Ornis Hungarica 2017. 25(2): 116–140.
DOI: 10.1515/orhu-2017-0019

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Exploratory analyses of migration timing and morphometrics of the Common Nightingale *(Luscinia megarhynchos)*

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Received: November 26, 2017 – Accepted: December 14, 2017

Csörgő, T., Fehérvári, P., Karcza, Zs. & Harnos, A. 2017. Exploratory analyses of migration timing and morphometrics of the Common Nightingale *(Luscinia megarhynchos)*. – Ornis Hungarica 25(2): 116–140. DOI: 10.1515/orhu-2017-0019

Abstract Ornithological studies often rely on long-term bird ringing data sets as sources of information. However, basic descriptive statistics of raw data are rarely provided. In order to fill this gap, here we present the fifth item of a series of exploratory analyses of migration timing and body size measurements of the most frequent Passerine species at a ringing station located in Central Hungary (1984–2016). First, we give a concise description of foreign ring recoveries of the Common Nightingale in relation to Hungary. We then shift focus to data of 3892 ringed and 1499 recaptured individuals derived from the ringing station, where birds have been trapped, handled and ringed with standardized methodology since 1984. Timing is described through annual and daily capture and recapture frequencies and their descriptive statistics. We show annual mean arrival dates within the study period and present the cumulative distributions of first captures with stopover durations. We present the distributions of wing, third primary, tail length and body mass, and the annual means of these variables. Furthermore, we show the distributions of individual fat and muscle scores, and the distributions of body mass within each fat score category. We distinguish the spring and autumn migratory periods and breeding season and age groups (i.e. juveniles and adults). Our aim is to provide a comprehensive overview of the analysed variables. However, we do not aim to interpret the obtained results, merely to draw attention to interesting patterns that may be worth exploring in detail. Data used here are available upon request for further analyses.

Keywords: Ócsa Bird Ringing Station, wing, third primary, tail length, body mass, fat, muscle, bird banding, capture-recapture, long term data, meta-analyses

Összefoglalás Madártani tanulmányokban gyakran elemeznek hosszútávú madárgyűrűzési adatsorokat, de az alapvető leíró statisztikák és exploratív elemzések általában nem hozzáférhetőek. E hiányt pótolandó, cikksorozatot indítottunk, melyben egy közép-magyarországi gyűrűző állomáson leggyakrabban előforduló énekesmadár fajok vonulás időzítésének és testméreteinek exploratív elemzéseit közöljük (1984–2016). A sorozat ötödik tagjaként szolgáló jelen cikkben először áttekintjük a fülemüle magyar gyűrűs külföldi és külföldi gyűrűs magyarországi megkerüléseit, majd rátérünk a faj egy magyarországi, 1984 óta standard módszerekkel dolgozó gyűrűzőállomásról származó 3892 gyűrűzött és 1499 visszafogott egyedétől származó adatainak elemzésére. Az időzítés és a fogásszám jellemzésére a napi és évi fogás és visszafogás gyakoriságokat használtuk. Ábrázoltuk az évenkénti átlagos érkezési időket és azok változását. Az éven belüli időzítést az első megfogások kumulatív eloszlásával ábrázoljuk feltüntetve a tartózkodási időket is. Közöljük a szárnyhossz, a harmadik evező hossz, a farokhossz és testtömeg leíró statisztikáit. Ábrázoljuk ezen változók éves átlagait, a zsír- és izomkategóriák gyakorisági eloszlását, valamint a testtömegek eloszlását zsírkategóriák szerinti bontásban. Az elemzésben elkülönítjük a vonulási (tavasz, ősz) és költési időszakokat és a korcsoportokat (fiatal, öreg). Célunk a vizsgált változók átfogó bemutatása és a bennük található mintázatok feltárása volt az eredmények interpretálása nélkül. Kérésre a cikkhez felhasznált adatsort rendelkezésre bocsátjuk.

