locality with five species.

Table 1. Checklist of birds identified in the Tamanrasset region, Algeria. Numbers corresponds to the list of localities in Materiel and Methods (* probably escaped from captivity) (IOC World Checklist version 11.2, Gill *et al.* 2021)

1. táblázat Az algériai Tamanrasset régióban talált madarak fajlistája. A helységek listája a Material and Methods fejezetben található (* valószínűleg fogságból szökött) (IOC World Checklist version 11.2, Gill *et al.* 2021)

Order	Family	Species	Common name	Localities
Anseriformes	Anatidae	*Anas crecca*	Eurasian Teal	9
Pterocliformes	Pteroclidae	*Pterocles coronatus*	Crowned Sandgrouse	5
Columbiformes	Columbidae	*Columba livia*	Rock Dove	1,2,3,6,7,8,9
		Streptopelia decaocto	Eurasian Collared Dove	1,2,3,5,6,7,8,9
		Spilopelia senegalensis	Laughing Dove	1,2,3,5,6,7,8,9
Gruiformes	Rallidae	*Fulica atra*	Eurasian Coot	9
Charadriiformes	Recurvirostridae	*Himantopus himantopus*	Black-winged Stilt	9
	Charadriidae	*Charadrius dubius*	Little Ringed Plover	9
	Scolopacidae	*Calidris temminckii*	Temminck's Stint	9
		Calidris minuta	Little Stint	9
		Tringa ochropus	Green Sandpiper	9
		Tringa nebularia	Common Greenshank	9
Ciconiiformes	Ciconiidae	*Ciconia ciconia*	White Stork	9
Pelecaniformes	Threskiornithidae	*Platalea leucorodia*	Eurasian Spoonbill	9
	Ardeidae	*Nycticorax nycticorax*	Black-crowned Night Heron	7
		Bubulcus ibis	Western Cattle Egret	5,7,9
		Ardea cinerea	Grey Heron	7
		Ardea purpurea	Purple Heron	7
		Egretta garzetta	Little Egret	9
Accipitriformes	Accipitridae	*Neophron percnopterus*	Egyptian Vulture	1,4,5
Strigiformes	Strigidae	*Asio flammeus*	Short-eared Owl	7
Bucerotiformes	Upupidae	*Upupa epops*	Eurasian Hoopoe	2,3,7
Coraciiformes	Meropidae	*Merops albicollis*	White-throated Bee-eater	3
Falconiformes	Falconidae	*Falco tinnunculus*	Common Kestrel	3,7,9
		Falco biarmicus	Lanner Falcon	3,7
Passeriformes	Laniidae	*Lanius excubitor*	Great Grey Shrike	2,3,5,6,7,9
	Corvidae	*Corvus ruficollis*	Brown-necked Raven	1,2,3,4,5,6,7,8,9
	Alaudidae	*Alaemon alaudipes*	Greater Hoopoe-lark	3,4,6
		Ammomanes deserti	Desert Lark	3,4,5,6,7
		Galerida cristata	Crested Lark	7

Order	Family	Species	Common name	Localities
Passeriformes	Hirundinidae	*Ptyonoprogne obsoleta*	Pale Crag Martin	1,2,3,5,6,7,8,9
		Hirundo rustica	Barn Swallow	5
	Phylloscopidae	*Phylloscopus bonelli*	Western Bonelli's Warbler	7
		Phylloscopus trochilus	Willow Warbler	3,5,7
		Phylloscopus collybita	Common Chiffchaff	1,2,3,5,7,8,9
	Sylviidae	*Sylvia borin*	Garden Warbler	2
		Curruca hortensis	Western Orphean Warbler	3
		Curruca melanocephala	Sardinian Warbler	1,2,3,5,6,7,8
		Curruca iberiae	Western Subalpine Warbler	2,3,7
	Leiothrichidae	*Argya fulva*	Fulvous Babbler	2,3
	Muscicapidae	*Muscicapa striata*	Spotted Flycatcher	7
		Luscinia svecica	Bluethroat	5
		Ficedula hypoleuca	European Pied Flycatcher	7
		Phoenicurus ochruros	Black Redstart	3
		Monticola solitarius	Blue Rock Thrush	3
		Oenanthe oenanthe	Northern Wheatear	3,7
		Oenanthe deserti	Desert Wheatear	3,5,6,7,8,9
		Oenanthe leucopyga	White-crowned Wheatear	1,2,3,4,5,6,7,8,9
	Passeridae	*Passer domesticus*	House Sparrow	5,7,8
		Passer simplex	Desert Sparrow	3,
		Passer luteus	Sudan Golden Sparrow	7,8,9
	Estrildidae	*Euodice cantans*	African Silverbill	1,3,5,7,8,9
		Lagonosticta senegala	Red-billed Firefinch	1,3,8
		* *Amadina fasciata*	* Cut-throat Finch	7
	Viduidae	* *Vidua chalybeata*	* Village Indigobird	1
	Motacillidae	*Motacilla flava*	Western Yellow Wagtail	9
		Motacilla alba	White Wagtail	3,5,7,9
		Anthus campestris	Tawny Pipit	7
		Anthus trivialis	Tree Pipit	9
		Anthus cervinus	Red-throated Pipit	9
	Fringillidae	*Bucanetes githagineus*	Trumpeter Finch	3,5,7,9
	Emberizidae	*Emberiza sahari*	House Bunting	1,2,3,5,6,7,8,9
13	29	62		

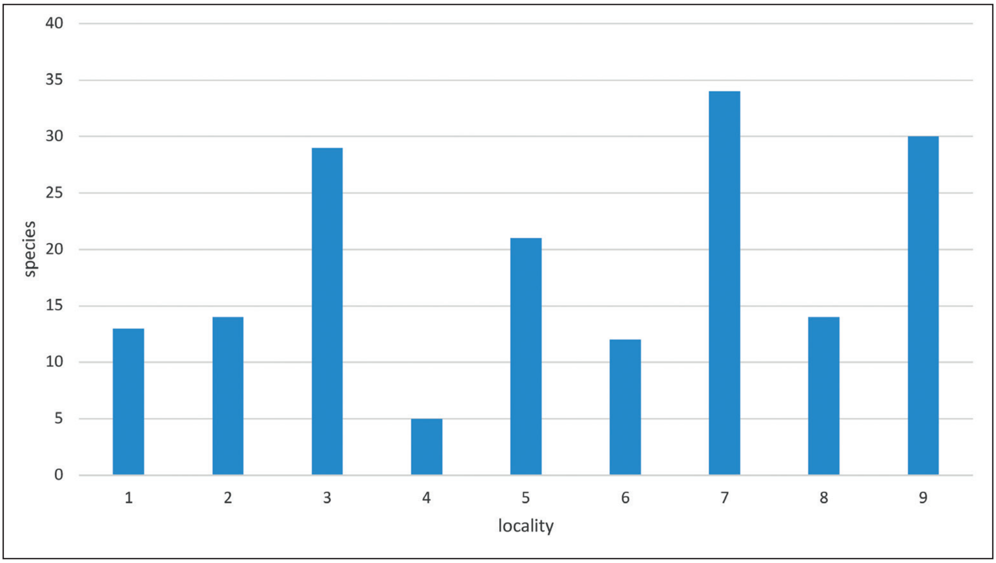

Figure 2. Distribution of the number of species per locality
2. ábra A vizsgált területek fajszámeloszlása

During this study, a new species were observed for the first time in Algeria *(Figure 3)* White-throated Bee-eater, and two probably escaped species: Cut-throat Finch, Village Indigobird and a new locality of distribution for the House Sparrow.

White-throated Bee-eater was observed at Oued Azerzi in the locality of Amsel in December 25th, 2021. Unfortunately, we could not spot this species after three days when we returned back to the same region.

Cut-throat Finch was recorded in an agriculture area situated in In Guezzam in December 28th, 2021 with a group of African Silverbill *(Euodice cantans)* perched on reed beds.

Village Indigobird was obserwed in Tamanrasset city in December 31st, 2021. This species was noted with the company of a group of Red-billed Firefinch *(Lagonosticta senegala)*.

House Sparrow was observed in three localities. Two groups was recorded in an agricultural zone (5. and 7. locality). The third group was in In Guezzam city.

Discussion

A total of 62 species were observed in the localities of the study area. The observed bird species represent 18.45% of the avifauna cited by Ledant *et al.* (1981) and 15.27% recorded by Isenmann and Moali (2000). A similar number of species (56) was observed in Tamanrasset (Boulaouad *et al.* 2021). For the northern part of the Algerian Sahara, Farhi and Belhamra (2012) counted 124 species belonging to 15 orders and 29 families and the most represented order was Passeriformes with 58 species. Guezoul *et al.* (2013) counted 59 species in the palm of Northern Algerian Sahara. Chedad *et al.* (2020) reported 55 species at Kef Doukhane. The southern part of the Algerian Sahara is a compulsory stopover point

Figure 3. New species for the avifauna of Algeria: White-throated Bee-eater, 25th December 2021, Oued Azerzi (photo Djamel Hadj Aissa)

3. ábra Új faj Algéria madárfaunájában: fehértorkú gyurgyalag, 2021. december 25., Oued Azerzi (fotó: Hamza Faidi és Djamel Hadj Aissa)

for all the birds on the trans-Saharan migratory pathway and it is considered as an important area for research of Afrotropical birds.

