WINTER DISTRIBUTION AND MIGRATORY STRATEGIES OF EURASIAN SPOONBILLS (*PLATALEA LEUCORODIA*) FROM THE PANNONIAN BREEDING POPULATION: ARE THEY LONG-DISTANCE MIGRANTS?

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In this paper, the wintering characteristics of the Eurasian Spoonbill (Platalea leucorodia) breeding in the Carpathian Basin (Pannonian population) were analysed. The data of 305 wintering Spoonbills marked with colour-rings in Hungary were used. A significant part, 80% of the Spoonbills wintered in Africa, while 20% spent the winter in Europe and only two birds in the Asian part of western Turkey. The most important wintering sites were in the central part of North Africa (in Algeria, Libya, but mainly Tunisia) and Italy. The tidal area in the Gulf of Gabes in Tunisia was the most important area where a significant proportion, 65% of all wintering Spoonbills spent the winter. This study provided new evidence of Spoonbills occurring in Saharan wetlands (Chott Tindla in Algeria) in winter. 2% of the resighted Spoonbills were reported from the wetlands of the Sahel in Sudan, Nigeria, Niger, Mali, Mauritania, and Senegal. European winterers were mainly found in Italy and, to a lesser extent, in the Balkans and the Carpathian Basin. The mean distance between the natal colonies and the wintering areas was 1,535 km. Spoonbills migrated in a south-southwestern direction (mean: 213°) to reach their wintering sites. In the Hungarian population, most specimens (94%) were short-distance migrants (wintered north of 22°N), 2% were long-distance migrants, and 4% were residents. However, the proportions of the residents and short-distance migrants are supposed to be overestimated and the proportion of the long-distance migrants is likely to be underestimated due to the lack of observation effort in sub-Saharan Africa. However, based on the winter census data and the proportion of ringed individuals of Hungarian origin in the wintering flocks, I estimated that the lack of observation effort would only slightly modify the result. There were two shifts in migratory strategies on an individual level: a resident Spoonbill became a short-distance migrant, and a short-distance migrant became a long-distance migrant by a following winter. While most of the East Atlantic Spoonbills are long-distance migrants, the results of this study indicate that most birds in the Pannonian population are likely to be rather short-distance migrants. The results of the GPS tracking also confirm that most Pannonian Spoonbills are short-distance migrants and support the main conclusion of this paper.

Key words: short-distance migration, long-distance migration, resident, avian migration, Mediterranean, Gulf of Gabes, Sahara, Sahel, Carpathian Basin.

INTRODUCTION

The nominate race of the Eurasian Spoonbill (*Platalea leucorodia leucorodia*) (hereafter Spoonbill) has a wide but patchy breeding range from Iberia and Atlantic West Europe east to Central and East Asia, and the breeding area extends south to the Persian Gulf, India, and Sri Lanka (Ткірlet *et al.* 2008). The Spoonbill is a specialist waterbird of wetlands with shallow water because it can forage only in water that is not deeper than 40 cm (Рідмісzкі & Végvári 2015, Sullender *et al.* 2016).

The nominate subspecies of the Spoonbill is a migratory race and has at least three distinct flyway populations in Europe (TRIPLET et al. 2008). 1) Generally, Spoonbills breeding in West Europe migrate along the East Atlantic coast and winter in the Netherlands, British Isles, France, Iberia, and the Atlantic coast of West Africa between Morocco and Senegal, with a significant density in Mauritania (de le Court & Aguilera 1997, Triplet et al. 2008, Lok et al. 2011). 2) Spoonbills breeding in East Europe (east of the Sea of Azov) are likely to move to the Indian subcontinent (Pakistan and India) to winter there (TRIPLET et al. 2008). 3) Breeders of Central and Southeast Europe mainly use the Central and East Mediterranean flyways. One of their most important flyways is the Adriatic Flyway which connects the Carpathian Basin and the wintering sites in the central part of the Mediterranean areas (PIGNICZKI et al. 2016). The Central and Southeast European birds migrate to South Europe, the Middle East (including Oman in the Arabian Peninsula), North Africa, and the Sahel (Müller 1984, CEPAK 2008, TRIPLET et al. 2008, VOLPONI et al. 2008, Pigniczki 2009, 2010, Kralj 2013, Pigniczki et al. 2016, Stanković 2018, Kiss et al. 2019). Recently, it has been proposed to split this flyway population into two separate flyway populations because the Central European (the breeders of Czechia, the Carpathian Basin, Italy, and Montenegro) and the Southeast European Spoonbills (the breeders of the eastern Balkans, and West Turkey) have quite different flyways with little overlap and between their distinct breeding areas the gene flow is marginal (PIGNICZKI et al. 2016, 2017, PIGNICZKI 2017b, CHAMPAGNON et al. 2019). The Central European breeding population (breeders of Czechia, Slovakia, Austria, Hungary, Western Romania, Croatia, Serbia, Montenegro, and Italy) was estimated at 1567-1657 breeding pairs in 2018 (CHAMPAGNON et al. 2019).