Kulcsszavak: Ócsai Madárvárta, szárnyhossz, harmadik evező hossza, farokhossz, testtömeg, zsír, izom, madárgyűrűzés, hosszútávú adatsor, meta-analízis, csalogány

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Introduction

Bird ringing or banding is one of the principal and oldest methods in use to study various aspects of avian populations (Robinson *et al.* 2009). Overwhelming amount of data has been collected by professional research entities and within citizen science projects Cooper *et al.* 2014) in over a century of bird ringing, and has been used excessively in a diverse array of disciplines. However, compared to the amount of data available throughout the world, concise descriptive information on measured parameters suitable for meta- or comparative analyses is sporadically available (Gienapp *et al.* 2007, Harnos *et al.* 2015). Though purely descriptive studies are often hard to publish within the framework of current hypothesis-focused science, we feel that such studies may well play an outstanding role in generating new hypotheses. Therefore, it is essential that descriptive studies apply the most appropriate statistical methodologies (Harnos *et al.* 2015, 2016). The bulk of currently available data is often collected at permanent, long-term ringing stations where large amount of individuals of various species are trapped simultaneously (Csörgő *et al.* 2016). These projects generally apply standardized methodologies in trapping, handling and data collection, thus information derived from these sites is suitable for location-wise comparisons (Schaub & Jenni 2000, Marra *et al.* 2004, Schaub *et al.* 2008, Tøttrup *et al.* 2010).

Here we present exploratory and descriptive statistics on the migration timing and morphometrics of the Common Nightingale *(Luscinia megarhynchos)* between 1984–2016 from a Central European ringing station (Ócsa Bird Ringing Station, Hungary, see Csörgő *et al.* 2016 for details).

The Nightingale is a sexually monomorphic, omnivorous, medium-sized species of the Turdidae family (Collar & Christie 2015). The upper parts are brown, the tail is chestnut-brown, the breast is uniform light buff-fish-brown without grey mottling, outer tertial feathers are bright rufous. The great-covers and tertials of adults are uniform brown. The juveniles' feathers are spotted until the postjuvenile moult. After the moult they are similar to adults, but tips of tertials and greater covers retain pale spots (Cramp 1988, Svensson 1992, Demongin 2016). The plumage of sexes is similar, but the males are slightly darker and larger than females, and the tarsi significantly longer than that of females. The exact sexing is only possible in hand using the incubation patch of breeding adults (Dittberner & Dittberner 1989, Svensson 1992, Demongin 2016, Hahn *et al.* 2016).

The Nightingale is a polytypical species, with 3 subspecies (*L. m. megarhynchos*, *L. m. african* and *L. m. hafizi*). The subspecies are quite similar in their appearance, making the identification of a single individual almost impossible (Cramp 1988, Svensson 1992, Demongin 2016). Intriguingly, mean wing and tail lengths vary with longitude for the nominate subspecies, creating and increasing pattern from west to east (Demongin 2016, Hahn *et al.* 2016).

The breeding area ranges from the Atlantic coast to Mongolia, from southern England to North-West Africa and Iran. The nominate subspecies breeds in Europe, North-Africa, and the Middle East, while *L. m. africana* breeds in Turkey, Caucasus, Iran, Kopet Dag, the *L. m. hafizi* in Central Asia, Mongolia (Cramp 1988, Tucker & Heath 1994, Grüll & Fracasso 1997, Collar & Christie 2015). In the Western Palearctic Nightingales breed in the middle and lower middle latitudes, Mediterranean and steppe climatic zones between July isotherms 17–30 °C. They occupy variable, densely vegetated habitats from lowland riverine woodland (here they overlap with the Thrush Nightingales - *Luscinia luscinia*), edges of broad-leaved woodlands to bushland, scrub, dry maquis and managed open woodland, suburban habitats and gardens (Cramp 1988, Tucker & Heath 1994, Grüll & Fracasso 1997).