White-throated Bee-eater *(Merops albicollis)*

Two species of bee-eater are present in Algeria: the European Bee-eater *(Merops apiaster)* and the Blue-cheeked Bee-eater *(Merops persicus)* (Isenmann & Moali 2000). The European Bee-eater is a widespread breeder from the coast to the northern edge of the Sahara and is present from April to September (Isenmann & Moali 2000). At Tassili, the White-throated

Bee-eater was observed both during post-breeding passage from August 25th to October 9th and eventually during pre-breeding passage from April 13th to May 11th in 1960. The Blue-cheeked Bee-eater present in the northern Sahara, stems its reproduction in three distinct regions (Biskra, Mzab and Figuig). Our observation of the White-throated Bee-eater is the first for Algeria. Its distribution ranges from southern Mauritania and Senegal in the west to south-western Saudi Arabia and western Yemen in the east (Jacobs *et al.* 2018). In the Western Sahara, this sub-Saharan species has recently occurred in two mentions Dakhla: a bird recorded in Gleib Jédiane on 5th and 6th December 2013 and another in Dakhla from 28th February to 1st May 2017 (Jacobs *et al.* 2018, Bergier & Thevenot 2019). According to the observations quoted above in Western Sahara, the species can be considered as accidental in the country.

Cut-throat Finch *(Amadina fasciata)*

The Estrildidae family is represented in Algeria by two species: the Red-billed Firefinch and African Silverbill (Belbachir 2000, Haddad & Afoutni 2020b). A third species, the Cut-throat Finch was observed in agricultural zones at In Guezzam. According to Borrow and Demey (2020), this is a sub-Saharian species which can be found particularly in the Sahel. Clouet and Joachim 2013 observed this species in Adrar of the Iforas, which is located in 150 km southwest of our study site in In Guezzam.

Figure 4. Probably escaped Cut-throat Finch with African Silverbill, 28th December 2021, In Guezzam (photo Karim Attouche)

4. ábra Valószínűleg fogságból szökött szalagpinty afrikai ezüstcsőrűpinty mellett, 2021. december 28., In Guezzam (fotó: Karim Attouche)

Village Indigobird *(Vidua chalybeata)*

The Village Indigobird is a breeding bird in most of Africa south of the Sahara Desert. According to Payne *et al.* (2000), the species is a host-specific brood parasite which deposits its eggs exclusively in the nest of an estrildid finch, the Red-billed Firefinch. The observation of Village Indigobird with a group of Red-billed Firefinch *(Figure 5)* in Tamanrasset city can lead to a new breeding bird for the avifauna of Algeria. Clouet and Joachim 2013 observed the Village Indigobird, in Aïr in the north of Niger. According to several observers of the Algerian avifauna, this species was found for sale (nearly 200 individuals for sale at 4.5 and 15 euros for one individual) in pet stores in the city of Tamanrasset.

House Sparrow *(Passer domesticus)*

According to Isenmann and Moali (2000), the House Sparrow is still absent from Tamanrasset and its surrounding (Ahaggar), and recall a potential overall competition with House Bunting *(Emberiza sahari)*. Haddad *et al.* (2021a) was recorded the species in the south-western part of the Algerian Sahara, exactly in Tindouf and its surroundings. The observation of these birds in In Guezzam are considered as new locality for Algeria.

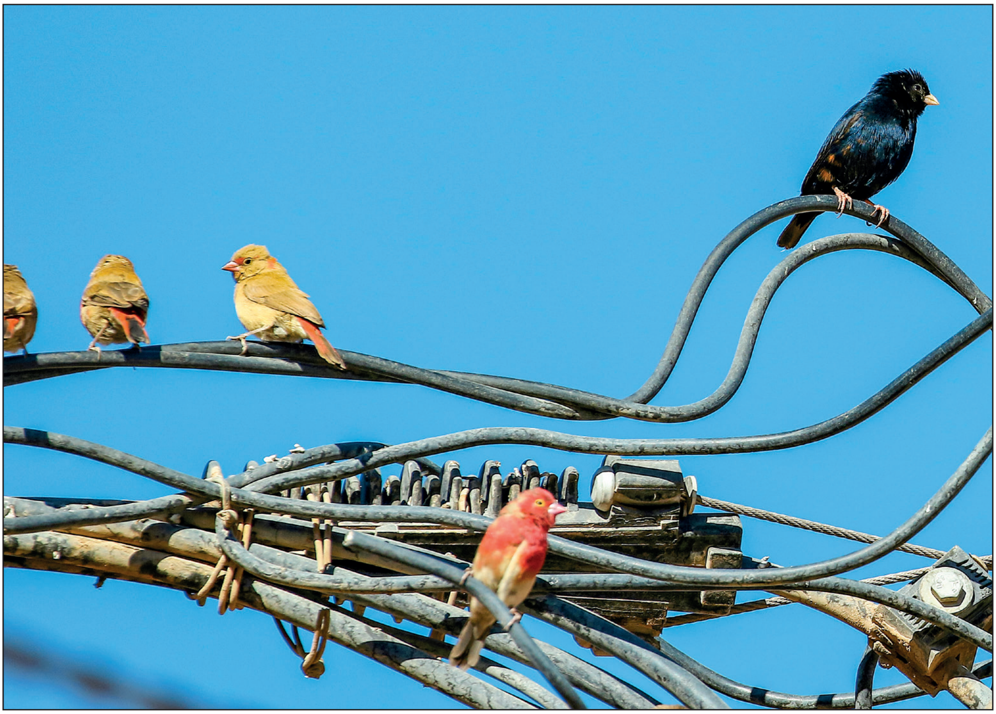

Figure 5. Probably escaped male Village Indigobird with two females and a male of Red-billed Firefinch, 31st December 2021, Tamanrasset city (photo Khaled Ayyach)

5. ábra Valószínűleg fogságból szökött hím piroslábú vidapinty két tojó és egy hím vörös amarant társaságában, 2021. december 31., Tamanrasset (fotó: Khaled Ayyach)

Figure 6. Male House Sparrow, 28th December 2021, Agricultural zone at In Guezzam (photo Bachir Harzallah)

6. ábra Hím házi veréb, 2021. December 28. In Guezzam (Fotó: Bachir Harzallah)

Conclusion

The results of this study revealed the presence of 3 new species for the Algerian avifauna and a new location of the House Sparrow. Note that the White-throated Bee-eater can be considered as an accidental species in Algeria. We must also note and conclude that Cut-throat Finch and Village Indigobird can be considered as cage releases and not migratory or accidental visitors in the region. They are indeed species introduced voluntarily, based on the big number of individuals sold in pet stores.

We would like this area to be a center of interest of specialists in the upcoming years in order to update our data on vertebrate fauna and find out whether the populations are in a phase of progression or regression.

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New species for the avifauna of adjoining coastal areas of Purba Medinipur district, West Bengal, India

Piklu Das[1*], Atish Manna[2] & Arajush Payra[3]

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Abstract To upgrade the known avifaunal assemblages of adjoining coastal areas of Purba Medinipur district, West Bengal, India, opportunistic survey were carried out during January 2020 to August 2022. The survey yielded additions of 36 bird species in 10 orders and 17 families to the coastal area of Purba Medinipur district, based on photographic evidences. Among these recorded birds, 30 species were classified as Least Concern, two species were Near Threatened *(Aythya nyroca, Calidris canutus)*, one species was Vulnerable *(Aythya ferina)*, two species were Endangered *(Calidris tenuirostris, Rynchops albicollis)* and one species was Not Assessed *(Porphyrio poliocephalus)*. Details of all the records are given here.

Keywords: additional records, opportunistic survey, West Bengal

Összefoglalás Az indiai Nyugat-Bengál térségében fekvő Purba Medinipur körzet eddig ismert madárfaunájának frissítése érdekében 2020 januárja és 2022 augusztus között opportunisztikus felméréseket végeztünk. A felmérések eredményeképpen 10 rend 17 családjába tartozó 36, a térségre új madárfajt találtunk Purba Medinipur körzet tengerparti területein, melyek határozása fotós bizonyítékokon alapszik. A felmért fajok közül 30 a legkevésbé veszélyeztetett, kettő a veszélyeztetettséghez közeli *(Aythya nyroca, Calidris canutus)*, egy a sérülékeny *(Aythya ferina)*, kettő a Veszélyeztetett *(Calidris tenuirostris, Rynchops albicollis),* egy nincs értékelve *(Porphyrio poliocephalus)* IUCN Red List védettségi kategóriába tartozik.

Kulcsszavak: új megfigyelések, opportunisztikus felmérés, Nyugat-Bengál

[1] Piklu Das, Wildlife Biologist of WNE, Sarisha, WB, 743368, India; Member of Wildlife Information and Nature Guide Society (WINGS), Paschim Bardhaman, WB, 713207, India
[2] Atish Manna, Wildlife Biologist of WNE, Sarisha, WB, 743368, India
[3] Arajush Payra, Ramnagar, Purba Medinipur, West Bengal, 721441, India; Faculty of Sustainable Studies, School of Ecology & Environmental Management, Dr. Vishwanath Karad MIT World Peace University, Kothrud, Pune, Maharastra, 411038, India
** corresponding author, e-mail: pikludas8348@gmail.com*

Introduction

Along the East coast of India, studies related to coastal bird diversity attains focus mainly on the Important Bird Areas (IBAs), namely Point Calimere Wildlife Sanctuary of Tamil Nadu, Chilika Lake and Bhitarkanika National Park of Odisha, and Sundarbans of West Bengal (Sivaperuman & Venkatraman 2015). Among the two coastal districts (Purba Medinipur & South 24 Parganas) of West Bengal, South 24 Parganas gained much more attention from researchers and naturalist owing to the presence of the world's largest coastal wetland: Sundarban Mangrove (home to about 360 bird species) (Venkatraman *et al.* 2019). In the Purba Medinipur district, which represents 27% coastal environment of West Bengal, only a few studies have been carried out on avifaunal diversity. Patra and Chakrabarti (2014) first reported 86 species of birds belonging to 10 orders and 35 families from Digha area.