Within the Central European breeding population, there is a geographically distinct breeding subpopulation, the Pannonian population, which breeds in the Carpathian Basin in Hungary, East Austria, South Slovakia, Western Romania, Croatia (north of the River Sava), and Serbia (north of the Danube) (PIGNICZKI & VÉGVÁRI 2015). The Hungarian population was estimated at 850–1,300 breeding pairs in 2002–2013 and 550–900 breeding pairs in 2014–2020 (PIGNICZKI 2021). The number of breeding pairs in Hungary fluctuates annually but had a declining trend during the last decade (PIGNICZKI 2021). The cause of the decline seems to be complex on the breeding grounds: ecological conditions (dry years), weather circumstances (hail, cold weather with rain), predation of eggs and chicks by wild boar (*Sus scrofa*), and collision with power lines affect the number of the breeding pairs, the breeding success, and the survival of individuals (TRIPLET *et*

al. 2008, PIGNICZKI 2015, 2017*a*, 2021, PIGNICZKI & VÉGVÁRI 2015, PIGNICZKI *et al.* 2017, 2019). Not only the circumstances in the breeding areas have an impact on the population dynamics, but threats also occur in wintering areas. In the case of several waterbirds, correlations were found between unfavourable wintering conditions and declining breeding populations during the following breeding season (Zwarts *et al.* 2009). Therefore, for nature conservation purposes, it is essential to map the exact wintering areas and study the wintering ecology of migratory birds because winter ecological conditions can have an impact on survival and even on subsequent breeding success (BAIRLEIN 2003).

Based on the results of colour-ringing, the migratory routes with the stopover sites (PIGNICZKI *et al.* 2016) and the dispersal of the Spoonbills in the Carpathian Basin hatched in Hungary were studied (PIGNICZKI & VÉG-VÁRI 2015). The origin of foreign marked individuals in Hungary was also described (PIGNICZKI 2017*b*). However, a detailed analysis of wintering is still missing in the case of the Hungarian population. The Hungarian Spoonbill database is the largest in continental Central Europe and has recoveries and resightings from the widest geographic area. The main purposes of this paper are to provide novel, extended information on the wintering areas of the Hungarian population and to estimate the proportion of different migratory strategies in the Pannonian breeding population.

MATERIAL AND METHODS

Study area – All the records of Spoonbills were used that were marked with colour-rings in Hungary when they were *pulli*. Individuals were captured in the heronries of the Great Hungarian Plain, the Kisalföld, and the heron colonies around Lake Balaton. The ringed individuals were recovered or observed later in several countries across Europe, Asia, and Africa.

Ringing Spoonbills and ring reading – The colour-ringing of Spoonbills started in Hungary in 2003. Three systems were used: 1) a combination of two plastic rings with the same or different colours on rings and with an engraved, two-character-long alphanumerical code (the same code on both rings of a single individual); 2) a unique colour-combination of six rings, one of them is a blue ring with a flag; 3) an engraved white plastic ring with a unique, black, four-character-long alphanumerical code which always starts with a 'J' (PIGNICZKI 2015, PIGNICZKI & VÉGVÁRI 2015).

Spoonbill chicks were captured in the colony in the reedbed while they were unable to fly. Spoonbill nestlings can be ringed when they are approximately three weeks old or older. Colonies were approached if the weather circumstances were favourable (not too cold or hot, with no strong sunshine, no rain, and no strong wind). Ringer teams tried to avoid visiting colonies if there were eggs or small, bare chicks in the nests because of their sensitiveness. During each ringing action, one or two teams ringed the chicks. Each ringing team consists of four to five persons: a licensed bird ringer, a person who holds the chicks during marking, and two to three persons responsible for capturing the chicks and letting them stay on their nests during the marking action. A single ringing action was not longer than 1–1.5 hours. Ringer teams might have returned to the same colony at least a week after the first ringing action to mark other chicks in a second ringing action.

The fledged, colour-ringed Spoonbills were reported by professional ornithologists, amateur birdwatchers, and nature photographers working in Europe, Asia, and Africa. Occasionally, dead Spoonbills were reported via the internet because their metal rings contain an address of a website to report the data. Generally, the ring reading and reporting efforts are unequal in the known and the potential wintering areas (KRALJ et al. 2012). Along the Adriatic/Central Mediterranean Flyway, a high observation effort is supposed in Italy and Hungary. In Tunisia, the ring reading effort was high during certain periods in winter. For example, a French Team from Tour du Valat had three, and I had seven expeditions together with Tunisian and British ornithologists to Tunisian wetlands in winter to find colour-ringed Spoonbills and read their rings. Local teams also observed Spoonbills in Tunisia and Libya during the International Waterbird Census (IWC). The ring reading effort is supposed to be lower in the Balkans, Algeria, and the central and eastern parts of the Sahel. Along the East Atlantic Flyway, the ring reading effort is very high in West European countries and relatively high in Morocco, Mauritania, and Senegal as well. Several ring reading expeditions have been organised to Mauritania and Senegal (Lok 2013). The effort to read colour-rings along the East Mediterranean Flyway is generally low but high in Israel (PIGNICZKI et al. 2016, KISS et al. 2019).

Data selection – The Hungarian dataset was used for this study. Bird ringers marked 2,512 chicks with colour-rings between 2003 and 2020 in Hungary. 1,653 (65.8%) of the ringed chicks were observed and/or recovered later 11,130 times. In this paper, data from the wintering areas during the core of the wintering period were used. The database contains records reported until the end of October 2021.