The Nightingale is widespread in southern and western Europe, complementing the more northerly and easterly distribution of the Thrush Nightingale. The Nightingale and the Thrush Nightingale are two ecologically and morphologically similar, closely related sister species (Sorjonen 1986). The two species diverged approximately during the Pleistocene (1.8 Mya) (Storchová *et al.* 2010). Both species have similar ecological requirements but partial habitat segregation has been observed in sympatry (Ranoszek 2001). The hybridisation of Nightingale on the overlapped breeding area is regular with Thrush Nightingale. Morphological as well as genetic studies indicate that approximately 3–5% of males in sympatry are hybrids. The hybrid males are fertile and can reproduce with either of the parental species (Becker 1995). The two species are isolated by incomplete prezygotic isolation and female hybrid sterility (Kverek *et al.* 2008, Storchová *et al.* 2010, Reifová *et al.* 2011). The F1 birds have intermediate wing formula (Kováts *et al.* 2013, Demongin 2016). The narrow hybrid zone ranges from Denmark to the west coast of the Black Sea.

North-Eastern Hungary lies in the contact zone of the two sister species, where recently only their hybrids and the *L. megarhynchos* could be found. Based on morphological and phylogenetic studies of four closely situated populations, the gene flow points from *L. luscinia* to *L. megarhynchos*. Recently cca. 7% of the this population are interspecific hybrids. The morphological character displacements and the proportion of hybrids refers a stable hybrid population (Ács & Kováts 2013, Kováts *et al.* 2013, Kováts & Harnos 2015).

The Nightingale is classified as Least Concern in the IUCN Red List (BirdLife International 2017). In Europe the overall trend was a moderate decline between 1980–2013 (EBCC

2015), but the population was estimated to be increasing between 2000–2012 (BirdLife International 2017). Recently the current European population trend is stable (Walther *et al.* 2010, EBCC 2015). The documented decline in the west of its range may have been driven by agricultural development, land-use and habitat changes, like the increasing tendency for 'tidying' of gardens and woodlands. For instance severe loss if breeding habitats along streams and rivers have been documented in Spain (Collar & Christie 2015). In the U.K. habitat modification as a result of grazing by deer may be a threat to this species (Newson *et al.* 2012). Poaching and hunting pressures along the migratory routes may also play a substantial part in driving overall breeding population decline; e.g. 36% of birds ringed in the Czech Republic (Kverek *et al.* 2008) were shot. The species may also be sensitive to climatic variations (Grüll & Fracasso 1997).

The mating system of Nightingales is social monogamy. Only females incubate, but both parents feed the offsprings. The pair-bond breaks down at the end of the breeding season (Cramp 1988). The Nightingale has a high breeding site fidelity (Henderson 2002, Barišić 2013). In the Czech Republic only 2% out of 351 adults have been found more than 10 km away, 91.2% of 34 juveniles settled less than 10 km from the natal site (Kverek 2008). Return rate of juveniles is lower (Henderson 2002).

The Nightingale is an obligate long-range migrant, wintering in Afro-tropics and Iraq. They winter in Sub-Saharan Africa in moist savannahs and savannah-forest mosaic mainly south of 10 °N, from Senegal to Kenya. The nominated subspecies winter between the Sahara and rainforest from West Africa east to Uganda. The other two subspecies *(L. m. hafizi, L. m. africana)* migrate and winter in East Africa, Kenya and Tanzania (Cramp 1988, Walther *et al.* 2010). The range of migration distances of the different populations are between 2500 and 4500 km. Western populations travel shorter, while northern-central European populations travel longer distances (Hahn *et al.* 2014, 2016). Recoveries and morphometric differences between autumn and spring suggest a general loop migration pattern in Africa (Spina & Volponi 2009, Jónás *et al.* 2018).

The Nightingale moves through Europe on a broad front and in a south-western direction in autumn (Cramp 1988, Bairlein *et al.* 2014, Hahn *et al.* 2016). Birds from the British Isles fly south-southwest through western France and Iberia, birds originating from Germany migrate south-west with a probable directional change in Portugal. A small part of Czech birds migrates via Italy, and a larger part moves in the south-western direction via France and Morocco. Birds ringed in northern Dalmatia have been recovered in Italy (Henderson 2002, Kverek 2008, Spina & Volponi 2009, Barišić 2013, Bairlein *et al.* 2014).