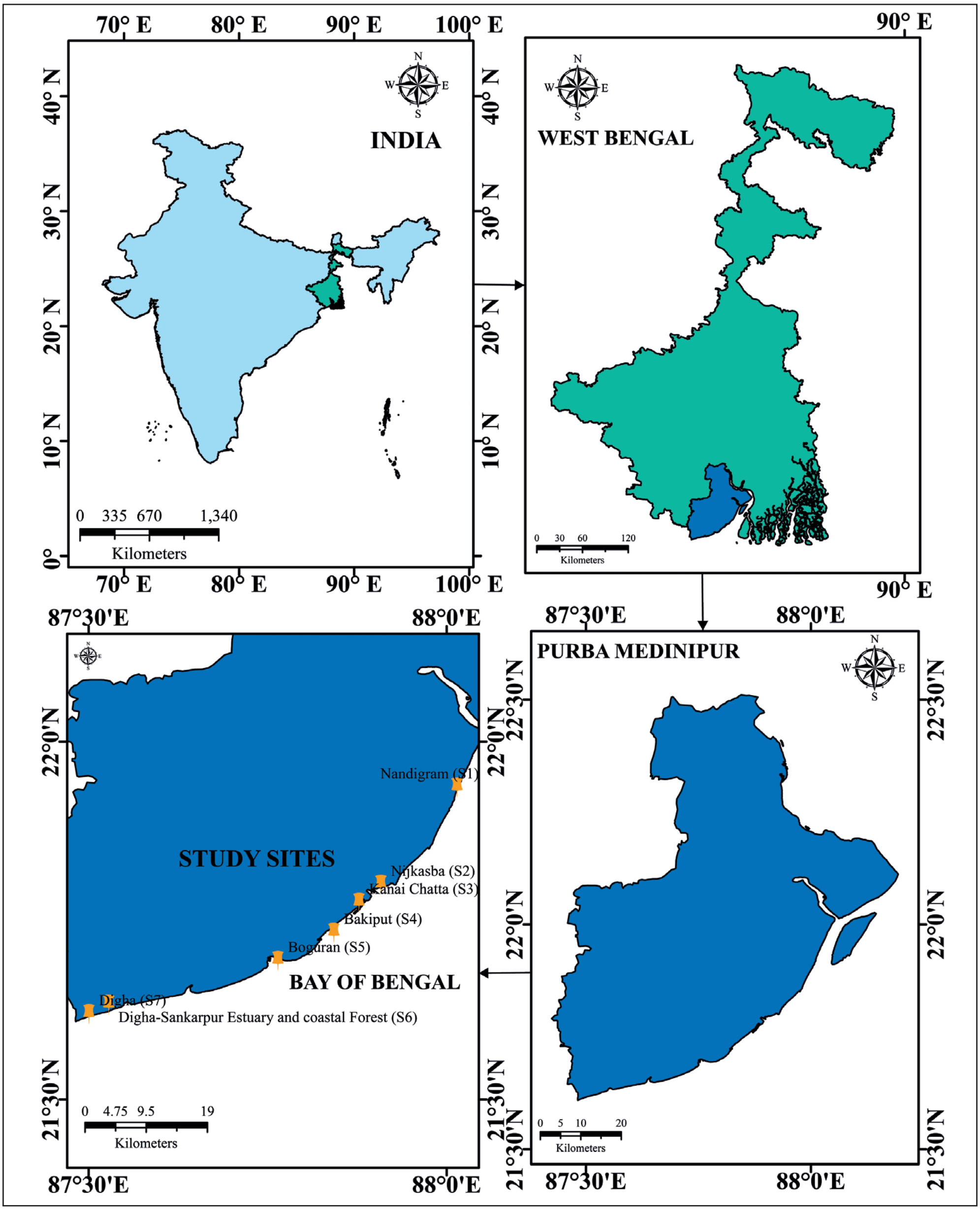

Figure 1. Location of the study area
1. ábra A vizsgált területek elhelyezkedése

Then Payra *et al.* (2017) reported 171 species of birds from six selected coastal sites of the district. In 2020, Payra (2020) reported 225 bird species from adjoining coastal areas of the district by compiling 29 newly recorded species, and all the previously published records from literatures and eBird. Recently, Abbott's Babbler *(Malacocincla abbotti)* has also been reported from the adjacent Coastal area of the district by Payra (2021a), and most recently, Payra (2021b) recorded Oriental Plover *(Charadrius veredus)* from Digha–Shankarpur estuary, which is an addition for the Indian mainland avifauna. Here in this paper, an attempt has been made to look into the complete avifaunal assemblages in adjoining coastal areas of the district.

Materials and Methods

Study area

Purba Medinipur district located at the southernmost part of West Bengal comes under the lower Indo-Gangetic Plain and Eastern coastal Plains. Covering an area of about 4,151.64 km^2, the district represents about 60 km of coastal tract. The eastern, northern and western parts of the district are dominated by almost entirely flat planes and the southern parts are covered by coastal plains. The tropical climate of this area provides annual rainfalls ranging between 1,400 mm and 1,700 mm. The temperature of the months of March to June usually ranges between 30 °C and 38 °C and remains lower (15–25 °C) during the months of November to February. Vegetation of the coastal forest of the district is chiefly dominated by *Casuarina equisetifolia*, but mixed vegetation of *Eucalyptus globulus* and *Acacia auriculiformis* are also seen. Undergrowth of the forest mainly consists of *Clerodendrum*, *Chromolaena*, *Lantana* and *Carissa* sp. Mangrove forest mainly composed of *Avicennia officinalis* and *Rhizophora mucronata.*

Data collection

Birds were monitored and recorded through opportunistic surveys between January 2020 and August 2022, at some selected places along the coast of Purba Medinipur district *(Table 1)*. Field surveys were mostly carried out between 6:00 a.m. to 11:00 am and 12:30 p.m. to 6:00 p.m., covering different types of habitat, such as coastal forest, freshwater wetlands, fish culture ponds, estuaries, mud flats, mangroves and sea beach. Identification was done with the help of guide books of Message and Taylor (2005), Grimmett *et al.* (2011) and Grewal *et al.* (2016). Systematic arrangement, scientific and common names follows Praveen *et al.* (2016). Threatened status of birds were adopted from the IUCN Red List (IUCN 2022). Residential status of the birds followed Grimmett *et al.* (2011).

Table 1. Details of the study sites along the coastal areas of Purba Medinipur district, West Bengal, India

1. táblázat A Purba Medinipur kerület part menti vizsgálati helyszínei (Nyugat-Bengál, India)

Study Sites	Latitude	Longitude	Altitude (Meter/Above the sea level)	Habitat
Nandigram (S1)	21°56′9.86″N	88° 0′52.09″E	0 – 8	Sea Shore (SS), Aquaculture land (AQ) and Agriculture field (AG)
Nijkasba (S2)	21°48′00.2″N	87°54′29.5″E	0 – 10	Sea shore (SS), Mangroves (MG) and Coastal Forest (CF)
Kanai Chatta (S3)	21°46′29.70″N	87°52′39.36″E	0 – 10	Sea shore (SS), Coastal Forest (CF), Mangroves (MG), Fresh Water Wetland (FW), Agricultural Field (AG), Aquaculture land (AQ) and Village woodland (VW)
Bakiput (S4)	21°43′58.6″N	87°50′32.9″E	0 – 4	Sea Shore (SS), Mangroves (MG) and Coastal Forest (CF)
Boguran (S5)	21°41′37.25″N	87°45′51.83″E	0 – 5	Sea Shore (SS), Coastal Forest (CF), Agricultural Field (AG) and Aquaculture Land (AQ)
Digha-Sankarpur Estuary and coastal Forest (S6)	21°37′56.68″N	87°31′41.19″E	0 – 6	Sea Shore (SS), Aquaculture Land (AQ), Agriculture Field (AG), Coastal Forest (CF) and Mangroves (MG)
Digha (S7)	21°37′9.23″N	87°30′1.82″E	0 – 15	Sea Shore (SS) and Coastal Forest (CF)

Results

36 species of birds belonging to 10 orders and 17 families are new additions to the area. Among these species, 30 species were classified as Least Concern, two species as Near Threatened *(Aythya nyroca, Calidris canutus)*, one species as Vulnerable *(Aythya ferina)*, two species as Endangered *(Calidris tenuirostris, Rynchops albicollis)* and one species as not assessed *(Porphyrio poliocephalus)*. Among these additional species, considering the species number, order Passeriformes was found to be richest with 10 species, followed by Charadriiformes with eight species, Anseriformes with seven species, Accipitriformes, Caprimulgiformes, Falconiformes, and Gruiformes each with two species, Columbiformes, Cuculiformes and Psittaciformes each with one species. Out of these 36 species, 17 species of birds were classified as waterbirds and the remaining 19 species were terrestrial. Details of the recorded bird species are given below.