The wintering records of Spoonbills ringed as chicks in the Hungarian colonies between 2003 and 2020 were used for this study. The core wintering period for Spoonbills was determined depending on geographic regions and age groups: 1) In the case of the Carpathian Basin, a bird was treated as a winterer if it was observed in December or January and in the case of immatures (2cy and 3cy) also in February. 2) It is difficult to separate the Spoonbills that winter in the Mediterranean areas from those that only stop there before/after their trans-Saharan migration (ISENMANN et al. 2005). The late autumn migration records of Spoonbills that were observed in Europe (except the Carpathian Basin), the Middle East, or North Africa were separated from wintering records by the following rules: juvenile Spoonbills were treated as wintering individuals if they were observed on or after 20 November, while non-juveniles were treated as winterers if they were seen on or after 5 November. These dates are practical to separate the wintering short-distance migrants from long-distance migrants that stopped in the Mediterranean sites while they are heading to the Sahel. Generally, the last non-juveniles leave Hungary by the first third of October, while the vast majority of the juveniles by the end of October. The main departure period of Spoonbills falls between the second half of August and the first days of October during the autumn migration in the Carpathian Basin (the median of the last observations in the Carpathian Basin: 15 September) (PIGNICZKI 2015). On spring migration, adults reach their breeding areas in the Carpathian Basin from the last third of February, while immatures appear there later, from April. The spring migration of most adults falls between the second half of February and the first half of April. Spoonbills reported from North Africa, the Middle East or Europe (except the Carpathian Basin) were treated as wintering birds by the following rule: all data of immatures (2cy and 3cy) were treated as wintering data in February, while observations were handled as wintering in the case of adults (4cy or older ones) until 10 February. 3) If a Spoonbill was reported from south of 22° N latitude at any time of the year, that record was also treated as a wintering record.

It might have happened that a small proportion of the individuals treated as winterers were on their late autumn or early spring migration in Europe or North Africa. Contrastingly, some individuals observed only outside the core wintering periods might have also been wintering individuals; however, their data were not used in this study.

Definitions – A European breeding bird is a short-distance migrant if it spends the winter north of the Sahara and a long-distance migrant if it moves to winter south of the Sahara, according to a widely accepted definition (JENNI & KÉRY 2003, ZWARTS *et al.* 2009). Based on that definition, a Spoonbill hatched in Hungary was treated as 1) a resident if it stayed in the Carpathian Basin during winter; 2) a short-distance migrant if it left the Carpathian Basin and wintered north of 22° N latitude; and 3) a long-distance migrant if it wintered south of 22° N latitude.

Statistical analysis – During data analysis, if percentage values were calculated, they were generally compared with the number of wintering birds (n=305) but also, in some cases, with the number of all marked individuals (n=2,512). To make it clear, it was always mentioned in the text.

Coordinates were collected in WGS84 coordinates. To calculate distance and direction, the 'fossil' package was used in the program R (VAVREK 2011, R CORE TEAM 2020). The distance and the direction of the movements were calculated for each record from the coordinates of the natal colony as the starting point and the coordinates of the wintering area as the endpoint. If a single individual had multiple wintering records, the record that belongs to the southernmost latitude was used for the descriptive statistics (mean, median, circular statistics). The PAST statistical programme (HAMMER *et al.* 2001) was used for the circular statistical analysis. For the entire wintering population and each group with different migratory strategies, the mean directions with 95% confidence intervals were determined in PAST.

RESULTS

The total database contained 684 wintering records of 305 individuals. 2,512 chicks got colour-rings in the Hungarian colonies; thus, we know the wintering areas of 12.1% of the colour-ringed population. 14 of 305 (4.6%) individuals were reported as carcasses during the winter; however, before they died, four were observed in their wintering sites.

Wintering areas and migratory strategies

Two (0.7%) of 305 specimens were reported as winterers from the Asian part of West Turkey, 59 (19.3%) individuals from Europe, and the majority, 245 (80.3%) birds from Africa (Figs 1 & 2, Table 1). Numbers, in the case of Europe and Africa, include one (0.3%) individual that was detected as a winterer both in Europe (Hungary) and in a following year in Africa (Tunisia). Two (0.7%) juvenile individuals were noted as European winterers that were detected during migration in a subsequent year in Africa. The new African wintering areas of those two individuals are not known exactly. One of them was seen on 20 October and 8 December in 2007 in Sardinia (Italy) during its first winter and was observed on 31 October and 1 November in 2009 at Lake

Tunis (Tunisia) when it was 3 calendar year (3cy) old. The other was detected in Sicily (Italy) on 22 January 2007 during its first winter and two years later, it was seen at Oued Lebna (Tunisia) on 10 August and 18 October 2009 when it was 4cy old. At least once, 245 of 2,512 (9.8%) colour-marked Spoonbills were observed in Africa in wintering time. The real number of African winterers must be even higher because 350 of 2,512 (13.9%) individuals were reported from Africa. 285 of 305 (93.4%) wintering Spoonbills were detected along the Adriatic Flyway in the Central Mediterranean areas in the Western Balkans, Italy, Northern Algeria, Tunisia, and Northern Libya.

Important European wintering areas of the Hungarian Spoonbills were in the mainland of Italy (n = 21; 6.9%), Sardinia (n = 13; 4.3%), and Sicily (n = 12; 6.9%), Sardinia (n = 13; 4.3%), and Sicily (n = 12; 6.9%), Sardinia (n = 13; 4.3%), and Sicily (n = 12; 6.9%), Sardinia (n = 13; 4.3%), and Sicily (n = 12; 6.9%), Sardinia (n = 13; 4.3%), Sardinia (n = 13; 4.3\%), Sardinia