Nightingale populations breeding in western, southern-central and eastern Europe use different flyways and wintering sites (Korner-Nievergelt *et al.* 2012, Hahn *et al.* 2014). Hahn *et al.* (2013) showed that different bird populations winter in population-specific clusters in Africa, indicating strong population level migratory connectivity.

The European breeding birds commence their migration in autumn between end of July and September (Cramp 1988). The peak passage in south and west coasts of the British Isles is in late August, early September, and in Central Europe in late August (Grüll &

Fracasso 1997, Henderson 2002, Bairlein *et al.* 2014). The autumn migration lasts from August to October in Spain and Italy (Bueno 1990, Spina & Volponi 2009). Juveniles precede adults in autumn on the Iberian peninsula (Bueno 1990). This may be caused by the fact that juveniles perform a partial moult prior to migration while adults undergo a rapid (cca. 45 days) complete moult (Ginn & Melville 1983, Svensson 1992, Jenni & Winkler 1994). After the seasonal peaks in August, the relative abundance of birds decreases in September and October, while body mass values reach maximum values, 5 g more on average compared to spring values and nearly 100% of the birds have fat reserves in Italy. Adults deposit fat reserves earlier than juveniles (Spina & Volponi 2009).

First arrivals at the African wintering grounds are in late August-early September, but the bulk of the birds arrive from late October to early December (Keith *et al.* 1992). In Nigeria, main passage is in the second half of October and November. The birds remain here for 1.5 months before travelling to Guinea in December (Cramp 1988, Newton 2008, Rappole 2013). Wintering birds are territorial (Keith *et al.* 1992), showing high within- and between-year site-fidelity (Salewski *et al.* 2000).

Yearly survival rate variability is associated with rainfall fluctuations in the Sahel region. After dryer winters, survival rates were lower than in others years with more precipitation (Boano *et al.* 2004).

The main northward passage is between mid-March and early April south of the Sahara. Last birds starts their journey back to Europe in May (Keith *et al.* 1992). The first arrivals in Europe are in March and the peak arrival time is in the last two decades of April in Italy, in April and May in Germany, late April and early May in Britain (Henderson 2002, Spina & Volponi 2009, Bairlein *et al.* 2014). Arrival dates may be considerably influenced by rainfall and temperature en route (Huin & Sparks 2000, Rubolini *et al.* 2007)

Spring migration shifted to earlier dates in the western Mediterranean between 1993–2007 (Robson & Barriocanal 2011), but no long-term trend in first arrival date (FAD) was observed in Italy (Rubolini *et al.* 2007) and in south-western Germany between 1970–2003 (Peintinger & Schuster 2005). While only a marginally significant trend toward earlier first arrival dates was observed in western Poland during the period of 1913–1996 (Tryjanowski *et al.* 2002), it was significant between 1983–2003 (Tryjanowski *et al.* 2005). The same trend in FAD could be observed in the second half of 20th century (Sparks *et al.* 2007) and in median passage dates between 2002–2011 in the UK (Eddowes 2012). Opposite trend was detected in Spain, where Nightingales showed a marked tendency to delayes arrival at the second half of 20th century (Gordo *et al.* 2005). A statistically significant advance of 11 days was recorded between two periods (1901–1917 and 1991–2005) in Central Croatia. The difference in the mean April temperature between two study periods was also significant (Kralj & Dolenec 2008).

The species is protected in Hungary (BirdLife Hungary 2017). The Nightingale is a common and widespread breeder of forest edge and floodplain forest, shrubs and bigger parks in Hungary. The Hungarian breeding population is estimated to 225000–280000 pairs (Hadarics & Zalai 2008). The population was stable between 1999–2016 (Szép *et al.*

2012). The species is a common migrant from early April until mid-May in spring peaking is at the end of April, and from the beginning of August until mid-September in autumn peaking in early August (Hadarics & Zalai 2008, Kováts & Csörgő 2009).

Nightingales are regular and common passage migrants at the Ócsa Bird Ringing Station, the source of data analysed in this paper.