Anseriformes: Anatidae

Common Shelduck *Tadorna tadorna*

This species breeds in Western Europe, the Mediterranean to central Asia through eastern Siberia and northeast China. Widespread during winter, migrates south to northern Africa, Iran, India, central China, south western Korea, Japan and Taiwan (Brazil 2009, Johnsgard 2010).

A total of 22 individuals of Common Shelduck were observed by PD, on 28 November 2020 at 6:44 am, at the coastline of Kanai Chatta. Then on 29 January 2021, four individuals were observed near the coast of Boguran. Between 11 to 28 February 2022, 13 individuals were frequently sighted at the sea beach in Kanai Chatta.

Ferruginous Duck *Aythya nyroca*

This species breeds in central and eastern Europe to central Asia and in northern Africa. During winter, it migrates southwards to Africa, the Mediterranean region, Persian Gulf, South and Southeast Asia (Vinicombe 2000, Brazil 2009).

Eight–nine individuals were observed by PD, between December 2020 and February 2021 at Kanai Chatta. AP observed about 15 individuals on 28 November 2020, at the fish pond near Digha-Shankarpur estuary, along with Gadwal, Red Crested Pochard and Lesser Whistling Duck. 12–13 individuals were frequently observed between 5 November 2021 and 15 March 2022 in Kanai Chatta.

Northern Shoveler *Spatula clypeata*

This species breeds in most areas of Nearctic and Palaearctic regions (Dubowy *et al.* 2020). Its wintering range extends from northern parts of North America, North and East Africa, Persian Gulf, South and Southeast Asia (Johnsgard 2010).

On 25 November 2020, PD observed one female individual in a freshwater wetland near the sea coast of Kanai Chatta.

Eurasian Wigeon *Mareca penelope*

The breeding range of this species extends from Iceland across northern parts of Europe and Palaearctic. In winter, it migrates to North Africa, east to India, Sri Lanka, Southeast Asia and Japan (Johnsgard 2010, Carboneras *et al.* 2020).

A single female was spotted on 28 November 2020 by AP, among the flocks of Ferruginous Duck and Lesser Whistling Duck in a fish pond near Digha-Shankarpur estuary. On 10 February 2022, PD observed two individuals of this species in Kanai Chatta. Again AM and PD observed near about 100 individuals in Haldi River, near Nandigram on 22 February 2022.

Northern Pintail *Anas acuta*

This dabbling duck breeds in northern parts of North America, Europe across the Palaearctic region. It spends the winter in North and Central America, North Africa, South and Southeast Asian countries (Johnsgard 2010).

On 24 October 2021, at 3:40 pm, PD noticed a female Northern Pintail sitting at sea beach of Bakiput coastal area.

Knob-billed Duck *Sarkidiornis melanotos*

This species is resident throughout sub-Saharan Africa, Madagascar, India, Nepal, and Bangladesh to Cambodia in Southeast Asia and in Southeast China (Johnsgard 2010, Birdlife International 2016a).

A single female was observed by AP, on 30 January 21, at 7:30 am, at Ghersai of Digha-Shankarpur Estuary.

Common Pochard *Aythya ferina*

The breeding range of this "Vulnerable" diving duck extends from western Europe, east through central Asia, Siberia and northern China. During winter a part of the whole population migrates to Europe, North Africa, the Mediterranean, Black and Caspian Seas, Indian Subcontinent to southern China and Japan (Brazil 2009, Johnsgard 2010).

Between 11 January 2022 to 16 January 2022, a male Common Pochard was frequently observed by PD, at Kanai Chatta, among the flock of Lesser Whistling Duck and Common Coot.

Columbiformes: Columbidae

Orange-breasted Green Pigeon *Treron bicinctus*

This species is found in the forests and well-wooded country. Resident in the Himalayas, hills of India, Bangladesh and Sri Lanka (Arlott 2015). In peninsular India, it is recorded from West Bengal and Chota Nagpur, south-eastern Ghats, also occurs in the western Ghats, hill ranges from northward Kerala through Karnataka to Goa (Kausik 2013).

PD observed one female on 11 April 2020, at 5:57 am, while feeding on the fruits of a fig tree at Kanai Chatta. Then, one male was recorded on 7 February 2021 at the same place. Further one female individual was sighted on 15 January 2022, at Digha-Sankarpur estuary.

Caprimulgiformes: Caprimulgidae

Jerdon's Nightjar *Caprimulgus atripennis*

This species is found on the forest edge. Resident in central and southern peninsular India (from Goa to Kerala, Tamil Nadu to eastwards Chota Nagpur Plateau) and Sri Lanka (Arlott 2015). The nearest known locality of this bird is located in Bhadutola Reserve Forest, Paschim Medinipur distrct, West Bengal (Giri & Maity 2021).

On 7 March 2022, at 6:30 pm, two individuals were noticed by PD, at Kanai Chatta. It was identified based on a call record and uploaded to eBird (Das 2022).

Indian Nightjar *Caprimulgus asiaticus*

This species is widespread resident throughout the south and Southeast Asia (BirdLife International 2016b, Grewal *et al.* 2016).

On 20 December 2020, at 5:35 pm a single individual was observed by AP. After that, two individuals were continuously sighted at the same place between 5:30 pm to 6:00 pm during 25 December 2020 to 7 January 2021.

Cuculiformes: Cuculidae

Common Cuckoo *Cuculus canorus*

The species has an extremely large range. Its breeding range extends from Iberia, Ireland, Russia, and Siberia to Japan. During winter, it migrates to Africa, south and Southeast Asia (Brazil 2009). In the Indian Subcontinent, it is known to breed in the hills of Pakistan, North, Central and Northeast India and the Himalayas (Grimmett *et al*. 2011).

One female individual was spotted by PD, on 2 November 2020 and 19 November 2020 respectively, at the mangrove forest, adjacent to the sea beach of Kanai Chatta. Again, AP and PD observed one individual at Digha coastal forest, on 11 March 2022.

Gruiformes: Rallidae

Grey-headed Swamphen *Porphyrio poliocephalus*

The species widely occurs from the Middle East countries to southern China and Thailand, throughout the Indian Subcontinent (Pranty & Callaghan 2020).

Single individual was observed by PD, on 11 April 2020 at Kanai Chatta. Then seven to nine individuals were frequently sighted by PD and AM at the same wetland from April 2021 to March 2022.

Slaty-breasted Rail *Lewinia striata*

In India, this species is confined to Indian Peninsula and Northeast India. It can also be found in Bangladesh, Sri Lanka, China and Southeast Asia (Grewal *et al.* 2016).

Two to four individuals were frequently sighted by PD, at Kanai Chatta, between 08 February 2022 and 15 March 2022.

Charadriiformes: Scolopacidae

Ruddy Turnstone *Arenaria interpres*

This species breeds near the Arctic coast of Northern Hemisphere (northern parts of North America, Europe and Asia). During winter, it moves south to the temperate and tropical regions South America, Africa, Asia and Australia (Brazil 2009). It is a scarce winter visitor to the Indian coast. Relatively common at northwest coast, as compared to eastern coastline of India (Grewal *et al.* 2016).

On 27 August 2021, at 2:58 pm, PD observed a single individual at Nijkasba. Again one individual (breeding plumage) was observed on 2 September 2021, at 9:50 am, in Bakiput.

Great Knot *Calidris tenuirostris*

The Great Knot is one of the long-distance migratory waders of the East Asian-Australian Flyway (Lisovski *et al.* 2016). It breeds in northeast Siberia and during winter it migrates to Australia, throughout the coastline of Southeast Asia, Indian Subcontinent and eastern coast of the Arabian Peninsula (Hayman *et al.* 2011).

The bird was continuously sighted by PD, during May 2020 to January 2022, at the coast of Kanai Chatta, Nijkasba, Bakiput and Boguran area.

In Kanai Chatta, eight individuals were observed on 10 May 2020 at 06:52 am. One individual was observed on 24 April 2021 at 01:07 pm. On 01 November 2021, 8:00 pm, about 33 individuals were recorded.

In Nijkasba, three individuals were recorded on 08 May 2021, at 12:34 pm. Similarly, on 22 June 2021, about 267 individuals (most of them were in non-breeding plumage, a few were in breeding plumage) were seen at the same place. On 05 July 2021, nine individuals were recorded. About 127 individuals were observed on 23 July 2021. On 11 August 2021, at 03:30 pm, 13 individuals were observed. About 47 individuals on 26 August 2021, at 01:00 pm. 24 individuals were observed on 03 November 2021, at 9:00 pm. Seven individuals were observed on 21 November 2021, at 11:00 pm. About 83 individuals on 21 December 2021, at 12:20 pm. and about134 individuals were observed on 02 January 2022, at 12:20 pm.

In Bakiput area, approximately 47 individuals were seen on 14 July 2021. Seven individuals were observed on 19 July 2021 at the same place. On 21 August 2021, at 01.00 pm, about 37 individuals were recorded.

In Boguran, approximately 31 individuals were observed on 04 November 2021, at 8:00 pm. Then, on 22 November 2021, at 3:00 pm, 11 individuals were seen at the same place.

Red Knot *Calidris canutus*

A medium sized shorebird which breeds in the high arctic region of Canada, Alaska, Greenland and Central and East Siberia. During winter, it migrates southward to the coastal zones of North and South-America, north-western Europe, West-Africa, South-Asia and Australia (Message & Taylor 2005, Hayman *et al.* 2011). In India, it is a rare winter visitor to the East Coast (Grewal *et al.* 2016).