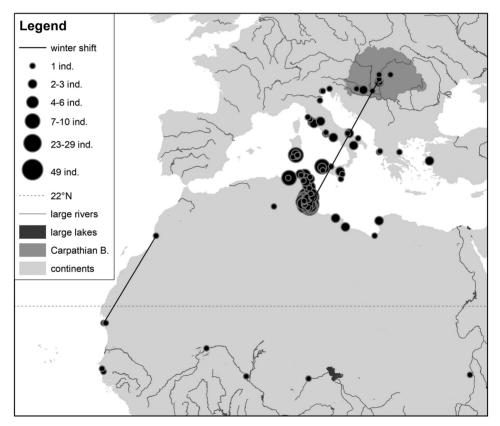


Fig. 1. Winter distribution of the Hungarian Spoonbills ringed between 2003 and 2020. The map contains all wintering data collected between the winters of 2003/2004 and 2020/2021. The lines of 'winter shift' indicate the shifts between winters when a resident became a short-distance migrant (shifted from Hungary to Tunisia) and a short-distance migrant became a long-distance migrant (shifted from Morocco to Mauritania). Abbreviations: ind. = individuals; Carpathian B. = Carpathian Basin

15; 4.9%) [including three (1.0%) specimens that were seen in both Sardinia and the mainland of Italy]. Two (0.7%) individuals spent the winter in the Balkans (Greece) and eleven (3.6%) in the southern part of the Carpathian Basin. The northernmost latitude where a Spoonbill belonging to the study population wintered was 47°01′N (Hungary). Two (0.7%) young individuals had Asian wintering areas in the Gediz Delta in Turkey. One was observed there on 9 January 2010 and the other on 3 February 2010.

Geographically, the most important wintering areas for the Hungarian Spoonbill population were in North Africa, especially in Tunisia, Northeast Algeria and Northwest Libya, while only one observation is known from Morocco (later, that individual wintered in Mauritania). The Gulf of Gabes (Tunisia) was particularly important as a wintering area. 65.2% (199 of 305) of all

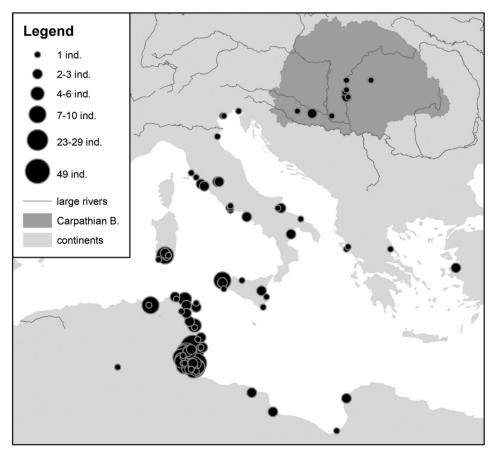


Fig. 2. Detailed map on the winter distribution of the Hungarian Spoonbills in the Carpathian Basin and the Central and East Mediterranean areas. Abbreviations: ind. = individuals; Carpathian B. = Carpathian Basin

Country	CR ind.	Notes about CR birds in 2003–2021	MS	MS Number of wintering individuals
Hungary	9	all in the Carpathian Basin	R	1–24 in 2004–2021, however, no available data in three winters (Pigniczki 2010, Birding.hu Team 2021)
Croatia	4	all in the Carpathian Basin	К	30 in 2016, 120 in 2017, 78 in 2018, 90 in 2019 (Wetlands International 2021)
Serbia	1	all in the Carpathian Basin	R	4 in 2018, 12 in 2019, 18 in 2020 (Wetlands International 2021)
Italy	46	13 in Sardinia, 15 in Sicily, 21 in the main- land	SD	max. 99 in 1991–1995, max. 304 in 1996–2000, max. 581 in 2001–2005, max. 794 in 2006–2010 (Zenatello <i>et al.</i> 2014), 1,027 in 2017, 1,365 in 2018, 1,236 in 2019 (Wetlands International 2021)
Greece	0		SD	750 in 2016 and 2017 (WETLANDS INTERNATIONAL 2021)
Turkey	7		SD	286 in 2017, 148 in 2018 (Wetlands International 2021)
Morocco	1		SD	849–1,498 in 2017–2020 (Wetlands International 2021)
Algeria	8	one in a North Saharan wetland (Chott Tindla)	SD	287 in 2016, 366 in 2017 (Wetlands International 2021)
Tunisia	225	199 in the wetlands of the Gulf of Gabes	SD	4,033 in 2008, 3,447 in 2014 (Azafzaf <i>et al.</i> 2015); 3,221 in 2016, 1,953 in 2017, 2,585 in 2018 (Wetlands International 2021)
Libya			SD	84–134 in 2005–2010 (Ѕмакт 2012); 135 in 2018 (К. Етахев <i>pers. comm.</i>)
Mauritania	7		LD	10,251 in 2017, 11,518 in 2020 (Wetlands International 2021) together with the local race (<i>P. l. balsaci</i>)
Senegal	1		LD	1,511 in 2019, 2,286 in 2020 (Wetlands International 2021)
Mali	1		LD	max. 75 in the central lakes of the inner Niger Delta between 1992 and 2005 ($T_{\rm WARTS}$ et al. 2009)