Our aim is to provide a comprehensive overview of migration timing, body size measurements and inter-annual changes in these variables. Hopefully, these patterns will help formulate research questions and provide information for further higher level analyses. However, we do not aim to interpret the obtained results, merely draw attention to interesting patterns, that may be worth exploring in detail.

Materials and methods

Bird ringing data

The Ócsa Bird Ringing Station is situated in Central Hungary (N47.2970, E19.2104) in the Duna-Ipoly National Park in the immediate vicinity of Ócsa town. The study site is characterized by a post-glacial peat bog with a mosaic of habitats including open water surfaces, reedbeds, bushy vegetation and forests. It is situated in a humid continental transitional climate zone (for further details see Csörgő *et al.* 2016, ocsabirdringing.org). Birds were trapped with standard mistnets placed at standard locations throughout the study period. Trapping effort is seasonal and changed over the years (see Csörgő *et al.* 2016 for details).

The day of the year of first capture in spring and in autumn were considered as arrival (migration) timing of individual birds. Stopover duration was calculated as the difference of within season last and first captures excluding within day recaptures. Biometric measurements were taken following strictly standardized methods (Szentendrey *et al.* 1979, EURING 2015). Only data of the first captures were used in the analysis. We distinguished first calendar year birds (juveniles) from adults upon plumage characteristics (Cramp 1988, Svensson 1992, Demongin 2016), and we present all results according to these groups. We present data for spring, breeding and autumn migratory seasons separately; birds caught after the 80th and before the 140th day of the year were considered to be spring migrants and birds caught after the 180th and before the 270th day of the year were considered to be autumn migrants. A total of 3892 Common Nightingales were captured and ringed between April and September; 508 in spring, 321 adults and 212 juveniles in the breeding season and 362 adults and 2443 juveniles in autumn (the rest of the birds was not aged) in the study period of 1984–2016. This total value constitutes ca. 18.9% of the 20,588 Common Nightingales ringed in Hungary in this period.

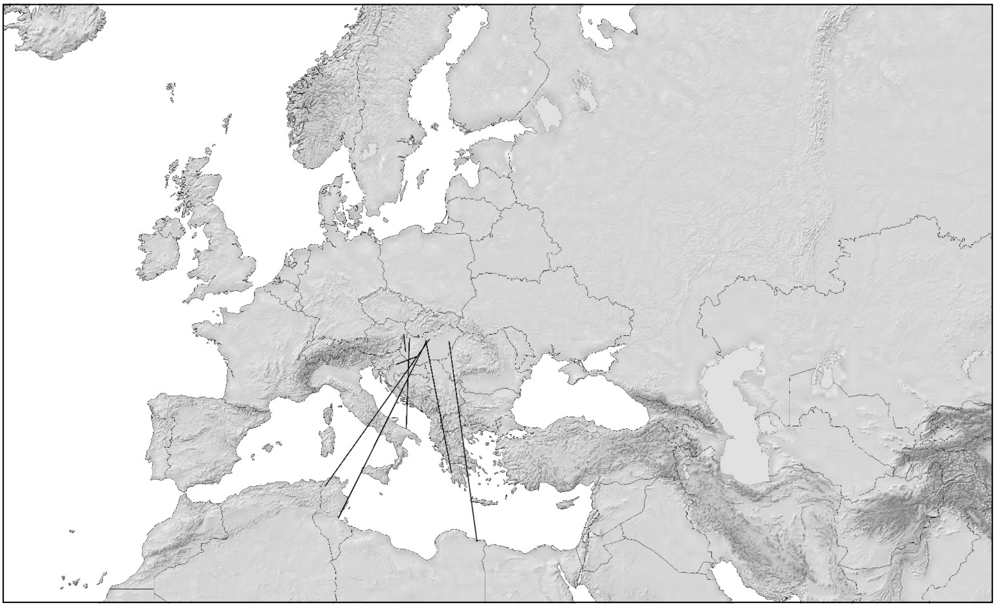
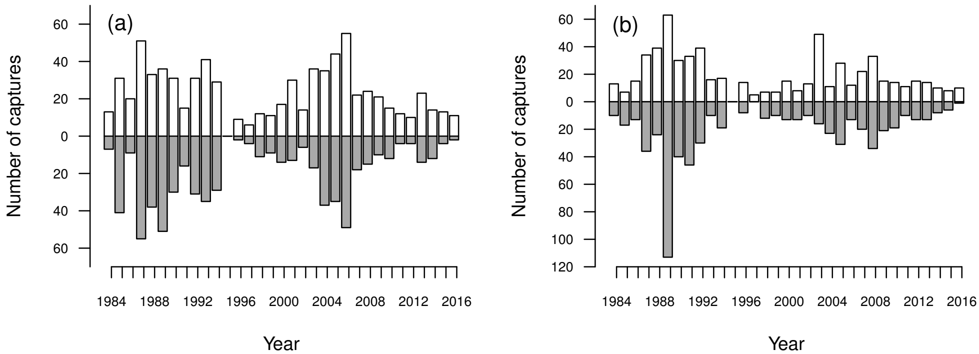