Aapproximately 21 individuals (one in breeding plumage) were observed by PD, at Bakiput on 14 July 2021, at 2:30 pm. On 19 August 2021, at 7:30 am, about 29 individuals were observed at the same place. Then, on 02 October 2021, at 11:00 am one individual was observed at the same place.

At Boguran, one individual was spotted on 08 October 2021, at 3:40 pm.

Broad-billed Sandpiper *Calidris falcinellus*

This small sized wader breeds in Northwest Europe and Siberia. During winter, it migrates south to the coasts of Africa, South and Southeast Asia and Australia, covering long distances (Message & Taylor 2005, Brazil 2009).

One individual was observed by PD at 3.00 pm on 11 April 2021 at Bakiput. One individual was observed by PD, at 12.30 pm on 21 September 2021 at Nijkasba.

At the same location, one individual was observed on 26 September 2021, at 9:00 am. Then, at the same place, two individuals were seen on 09 October 2021, at 13:45 pm. One individual was observed on 19 October 2021, at 11:30 am. On 6 November 2021, at 11.30 am, 16 individuals were recorded. On 20 November 2021, at 12:00 pm, seven individuals were observed. On 21 December 2021, at 12:20 pm, about 27 individuals were seen. On 02 January 2022, at 12:20 pm, about 43 individuals were observed. On 02 February 2022, at 8:00 am about 36 individuals were recorded.

Dunlin *Calidris alpina*
This species breeds along the coastline of the Northern Hemisphere in Arctic and sub-Arctic region of northern Europe and Asia. During winter, it migrates southward to the coastal areas of North America, Africa, South and Southeast Asia and the Middle East countries (Message & Taylor 2005). This species is a common winter visitor to the Indian coast and comparatively common at northwest coast (Grewal *et al.* 2016).

From Nijkasba, two individuals (breeding and non-breeding plumage) were observed by PD, on 21 September 2021, at 11:30 pm. Again, two individuals (breeding and non-breeding plumage) were sighted at the same place on 26 September 2021, at 8.00 am. Four individuals were recorded on 09 October 2021, at 1:00 pm. on 19 October 2021, at 11:30 am, seven individuals were seen. On 06 November 2021, at 12:00 pm, six individuals were sighted. On 20 November 2021, at 12:00 pm, six individuals were observed. On 21 December 2021, at 12:20 pm, about three individuals were observed. On 02 January 2022, at 12:20 pm, three individuals and on 02 February 2022, at 8:00 pm, about six individuals were recorded.

Two individuals were observed at Kanai Chatta, on 18 October 2021, at 10:00 am.

Charadriiformes: Laridae

Indian Skimmer *Rynchops albicollis*
This globally 'Endangered' bird is confined to Bangladesh, India, Myanmar and Pakistan. Currently, its breeding range is restricted to India and western Bangladesh (Kabir *et al.* 2016). In India, it is known to breed in National Chambal Sanctuary, Narora Ramsar site, River Mahanadi, Son Gharial Sanctuary, River Ganga, Turtle Wildlife Sanctuary and Pong Dam (Ankit *et al*. 2018, Debata *et al*. 2019, Mital *et al.* 2019).

A single individual was continuously observed by PD, between 13 April and 16 April 2021 at sea beach of Nijkasba, during low tide between 12:00 pm and 5:30 pm. Most of the time, it was seen sitting among the mixed flock of Whiskered Tern, Common Tern, White-winged Tern and Black-headed Gull.

Bridled Tern *Onychoprion anaethetus*
This species widely occurs in Central American coast, western and eastern Africa coast, the Middle East, Southeast Asian and Australian coast (Brazil 2009, BirdLife International 2019). In India, it breeds on the West coast (Maharashtra coast and Lakshadweep), Andaman and the Maldives (Arlott 2015).

On 30 September 2021, at 8.30 am, a single individual was observed by PD and AM, at sea beach of Digha.

Slender-billed Gull *Chroicocephalus genei*
This species is resident in Pakistan and winter visitor to Bhutan, India, Nepal and Sri Lanka (Grewal *et al.* 2016).

During survey on 22 February 2022, at 12.30 pm, one individual was spotted by PD and AM, at the Junction of Hooghly River and Bay of Bengal, Nandigram.

Accipitriformes: Accipitridae

Changeable Hawk-eagle *Nisaetus cirrhatus*
This large bird of prey species widely distributed, ranging from eastwards India through Southeast Asia to Philippines and Greater Sundas (Gunawan & Noske 2017).

One individual was sighted by PD, on 26 August 2022, while sitting on a *Casuarina equisetifolia* tree at Kanai Chatta coastal forest.

White-eyed Buzzard *Butastur teesa*
This species occurs in Iran, Pakistan, throughout India, Nepal east to Bangladesh, Myanmar and China (BirdLife International 2016c).

One individual was sighted by PD, on 11 January 2022 at Kanai Chatta. Later, the bird was frequently observed at the same place between 13 January 2022 and 27 February 2022.

Falconiformes: Falconidae

Amur Falcon *Falco amurensis*
This species breeds in the Palaearctic region of East Asia from Transbaikalia to Ussuriland, and northeast Mongolia to North Korea and eastern China. During winter, it migrates to Sub-Saharan Africa via Indian Subcontinent (Ferguson-Lees & Christie 2001, Brazil 2009).

One individual was sighted by PD, on 19 November 2021 at 8.21 am while hovering at the sky in Kanai Chatta. A single female was recorded by AP on 26 November 2020, at the coastal fishery pond near Digha-Shankarpur estuary. Then, on 27 November 2020, five to six individuals were observed near the Digha Coastal Forest.

Eurasian Hobby *Falco subbuteo*
The distribution range of this bird extends from Europe, eastwards through central Asia and northern Africa. In winter, the species migrates to central and southern Africa, India and southern China (Brazil 2009). In the Indian Subcontinent, it breeds in the Himalayan region and widespread during winter (Arlott 2015).

One individual was sighted on 28 October 2020, at 7:16 am, in Kanai Chatta by PD. Then, a single individual was spotted by AP, on 27 November 2020, at about 2:54 pm while the bird was hovering along with the flock of Amur Falcon, near the Digha Coastal Forest. Again PD observed one immature individual at Dariyapur, on 31 March 2021, at 4.30 pm.

Psittaciformes: Psittaculidae

Plum-headed Parakeet *Psittacula cyanocephala*
This species is endemic to the Indian Subcontinent, distributed from northeast Pakistan to Bhutan and south to Sri Lanka (Collar & Boesman 2020).

On 23 September 2021, at about 8:00 am, PD observed one male Plum-headed Parakeet sitting on a bamboo tree, at Kanai Chatta.

Passeriformes: Dicruridae

Lesser Racket-tailed Drongo *Dicrurus remifer*
This species is a breeding resident in the Himalayan foothills, from Uttarakhand east to Myanmar (Grewal *et al.* 2016).

On 31 October 2020, PD observed one immature individual at the sea beach of Kanai Chatta.

Passeriformes: Irenidae

Jerdon's Leafbird *Chloropsis jerdoni*
This species is found in open forests and woodlands. The distribution of this bird restricted to Peninsular India and in Sri Lanka (Grimmett *et al*. 2011, Arlott 2015).

Single male was observed by PD, on 17 September 2020, at 01:36 pm, at Kanai Chatta. Again, it was sighted at the same place on 06 May 2021, at 7.00 am.

Passeriformes: Emberizidae

Black-headed Bunting *Emberiza melanocephala*
This species breeds in south-eastern parts of Europe to Iran. During winter, it migrates to northern, western and central India and Southeast-Nepal via Southern Pakistan (Grimmett *et al*. 2011, BirdLife International 2016d). In the Bengal plains of eastern India, it is an uncommon but widespread visitor with scattered wintering records (Adhurya *et al.* 2015).

On 27 September 2021, at 01:00 pm, one individual of Black-headed Bunting was observed by PD, at Kanai Chatta, while sitting on an electric wire along with the Scaly-breasted Munia and Baya Weaver.

Passeriformes: Phylloscopidae

Yellow-browed Warbler *Phylloscopus inornatus*
The species breeds in the forest of Ural Mountains to eastwards Republic of Sakha and Sakhalin, Northeast China. During winter, it migrates to South and Southeast Asia (Brazil 2009, Sander *et al*. 2017). In the Indian Subcontinent, it is distributed from central Nepal to Northeast India, Bangladesh.

On 13 November 2020, at about 12:10 pm, a single individual was sighted by AP, at the coastal forest of Shankarpur foraging among the canopies of *Casuarina* and *Eucalyptus* trees.

Green-crowned Warbler *Seicercus burkii*
This species is found in forest undergrowth and secondary growth. It breeds in the Himalayas wintering at lower elevations and in the northeast, and is sporadically recorded elsewhere in Indian Subcontinent (Arlott 2015).

On 13 November 2020, two individuals were observed by AP, between 12:40 pm to 01:20 pm, at coastal forest of Shankarpur foraging among the dense undergrowth of the coastal forest.

Greenish Warbler *Phylloscopus trochiloides*
This species is a breeding resident in the Himalayas. During winter, it is widespread in the lowland of peninsula India and Sri Lanka (Grewal *et al.* 2016).

A single adult individual was observed on 19 October 2020, at 3:41 pm while foraging among the canopy of *Vachellia nilotica* tree at Kuliyata, Purba Medinipur.