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CountryCRNotes about CR birdsMSNumber of wintering individualsind.in 2003-2021LDestimated at 100-200 for the whole country in 1994-1997 (BROUWER & MUL- LIFNiger1LDestimated at 100-200 for the whole country in 1994-1997 (BROUWER & MUL- LIFNigeria1LDestimated at 100-200 for the whole country in 1994-1997 (BROUWER & MUL- LIFNigeria1LDNatAbase 2021)Nigeria1LDmax: 52 in Hadejia-Nguru floodplains in 1988-1998 (ZwARTS <i>et al.</i> 2009)Sudan1LD1,299 in February 2018 (H. AZAFZAF <i>pers. comm.</i> , WFTLANDS INTERNATIONAL 2021)Total*305ILD1,299 in February 2018 (H. AZAFZAF <i>pers. comm.</i> , WFTLANDS INTERNATIONAL 2021)Table 2. The most important characteristics of wintering colour-ringed Sponbills of Hungarian origin for the three migration	birds MS LD LD LD LD LD LD Rcstaents Residents	MS Number of wintering individuals LD estimated at 100–200 for the whole LE estimated at 100–200 for the whole LE max. 52 in Hadejia-Nguru floodpl LD 1,299 in February 2018 (H. Azarzar LD 1,299 in February 2018 (H. Azarzar of wintering colour-ringed Spoonbills of strategies and the total population lents Short-distance Long-dist	ndividuals or the whole country during the winter c uru floodplains in 19 H. Azarzar <i>pers. com</i> P. Azarzar <i>pers. com</i> Dulation Long-distance	Number of wintering individuals estimated at 100–200 for the whole country in 1994–1997 (BROUWER & MUL- LIÉ 2001), 26 in 2002, 27 during the winter of 2006–2007 (WEST AFRICAN BIRD DATABASE 2021) max. 52 in Hadejia-Nguru floodplains in 1988–1998 (ZWARTS <i>et al.</i> 2009) 1,299 in February 2018 (H. AZAFZAF <i>pers. comm.</i> , WETLANDS INTERNATIONAL 2021) 1,299 in February 2018 (H. AZAFZAF <i>pers. comm.</i> , WETLANDS INTERNATIONAL 2021) 1,299 in February 2018 (H. AZAFZAF <i>pers. comm.</i> , WETLANDS INTERNATIONAL 2021) thering colour-ringed Spoonbills of Hungarian origin for the three migration thegies and the total population Short-distance Long-distance All wintering individuals
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Number of individuals	$10 + 1^{*}$	287 + 2**	$6 + 1^{***}$	305
Mean distance ± SD [km]	168.1 ± 86.3	$1,520.3\pm 283.7$	$4,291.4\pm461.2$	$1,534.5\pm555.5$
Median distance [km]	155	1,593	4,215	1,592
Minimum distance [km]	76	558	3,848	76
Maximum distance [km]	374	3,121	5,135	5,135
Range of direction	74.0°–235.3°	° 140.7°–261.1°	159.0°-240.6°	74.0°–261.1°
Mean direction	193.7°	213.5°	214.9°	213.1°
95% confidence interval of direction	141.6°–245.8°	° 207.2°–219.9°	166.8°–263.0°	206.8°-219.4°

WINTERING OF THE PANNONIAN SPOONBILLS

wintering individuals were observed there at least once. An immature (3cy) wintered on 25 January 2011 at Chott Tindla (33°40′N, 6°3′E), a Saharan wetland in Algeria, south of the Atlas Mountains. Seven (2.3%) individuals were found in a nearly 5,300 km wide-ranged area in the Sahel, between Sudan and the Atlantic coast of West Africa (Mauritania and Senegal). Wintering individuals in the Sahel were reported from the catchment area of the White Nile in Sudan (n = 1) in February, the Hadejia-Nguru floodplains in Nigeria (n = 1) in February, the River Niger in Niger (n = 1) in November and in Mali (n = 1; the exact month is not known), the Banc d'Arguin in Mauritania (n = 2) in November, December, January, and June, and finally, the Sine-Saloum Delta in Senegal (n = 1) in October and March. The southernmost latitude where a Spoonbill belonging to the Hungarian population wintered was 12°49′N (Nigeria).

Three migratory strategies were recognised: eleven of 305 (3.6%) individuals were residents at least during one winter, 289 (94.8%) were short-distance migrants, and seven (2.3%) were long-distance migrants (Table 2). Those data include two shifts in the migratory strategies: a juvenile spent its first winter as a resident between December 2006 and February 2007 in South Hungary, in the Carpathian Basin and later was observed as a short-distance migrant in January 2014 in Djerba (Tunisia) (Fig. 1). The distance between the two wintering areas was 1,632 km. Another juvenile was detected as a short-distance migrant during its first winter at the Atlantic coast of Morocco in November and December 2007, and later that bird was seen as a long-distance migrant between 2008 and 2012 at the Banc d'Arguin in Mauritania (Fig. 1). The distance between the Moroccan and the Mauritanian wintering site was 1,350 km.

Distance and direction of the wintering areas from the natal colonies

The mean (\pm SD) distance between the natal colonies and the wintering areas was 1,534.5 \pm 555.5 km. The median was a similar value, 1,592.0 km. The shortest distance between the natal colony and the wintering area was only 76 km (in Hungary), while the longest one was 5,135 km (between Hungary and Senegal). Most Spoonbills migrated in a south-southwestern direction (mean: 213.1°) to reach their wintering sites. The 95% confidence interval falls between 206.8° and 219.4° (directionality south-southwest and southwest) (Table 2).

DISCUSSION

In this study, I determined the winter distribution of Spoonbills marked in Hungary. Africa was the most important wintering continent, holding 80% of the observed individuals with known wintering areas, while 20% of the birds were observed in Europe and less than 1% in Asia. The proportion of the African winterers could be even higher than 80% because many individuals were observed there before or after the wintering period but not during the wintering time, and specimens that reached Africa are supposed to be African winterers.

The role of North Africa in the wintering

Based on ring recoveries and colour-ring readings, Tunisia is the most important North African wintering area for the Pannonian population (Mül-LER 1984, SMART et al. 2007, TRIPLET et al. 2008, PIGNICZKI 2009, 2010, 2015, 2017b, KRALJ et al. 2012, STANKOVIĆ 2018). The wintering population in Tunisia was 4,033 individuals during the waterbird census in 2008 (Azafzaf et al. 2015) and counted between 1,953 and 3,221 individuals during 2016–2018 (WETLANDS INTERNATIONAL 2021). Not only the Pannonian Spoonbill population winters in Tunisia but a sizeable part of the Czech, Italian, and the Camargue population as well, and a few individuals from the Danube Delta (Romania), Greece, and the Netherlands (AZAFZAF et al. 2006, SMART et al. 2007, CEPAK 2008, VOLPONI et al. 2008, LOK et al. 2011, BLANCHON et al. 2017, PIGNICZKI 2017b, Kiss et al. 2019). Spoonbills find perfect foraging possibilities in the tidal area of the Gulf of Gabes, where the tidal range of up to 2 m is unique for the Mediterranean Sea (SMART et al. 2007, HAMZA et al. 2016). From the nature conservation approach, it is an important result that a significant part of the Pannonian Spoonbill population winters in the Gulf of Gabes, which shows the importance of that area at an international level. The recent results indicate that Tunisian nature conservation has to play a key role in protecting and sustaining the Central European Spoonbill population that is wintering there.

Compared to Tunisia, the number of Libyan and Algerian colour-ring observations and the wintering population are also smaller. A few Spoonbills (84-135 individuals) spend the winter in Libya (SMART 2012, K. ETAYEB pers. comm.). Ring recoveries indicate that they came from the Pannonian and the Italian breeding population (PIGNICZKI 2009, 2010, 2015, KRALJ et al. 2012, SMART 2012, ISENMANN et al. 2016). In Algeria, 287–366 wintering Spoonbills were reported (2016–2017) (Wetlands International 2021). Previously, the origin of the wintering Spoonbills in Algeria was completely unknown; however, it was supposed that individuals might arrive from the Pannonian population (ISENMANN & MOALI 2000). My study confirmed that at least a part of the Algerian wintering Spoonbills came from the Carpathian Basin. Another essential finding of this paper is that a few Spoonbills occur in the Saharan wetlands south of Atlas Mountain in winter, as was found in the case of Chott Tindla. Based on ringed individuals, Morocco is only marginal for the Pannonian Spoonbill population; that area is mainly used by the breeders of the East Atlantic population (TRIPLET *et al.* 2008, Lok *et al.* 2011).

There are no confirmed fresh records of Spoonbills of Hungarian origin in Egypt, however, two specimens with white rings were observed there, but unfortunately, their codes were not read. Based on the colour of the rings, it can be assumed that these two individuals may have originated from the Pannonian population (PIGNICZKI 2015). Old metal ring recoveries of wintering Pannonian individuals (including Hungarian ones) are known from Egypt between the 1930s and the 1950s, mainly along the Nile (Müller 1984, Mul-LIÉ 1989, PIGNICZKI 2010, 2015). Recently, only one colour-ringed individual from the Pannonian population (ringed in Serbia) was photographed at Aswan in December 2007 (PIGNICZKI et al. 2016). Two old recoveries of metalringed Spoonbills that were marked in the Danube Delta (Romania) are also known from Egypt (Kiss et al. 2019). Based on data available until the late 1980s, the number of Spoonbills was high only during the autumn and spring migrations and was lower between November and February, suggesting that the majority migrate through Egypt and only a few stay there in the winter (GOODMAN & MEININGER 1989). The number of reported wintering Spoonbills in Egypt is quite low; they seem missing from the Nile Delta and are generally observed in the southern part of the Nile (GOODMAN & MEININGER 1989, SMART et al. 2007, TRIPLET et al. 2008). During the waterbird census, only 51 wintering individuals were reported in Egypt in January 2016 (WETLANDS IN-TERNATIONAL 2021).

The role of the Sahel in the wintering

The results of this study indicate that only a few specimens crossed the Sahara and migrated to the wetlands in the Sahel. A part of the Pannonian Spoonbills went to the central part of the Sahel in Mali, Niger, and Nigeria. One colour-ringed individual of Hungarian origin was observed at the Hadejia-Nguru floodplains in Nigeria, and two were reported from the river Niger in Niger and Mali. Old metal-ringed recoveries of individuals from Hungary are also known along the River Niger from Mali and Niger (PIGNICZKI 2009, 2010, 2015). Two Spoonbills from the Pannonian population (one from Croatia and one from Serbia) were found dead in Niger (KRALJ et al. 2012). Crossing the Sahara is a risky journey: two ringed specimens from the Pannonian population were found dead in the Algerian Sahara (Müller 1984, PIGNICZKI 2017b). Besides the Carpathian Basin population, Spoonbills that were marked in Italy also migrated through the Sahara: two were found in Mali and one in Nigeria (VOLPONI et al. 2008). A low number of Spoonbills was reported from the wetlands in the central part of the Sahel: a maximum of 75 individuals were counted in the central lakes of the inner Niger delta in Mali between 1992 and 2005, and a maximum of 52 individuals in the Hadejia-Nguru floodplains in Nigeria between 1988 and 1998 (ZWARTS *et al.* 2009). Data on wintering Spoonbills are not available from Lake Chad (ZWARTS *et al.* 2009, WEST AFRICAN BIRD DATABASE 2021). In Niger, 26 wintering Spoonbills were reported in 2002 and 27 during the winter in 2006–2007 (WEST AFRICAN BIRD DATABASE 2021). From Chad, only one specimen was reported in 2019 (WEST AFRICAN BIRD DATABASE 2021). Not only the winter surveys but the estimations also indicate a low number of Spoonbills in the central part of the Sahel: the total number of wintering Spoonbills between 1994 and 1997 was estimated at 100–200 individuals in Niger across the whole country (BROUWER & MULLIÉ 2001).