Passeriformes: Sturnidae

Bank Myna *Acridotheres ginginianus*
This is a resident species occuring mainly in the Indian subcontinent from Pakistan in west, through India to Bangladesh, Nepal and Bhutan and with old records of this species in southern Afghanistan (Abed & Salim 2019). In India, distribution records has been reported in the planes of northern and central India from the Himalayan foothills, Terai to a line from Mumbai to Balasore in Odisha and Visakhapatnam, Srikakulam and Chennai in the southernmost distribution (Ali & Ripley 2007, Taher *et al.* 2010).

A single individual was spotted by AP, on 8 December 2020, among a flock of Common Myna, near the sea beach of Shankarpur. The individual was foraging on the ground along with Common Myna. Again on 15 April 2022, at 10:00 am, one individual was sighted at Kanai Chatta.

Passeriformes: Muscicapidae

Red-breasted Flycatcher *Ficedula parva*
This species breeds across Eastern Europe and Central Asia. Non-breeding found mainly Pakistan and northern, western and central part of India, locally in southeastern Arabia (Mitrus *et al*. 2005, Porter & Aspinall 2010).

On 3 November 2020, a single individual was observed by AP at the coastal forest of Shankarpur.

Blue Rock-Thrush *Monticola solitarius*
This species is recorded from Southern Palearctic, Northern Afrotropics and Oriental regions (Choi *et al.* 2011). In the Indian region, it breeds in the Himalayas and during winter, it is widespread throughout the peninsula (Grewal *et al.* 2016).

One young individual was observed by AP, at the coastal forest of Shankarpur on 21 December 2020. It was foraging on the ground.

Passeriformes: Turdidae

Scaly Thrush *Zoothera dauma*

This species breeds in Western Himalaya and in east to Assam, south-central China, North-Indochina, Taiwan, West and North-Myanmar and North and West-Thailand. Non-breeding ranges recorded in Himalaya foothills, south China, lowlands of Northeast Indian Subcontinent and Southeast Asia (Robson 2014, Collar *et al.* 2020).

A single individual was observed by AP, on 14 November 2020, at 12:40 pm in the Shankarpur coastal forest feeding on ground under the dense bushes of Cashew tree. Later, on 19 December 2020, one individual was observed at the coastal forest of Shankarpur estuary. On 15 January 2022 at 1:00 pm, PD was observed one individual sitting on a *Casuarina equisetifolia* tree at Shankarpur coastal forest.

Discussion

As a result of current additional records of 36 bird species, 15 species have been recorded for the first time from Purba Medinipur. Thus, the total species richness of the avifauna in adjoining coastal areas of Purba Medinipur district increases to approximately 263 species (Payra 2020, 2021a, 2021b). The coastal area of Purba Medinipur district is located at the overlapping area of East Asia-Australasia Flyway and Central Asian Flyway, thus, the coastal area of the district comes under migratory flyways of many species of waders and waterbirds and served as an important stop-over and wintering site. Our present records with new locality of bird species will serve as valuable information to understand and monitor their distribution pattern and movement over time and place. The coast of Purba Medinipur possesses many coastal wetlands, including mudflats, freshwater wetland, fishery ponds, estuaries, mangroves and as well as coastal forests, are most likely major attractions for many bird species for roosting, feeding, and nesting. Thus, conserving such habitats will be a significant stepping stone towards the conservation and protection of birds of coastal area of the district.

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Table 2. List of the newly recorded birds from the adjoining coastal areas of Purba Medinipur district, West Bengal, India. Study Sites: S1-Nandigram; S2-Nijkasba; S3-Kanai Chatta; S4-Bakiput; S5-Boguran; S6-Digha-shankarpur Estuary; S7-Digha; Habitat: SS-Sea Shore; FW-Fresh Water Wetland; AQ-Aquaculture Land; CF-Coastal Forest; AG-Agricultural Field; VW-Village Woodland; MG-Mangroves; Residential Status: RE-Resident; WM-Winter Migrant; PM-Passage Migrant (Grimmett *et al.* 2011); IUCN Status: LC-Least Concern; NT-Near Threatened; VU-Vulnerable; EN-Endangered; NA-Not Assessed (IUCN Red List). ** = New records from Purba Medinipur District

2. táblázat Az újonnan rögzített madarak listája a nyugat-bengáli Purba Medinipur körzet szomszédos tengerparti területeiről. Területek: S1-Nandigram; S2-Nijkasba; S3-Kanai Chatta; S4-Bakiput; S5-Boguran; S6-Digha-shankarpur torkolat; S7-Digha; Élőhely: SS-tengerpart; FW-édesvizes élőhely; AQ-vízgazdálkodási terület; CF-parti erdő; AG-mezőgazdasági terület; VW-kezelt erdő; MG-Mangrove erdő; Lakossági állapot: RE-állandó; WM-téli migráns; PM-ideiglenesen itt tartózkodó (Grimmett *et al.* 2011); IUCN állapota: LC-Nem Fenyegetett; NT-Mérsékelten Fenyegetett; VU-Sebezhető; EN-Veszélyeztetett; NA-Nem értékelt (IUCN Red List). ** = Új adatok Purba Medinipur területéről

Sl. No.	Order/Family	Species name\ Scientific Name	Study Sites	Habitat	Residential Status	IUCN status
1	Anseriformes: Anatidae	Common Shelduck *Tadorna tadorna*	S3, S5	SS	WM	LC
2		Ferruginous Duck *Aythya nyroca*	S3, S6	FW,AQ	WM	NT
3		Northern Shoveler *Spatula clypeata*	S3	FW	WM	LC
4		Eurasian Wigeon *Mareca penelope*	S1,S3, S6	SS,FW,AQ	WM	LC
5		Northern Pintail *Anas acuta*	S4	SS	WM	LC
6		Knob-billed Duck *Sarkidiornis melanotos*	S6	AQ	WM	LC
7		Common Pochard *Aythya farina*	S3	FW	WM	VU
8	Columbiformes: Columbidae	Orange-breasted Green *Treron bicinctus***	S3, S6	CF,VW	RE	LC
9	Caprimulgiformes: Caprimulgidae	Jerdon's Nightjar *Caprimulgus atripennis***	S3	CF,MG	RE	LC
10		Indian Nightjar *Caprimulgus asiaticus***	S6	CF,VW	RE	LC
11	Cuculiformes: Cuculidae	Common Cuckoo *Cuculus canorus*	S3, S7	MG,CF	RE	LC
12	Gruiformes: Rallidae	Grey-headed Swamphen *Porphyrio poliocephalus*	S3	FW	RE	NA
13		Slaty-breasted Rail *Lewinia striata*	S3	FW	RE	LC
14	Charadriiformes: Scolopacidae	Ruddy Turnstone *Arenaria interpres*	S2, S4	SS	WM	LC
15		Great Knot *Calidris tenuirostris***	S2, S3, S4, S5	SS	WM	EN

Sl. No.	Order/Family	Species name\ Scientific Name	Study Sites	Habitat	Residential Status	IUCN status
16		Red Knot *Calidris canutus* **	S4, S5	SS	WM	NT
17		Broad-billed Sandpiper *Calidris falcinellus***	S2	SS	WM	LC
18		Dunlin *Calidris alpine***	S2, S3	SS	WM	LC
19	Charadriiformes: Laridae	Indian Skimmer *Rynchops albicollis***	S2	SS	RE	EN
20		Bridled tern *Onychoprion anaethetus***	S7	SS	RE	LC
21		Slender-billed Gull *Chroicocephalus genei***	S1	SS	WM	LC
22	Accipitriformes: Accipitridae	White-eyed Buzzard *Butastur teesa*	S3	AG,FW,VW	RE	LC
23		Changeable Hawk-eagle *Nisaetus cirrhatus*	S3	CF	RE	LC
24	Falconiformes: Falconidae	Amur Falcon *Falco amurensis*	S3,S6,S7	CF,AG,VW	PM	LC
25		Eurasian Hobby *Falco subbuteo*	S3, S7	FW,CF	WM	LC
26	Psittaciformes: Psittaculidae	Plum-headed Parakeet *Psittacula cyanocephala*	S3	VW	RE	LC
27	Passeriformes: Dicruridae	Lesser Racket-tailed Drongo *Dicrurus remifer***	S3	CF	RE	LC
28	Passeriformes: Chloropseidae	Jerdon's Leafbird *Chloropsis jerdoni*	S3	FW	RE	LC
29	Passeriformes: Emberizidae	Black-headed Bunting *Emberiza melanocephala***	S3	AG	WM	LC
30	Passeriformes: Phylloscopidae	Yellow-browed Warbler *Phylloscopus inornatus***	S6	CF	WM	LC
31		Green-crowned Warbler *Phylloscopus burkii***	S6	CF	WM	LC
32		Greenish Warbler *Phylloscopus trochiloides*	S6	VW	WM & PM	LC
33	Passeriformes: Sturnidae	Bank Myna *Acridotheres ginginianus*	S6,S3	AG	RE	LC
34	Passeriformes: Muscicapidae	Red-breasted Flycatcher *Ficedula parva***	S6	CF	WM & PM	LC
35		Blue Rock Thrush *Monticola solitaries*	S6	CF	RE & WM	LC
36	Passeriformes: Turdidae	Scaly Thrush *Zoothera dauma*	S6	CF	WM	LC

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The Wilson's Phalarope *Phalaropus tricolor* population and feeding activity at Lake Titicaca

Angel CANALES-GUTIÉRREZ[1]*, Gelvi CANALES-MANCHURIA[2] & Fabrizzio CANALES-MANCHURIA[3]

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Abstract A population estimation of Wilson's Phalaropes was conducted in the Confinada Lagoon of the inner bay of Lake Titicaca in the city of Puno between August and May of 2016/2017, 2017/2018 and 2018/2019. We employed the quadrat method of population estimation with three repetitions using 10×50 mm binoculars between 06:00 and 08:00 h. We recorded population fluctuations in August and September (immigration season) and April and May (emigration season). We counted a maximum population of 112,000 Wilson's Phalaropes during the immigration season, and then in the emigration season. During their stay of approximately 8 months, the birds feed on water fleas, insects and detritus amounted to 146,496 t. The inner bay of Lake Titicaca is an important aquatic habitat for these migratory birds, which has a positive impact on the contribution to the decontamination of the lake.