In Sudan, a new and two old observations of ringed Spoonbills prove that a part of the Hungarian population still uses wetlands in the Eastern Sahel (Рідмісткі 2010). There is a considerable wintering population in Sudan: 1,299 wintering individuals were reported there in February 2018 (H. AzaFzaF pers. comm., WETLANDS INTERNATIONAL 2021). Approximately 80% of the Sudanese winterers (roughly 1,000 individuals) were carefully checked for rings during February 2018, and only one individual had a colour-ring (0.1%) (H. AZAFZAF pers. comm.). Contrastingly, 30 of 1,400 carefully checked Spoonbills (2.1%) had Hungarian rings in Tunisia in 2013, 29 of 1,290 (2.2%) in 2014, and 57 of 1,950 (2.9%) in 2018 (Cs. PIGNICZKI unpublished data). This result likely indicates that most of the Sudanese winterers came from regions where the colour-ringing effort is low. I assume that the wintering areas in Sudan are only marginal for the Pannonian population. One Spoonbill from the Danube Delta (Romania) also reached Sudan, and another one moved to Kenya (Kiss et al. 2019). Interestingly, three individuals from the Camargue (France) appeared in South Sudan, which is quite extraordinary data (BLANCHON et al. 2017).

Three Spoonbills from the Carpathian Basin reached the Western Sahel at the East Atlantic coast of Africa and wintered in Mauritania and Senegal. Besides two Hungarian birds, a Spoonbill from Serbia also wintered in Mauritania (STANKOVIĆ 2018). A large number of observations and ring recoveries prove that the Atlantic coast of West Africa is the most important wintering area of the West European Spoonbill population that breeds between Iberia and Denmark (DE LE COURT & AGUILERA 1997, LOK *et al.* 2011, LOK 2013). In West Africa (Mauritania, Senegal, and The Gambia), the number of wintering Spoonbills together with the resident West African subspecies (*Platalea leucorodia balsaci*) was 11,209 individuals in 2017 and 13,860 birds in 2020 (WET-LANDS INTERNATIONAL 2021), which is a remarkable concentration.

The role of the Middle East in the wintering

Spoonbills observed in the Gediz Delta in Turkey provided novel information on the wintering areas of the Pannonian population in the Middle East. 148–286 wintering individuals were reported from Turkey (2016–2018) (WETLANDS INTERNATIONAL 2021). In Israel, despite the high observation effort and quite a large number of wintering Spoonbills (256–604 wintering birds in 2017–2020 (WETLANDS INTERNATIONAL 2021)), there are no winter records of colour-ringed individuals from the Pannonian population; however, two individuals appeared there during migration (PIGNICZKI *et al.* 2016). The wetlands of the Middle East are likely to be of marginal importance for the wintering Pannonian Spoonbills.

The role of Mediterranean Europe in the wintering

48 colour-ringed Spoonbills of Hungarian origin wintered in Mediterranean Europe, south of the Carpathian Basin. Italy was their most important wintering area. Most of the colour-ringed winterers were reported from southern Italy (including Sicily and Sardinia) (PIGNICZKI 2009, 2010, 2015, KRALJ *et al.* 2012, PIGNICZKI *et al.* 2016, IENTILE *et al.* 2020). The number of Italian winterers increased from 99 individuals to 1,365 between 1991 and 2019 (ZENATELLO *et al.* 2014, WETLANDS INTERNATIONAL 2021).

Two colour-ringed birds of Hungarian origin were reported from the Balkans (Greece). Old recoveries of metal-ringed individuals from Hungary are also known from Western Greece in the winter (PIGNICZKI 2010). In Greece, the number of wintering Spoonbills was estimated at 750 individuals (2016–2017) (WETLANDS INTERNATIONAL 2021). However, there are wintering Spoonbills in the Western Balkans [33–36 in Bosnia & Herzegovina (2018–2019), 8–14 in Montenegro (2018–2021), 46–86 in Albania (2017–2020) (WETLANDS INTERNATIONAL 2021)], no wintering Pannonian individuals were observed there because of the low ring-reading effort.

In South-Western Europe, many wintering Spoonbills were detected [1,335–2,102 in France (2017–2020), 1,917–2,341 in Portugal (2017–2020), and 3,735 in Spain (2017) (WETLANDS INTERNATIONAL 2021)], however, despite the high effort, winterers of Hungarian origin were not observed because South-Western Europe is unimportant for the wintering Pannonian birds.

The role of the Carpathian Basin in the wintering

In the winter, eleven colour-ringed Spoonbills of Hungarian origin stayed in the Carpathian Basin, in Serbia, Croatia, and Hungary. They were residents with no significant migratory movement. In the 1920s and 1930s, overwintering individuals ringed at the Kis-Balaton were found occasionally in small numbers in the southern part of the Carpathian Basin, in Serbia and Croatia (PIGNICZKI 2010). In the 2000s, no ringed residents of Serbian and Croatian origin were found in the Carpathian Basin (KRALJ *et al.* 2012). During the last decades, the importance of the Carpathian Basin for the wintering Spoonbills seems to have gotten larger. In the mild winter of 1960–1961, 2–5 wintering juveniles were reported from the Zicksee (Eastern Austria) (LEISLER 1966). Recurrently, 1–24 individuals overwintered in Hungary; however, in some years, the confirmed wintering records are absent (PIGNICZKI 2010, BIRDING.HU TEAM 2021). In the winters between 2018 and 2020, 4–18 birds spent the winter in Serbia (WETLANDS INTERNATIONAL 2021). In Croatia, 30–120 wintering specimens were found on the fishponds located between the River Drava and River Sava in January 2016–2019 (WETLANDS INTERNATIONAL 2021, T. MIKSUKA *pers. comm.*). The observations of colour-ringed individuals indicate that they had a good chance of successfully surviving mild winters in the Carpathian Basin. However, if the winter was harsh, they had a higher chance of death because of the lack of available food due to the frozen waters (PIGNICZKI 2010).