Keywords: behavior, emigration, immigration, feeding, migratory species

Összefoglalás A Wilson-víztaposó populációjának becslését 2016/2017, 2017/2018 és 2018/2019 augusztusa és májusa között végeztük Puno városában, a Titicaca-tó belső öblének Confinada lagúnájában. A populációbecsléshez kvadrát-alapú módszert alkalmaztuk három ismétléssel, 10×50 mm-es kézitávcső használatával, 06:00 és 08:00 óra között. Augusztus és szeptember (érkezési időszak), illetve április és május (távozási időszak) között rögzítettük az állomány egyedszámának ingadozását. Az érkezési időszakban, majd a távozási időszakban számláltuk a legtöbb, mintegy 112 000 Wilson-víztaposót. A madarak a Titicaca-tó belső öblének környezetében való nyolc hónapos tartózkodásuk alatt becslésünk szerint 146 496 tonna szerves törmeléket, rovarokat, vízibolhákat, rákféléket és egyebeket fogyasztanak. A Titicaca-tó belső öble fontos élőhely ezeknek a madaraknak, amelyek pozitív hatással vannak a tó vízminőségére.

Kulcsszavak: viselkedés, kivándorlás, bevándorlás táplálkozás, vonuló faj

[1] *Ecology Program, Faculty of Biological Sciences, Universidad Nacional del Altiplano de Puno, Peru*
[2] *Professional School of Environmental Engineering, Universidad Nacional Jorge Basadre Grohmann de Tacna, Peru*
[3] *Master of Science: with mention in Safety and Environment, Graduate School, Universidad Nacional San Agustín de Arequipa, Peru*
** corresponding author, e-mail: acanales@unap.edu.pe*

Introduction

Wetlands have a high diversity of wild flora and fauna and act as breeding, feeding and resting areas for migratory birds, and these types of ecosystems are important to migratory shorebirds such as Wilson's Phalaropes *(Phalaropus tricolor)*, which start their journey in the Northern Hemisphere and then migrate to South America (Miranda *et al*. 2015). They reproduce in the United States and Canada, and spend their winters mainly in saline lakes in the Andes of South America. Their estimated population is 1.5 million individuals; however, they have suffered a significant decline (Lesterhuis & Clay 2010). This species feeds on small crustaceans, larvae and adults of insects (De la Peña 2016).

Out of the birds reported at Lake Titicaca, there are 95 resident species and 40 species come from other latitudes: 17 species are Nearctic migrants, 10 species are austral migrants, and 13 species perform latitudinal migration from the Peruvian Andes to the coastal region. Nearctic migrants are at Lake Titicaca from September to March, and southern migrants are from April to August (Pulido 2018). Saline plants provide refuges and feeding grounds for migratory shorebirds in the tropics, and up to 107,081 Wilson's Phalaropes individuals have been recorded (Del Pezo 2018).

Wilson's Phalaropes usually exhibit a twisting and turning behavior when feeding in freshwater sites for several days, converging on eddy fronts and internal waves that apparently provide an easily accessible and constant supply of food (DiGiacomo *et al*. 2002). In Cuba, Wilson's Phalaropes are a rare species with only two previous records in the country (González *et al*. 2018). Additionally, in Argentina, they are rare in the RAMSAR site and Vicuña Provincial Reserve of Argentina (Lobo & Marano 2017), while in Colombia, they have a distribution range including several localities (Ruiz-Guerra 2012). In the Pisco area of Peru, this species is habituated to human presence (Astohuaman & Espejo 2003), phalaropes having the highest abundance of all shorebirds (Podestá *et al.* 2017).

Wetlands are important habitats for aquatic birds, which are some of the most charismatic fauna inhabiting wetlands, with a greater flexibility than that of fish because they can make use of these environments during only part of their annual cycle (López-Lanús & Blanco 2005).

Freshwater wetlands are feeding areas where there are high concentrations of the Scolopacidae family (Pulido *et al.* 2020, Ruiz-Guerra & Cifuentes 2021), which dominate the avifauna assemblages with a high abundance and diversity of boreal and austral migrants (Pisconte *et al*. 2020). Additionally, in some lagoons, there is a greater representation of the Scolopacidae family (Ruiz-Santillán *et al*. 2020). In Argentina, Wilson's Phalaropes are observed in high numbers in hypersaline lagoons; within a total of 502 habitats, 51 (10.1%) represent feeding areas of phalaropes, with more than 10,000 individuals recorded in each area (Dodyk 2020). In Central America, there are 68 nonbreeding migratory species such as Wilson's Phalaropes (Herrera 2021), of which up to nine have been recorded in the migratory flyways of Argentina, Paraguay and Brazil. However, these habitats are being fragmented by agricultural activities and inadequate water resource management (Pulido *et al*. 2021).

Many species of migratory birds feeding on invertebrates, including mollusks, crustaceans and insects (Villavicencio 1989) in the inner bay of Lake Titicaca in the city of Puno have been observed (Canales 2004), being an important component of the water pollution process (Rodríguez-Guzmán & Gilbes-Santaella 2009), as they are related to the production and flow of pollutants in the water (Ekercin 2007), which mainly restricts the use of water for human consumption (Torres-Dowdall *et al*. 2010). Organic and inorganic pollutants discharged into domestic water or run-off water (Kutschker *et al.* 2009) affect the population dynamics of aquatic flora and fauna (Quintero *et al.* 2010, Bracho *et al*. 2016) and have a negative impact on the quality of the aquatic ecosystem (González 2012).

Our research objective was to quantify the amount of feeding (detritus, water fleas, insects and crustaceans) by Wilson's Phalaropes individuals in the inner bay of Lake Titicaca in the city of Puno.

Materials and Methods

Study area

The research was carried out in the Confinada Lagoon Bay of Lake Titicaca in the city of Puno, located at 3,810 m above sea level, with the coordinates of 15°49'58.95"S and 70°01'01.67"W and a temperature range between 5 and 20 °C. This lagoon was formed by the filtration of the lake, the addition of rainwater and the wastewater from the city of Puno. It has an area of approximately 20 ha and an average depth of 2.5 m.

We recorded the presence of Wilson's Phalaropes from 06:00 to 08:00 h during August and September (immigration stage) and April and May (emigration stage) in 2016, 2017, 2018 and 2019. For the counting of individuals, we applied the quadrat method, starting

Figure 1. Study location, Confinada Lagoon in the inner bay of Titicaca ake Puno, Peru
1. ábra A vizsgálati terület, Confinada laguna a Titicaca Puno-tó belső öblében, Peruban

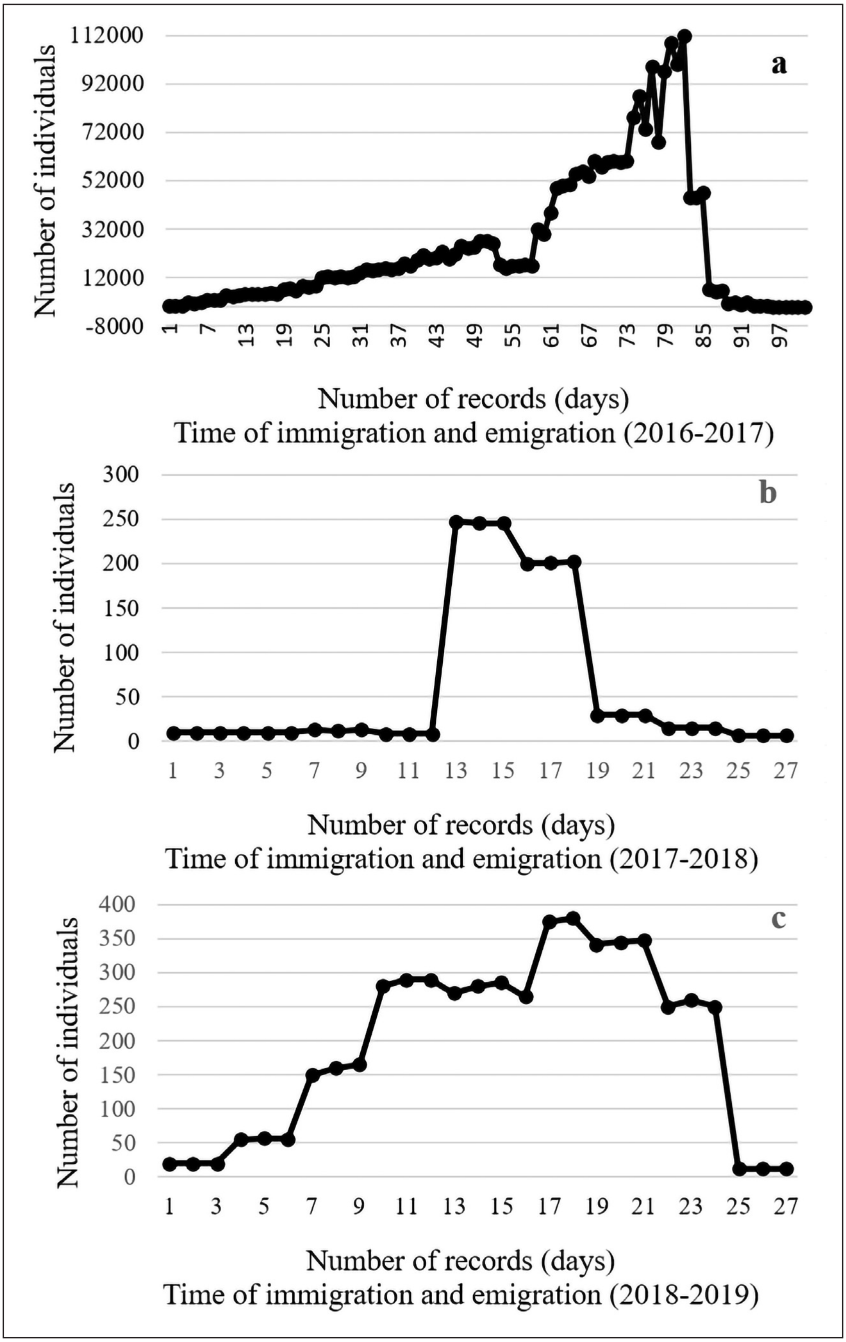


Figure 2. Population estimation of the number of individuals during immigration and emigration of Wilson's Phalaropes in the inner bay of Lake Titicaca, Puno. (a), 2016/2017 (b) 2017/2018 (c) 2018/2019

2. ábra A Wilson-víztaposók egyedszámának becslése a bevándorlás és a kivándorlás során a Titicaca-tó belső öblében, Punóban. (a) 2016/2017, (b) 2017/2018, (c) 2018/2019 from a fixed point located in the central part of the lagoon after dividing the lagoon into four quadrants. For the population estimation of this migratory species, we used Bushnell 10×50 mm binoculars.

We counted the number of individuals in all samples beginning in the southern part of the lagoon and ending in the northern zone. In each of the quadrants, we recorded three replicate counts, and then we obtained the average number of individuals for each quadrant *(Figure 1)*. The replicates allowed us to have a better approximation of the population estimate of Wilson's Phalaropes when they were carrying out their feeding activities (capturing water fleas, insects and detritus) in the confined lagoon.

The consumption of organic detritus, insects, water fleas, crustaceans, among others, by migratory birds has been calculated on the basis of 10% of the average weight of the migratory bird species evaluated (Canales 2004).

Results

Population estimation

The number of individual Wilson's Phalaropes during the 2016/2017 immigration and emigration season had a mean of 24,558.44 individuals, with a minimum value of 10 individuals and a maximum value of 112,000 individuals *(Figure 2a)*, while the population estimate of Wilson's Phalaropes during the 2017/2018 immigration and emigration season had a mean of 60.04 individuals, with a minimum value of seven individuals and a maximum value of 247 individuals arriving in the Confinada Lagoon *(Figure 2b)*.

The number of Wilson's Phalaropes during the 2018/2019 immigration and emigration season had a mean of 194.13 individuals, with a minimum value of 12 individuals and a maximum value of 380 individuals arriving in the Confinada Lagoon *(Figure 2c)*. The presence of Wilson's Phalaropes in this area occurs from August onward, when the immigration of thousands of individuals of Wilson's Phalaropes begins. After feeding, they emigrate to the United States and Canada between April and May.

Feeding activity

During their stay in the bay, Wilson's Phalaropes feed on Water Fleas *(Daphnia pulex)*, detritus, insects, algae and crustaceans, and this species is also beneficial for oxygenating the waters, reducing inappropriate odors, promoting birdwatching tourism, improving the landscape and interacting with other bird species, which are associated with the presence of this migratory bird.

The 112,000 migratory individuals of Wilson's Phalaropes have fed on organic detritus, insects, water fleas, crustaceans and others during an eight-month stay in the inner bay of Lake Titicaca, a total of 146,496 kg *(Table 1)*.

Table 1. Amount of feeding of organic detritus, water fleas, insects, crustaceans, etc. by individuals of Wilson's Phalaropes

1. táblázat A Wilson-víztaposók táplálékbázisaként szolgáló szerves törmelék, vízibolhák, rovarok, rákfélék stb. mennyiségi eloszlása

Species	Number of individuals	Daily consumption in kg (10% of their weight corporal= 0.00545 kg)	Total month (kg)	Total for 8 months (kg)
P. tricolor (Average weights 0.0545 kg)	112,000	610.4	18,312	146,496

Discussion

Population estimation

This migratory bird arrives to feed (Lesterhuis & Clay 2010) on small crustaceans, larvae and adult insects (Miranda *et al.* 2015). Wetlands have a great diversity of flora and act as breeding, feeding and resting centers for these migratory birds, whose estimated population is 1.5 million individuals (Lesterhuis & Clay 2010); however, the migration of 2016/2017 was unusual for Lake Titicaca Bay in the city of Puno (Confinada Lagoon) due to the high number of individuals, i.e., reaching up to 112,000 individuals, while in 2017/2018 and 2018/2019, only very few individuals arrived (not exceeding 380 individuals). This phenomenon could be due to environmental factors such as the disturbance of their habitat that they use as stopover sites on their migratory route; or due to a greater availability of food that could have been found at Lake Titicaca. Moreover, Ocampo-Peñuela (2010) suggests that the presence of water is the main compass of the migratory movements of many birds, where, in a dry season, large numbers of individuals are observed in a single habitat. Furthermore, according to Torres *et al.* (2006), sexual maturity and the accumulation of fat could influence the abundance of migrating individuals.

The Confinada Lagoon, where this species feeds from August to May, is an important habitat for aquatic birds (López-Lanús & Blanco 2005).

Similarly, in an artificial pool of a salt company in Ecuador, up to 10,7081 individuals of Wilson's Phalaropes have been recorded (Del Pezo 2018).

Feeding activity

The 112,000 individuals of Wilson's Phalaropes, in the eight months of permanence in the surroundings of the inner bay of Lake Titicaca in the city of Puno, feed on organic detritus, insects, water fleas, crustaceans and others, consuming about 146.496 t, this result has been estimated based on the average of 54.45 g, weight of males and females of Wilson's Phalaropes individuals (Salvador 2014), considering the minimum consumption of each individual in at least 10% of its weight, which corresponds to 5.45 g/each individual/day *(Table 1)*.

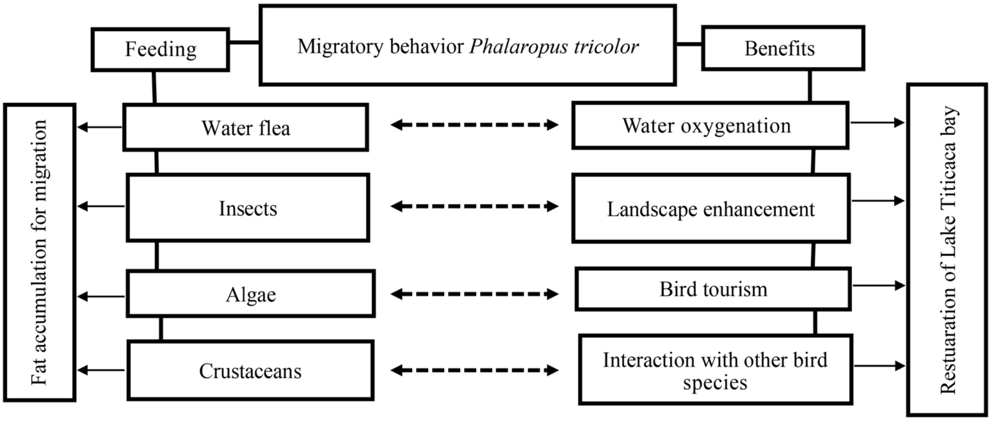
According to De la Peña (2016), Wilson's Phalaropes feed on small crustaceans, larvae, insects and also have a preference for sites with abundant flies and microbial substrates

(Franco & Conover 2019), and also, they depend on abundant invertebrate prey (Franco & Conover 2021), because shorebirds increase their ability to replenish energy reserves, while migrating to North America and Canada (Andrei *et al*. 2009) and they must accumulate fat during the premigratory period (Harrington *et al.* 1991).

Therefore, the inner bay of Titicaca is an important feeding habitat for migratory birds, which accumulate fat as an energy reserve that serves for oxygen transport, hypertrophy of flight muscles and the development, integration and synchronization of migratory behaviour (Villaseñor 1994), using the accumulated fat as the "fuel load" for migration (Grandío 1998), presenting good conditions of fat status and physical condition of the migrants (Pérez 1999).

Finally, these migratory birds have a positive impact on the contribution to the decontamination of the inner bay of Lake Titicaca in the city of Puno, due to the type of food they eat (Canales 1989), such as insects and detritus, among others (Canales 2004), also providing the benefits of oxygenation of the water. Water oxygenation is a fundamental aspect for aquatic life, where its absence can cause reduction and death of the species present in the body of water (Shaghaghi *et al.* 2020).

Graphical abstract



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