Migration strategies in the Hungarian Spoonbill population

Most colour-ringed Spoonbills of Hungarian origin were short-distance migrants. The majority of them were seen in the Central Mediterranean areas during winter. This southwestern migratory direction was confirmed by GPStracking and colour-ring readings as well. Most Pannonian birds moved along the Adriatic Flyway (Kralj et al. 2012, Pigniczki et al. 2016, Cs. Pigniczki unpublished data). Of the twelve Spoonbills equipped with GPS devices in Hungary, only one (8%) started to cross the Sahara (the last signal of its GPS device was detected above the Libyan Sahara). Therefore, this bird can be treated as a long-distance migrant. Ten individuals were short-distance migrants (83%), and one was a resident (8%) (Cs. PIGNICZKI unpublished data). An adult bird equipped with a GPS device in Italy appeared in Hungary in two summers, moved to winter to Tunisia and was a short-distance migrant (PIGNICZKI et al. 2016). Twelve Spoonbills equipped with GPS devices moved to the southwestern direction when they left the Carpathian Basin (eleven individuals belong to a Hungarian, one belongs to an Italian project) (PIGNICZKI et al. 2016, Cs. PIGNICZKI unpublished data). The first results of GPS tracking also support that the Pannonian Spoonbills are mainly short-distance migrants.

The results of this paper indicate that the vast majority, 94% of the Spoonbills were short-distance migrants, 2% were long-distance migrants, and 4% were residents. The proportions of the residents and short-distance migrants are probably overestimated, while the rate of long-distance migrants seems to be underestimated. The ratio of the trans-Saharan migrants probably can be higher because they could be in a fair-sized area in the Sahel where the observation effort is generally low (REICHLIN *et al.* 2013). However, based on the winter census data of Spoonbills and the proportion of ringed individuals of Hungarian origin in the flocks, I estimate that the lack of observation effort would only slightly modify the result given above. Only a small part (3%) of the African wintering birds occurred in the central part of the Sahel from the South Pannonian (Serbian and Croatian) population (KRALJ *et al.* 2012). The Pannonian population of Spoonbill was treated as a long-distance migratory population in several studies (Végvári *et al.* 2010, Végvári & BARTA 2016). However, the result of this paper highlighted that this is rather a short-distance migratory population. The migration strategy of the Pannonian population seems to be different from the Dutch population. In the Dutch population, the proportion of long-distance migrants was 52% during their first winter, however, during their following winters, it was 66%. Thus, the Dutch population is rather a long-distance migratory population (Lox *et al.* 2011).

Two shifts were recognised in the migratory strategies on an individual level. Both shifts happened in a southward direction: a resident juvenile became a short-distance migrant (shifted from Hungary to Tunisia), and a short-distance migrant juvenile became a long-distance migrant (shifted from Morocco to Mauritania). Furthermore, two individuals with European wintering areas during their first winter appeared later in North Africa, thus I assume that they became African winterers. It was also described in the Dutch population that some juvenile birds shifted their wintering regions and moved southward from their first wintering area in the following winters. From their second winter, Spoonbills were faithful to their wintering sites (Lox *et al.* 2011).

The mean distance between the natal and wintering sites covered by Spoonbills hatched in Hungary was 1,530 km. In the case of the Serbian and Croatian populations, it was found that most individuals migrate only 700-1,200 km to the Italian wintering sites, while 1,200-1,600 km to the Tunisian ones (KRALJ et al. 2012). Generally, the Pannonian population took shorter distances than the Iberian or the Dutch population. Iberian birds crossing the Sahara fly 2,500 km to their wintering areas in Senegal (DE LE COURT & AGUILERA 1997). Most Spoonbills from the Netherlands have even longer trans-Saharan migration because they fly 4,500 km to their Mauritanian and 5,000 km to their Senegalese wintering areas, however, they migrate only 1,000 km to winter in France, while they cover 2,000 km to winter in Iberia (Lox 2013, Lox et al. 2015). The entire Hungarian population migrated in a south-southwest (SSW) direction (mean: 213°). The mean direction between the South Pannonian (Croatian and Serbian) natal areas and the African wintering locations was nearly the same value (211°, SSW) (KRALJ et al. 2012) as it was found for the Hungarian population.

In this article, I described the wintering areas and some wintering parameters (distance and direction) of the Pannonian Spoonbills based on the recoveries and resightings of the Hungarian individuals. The main result of this paper is that the Spoonbills in the Hungarian (Pannonian) population are likely to be rather short-distance migrants; however, some long-distance migrants and residents also exist among them. Despite the limited data available from sub-Saharan Africa, this result is supported by the estimations of wintering birds in the central area of the Sahel, the analysis of the origin of colour-ringed Spoonbills in the entire wintering areas, and the first results of GPS telemetry.

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