Figure 1. Foreign ring recoveries of Common Nightingales. The data of birds ringed in Hungary and recovered abroad and the birds ringed abroad and recovered in Hungary are depicted

1. ábra Magyarországon jelölt és külföldön megkerült, illetve külföldön jelölt és Magyarországon megfogott fülemülék

Statistical methods

To describe daily and yearly capture frequencies and the cumulative distribution of the date of first captures with recaptures, we used the functions of the `ringR` package (Harnos *et al.* 2015). Descriptive tables (mean, median, standard deviation (SD), minimum (min), maximum (max) values and sample size (N)) on the timing of migration, stopover duration, the length of wing, third primary and tail, and body mass were created by the `data.table` package (Dowle *et al.* 2013), which is highly effective in calculating summary statistics for different groups and subsets. The annual mean values of timing, body mass, wing-, third primary and tail lengths are plotted against time (year) on scatterplots. Loess smooth lines were fitted to highlight trends (Cleveland *et al.* 1992). The distribution of the same variables were represented with histograms and overlaid smoothed histograms. Boxplots were used to show the body mass distributions by fat score categories. Fat and muscle score frequencies are shown using barplots. We distinguished seasons and age groups throughout the analyses. For more details on the analysis, please visit ocsabirdringing.org. All analyses were carried out in R 3.4.0 (R Core Team 2017).



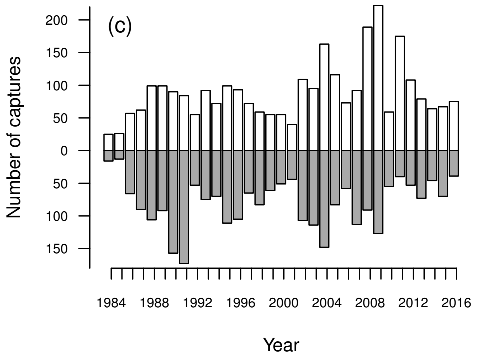


Figure 2. Annual capture (white bars) and recapture (grey bars) frequencies in spring (a), in the breeding period (b), and in autumn (c)

2. ábra Éves fogás (fehér oszlopok) és visszafogás (szürke oszlopok) gyakoriságok tavasszal (a), a költési időszakban (b) és ősszel (c)

Results

A total of 9 foreign recaptures were recorded between 1951 and 2016 in relation to Hungary *(Figure 1)*. Birds ringed is Hungary have been recovered on the middle Mediterranean, in Tunisia, Italy, Greece, and Lybia (Kováts & Csörgő 2009, BirdLife Hungary 2017). Annual capture and recapture frequencies at the study site are shown in *Figure 2*. Within-year capture and recapture frequencies, together with cumulative distributions of individual first and last captures are depicted in *Figure 3*, while their respective descriptive statistics are presented in *Table 1–2*. Changes in annual mean arrival dates throughout the study period and the distribution of within-year migration timing according to season and age are presented in *Figure 4*. The trend of annual mean wing lengths and the distributions of wing length measurements according to season and age are shown in *Figure 5*, while their respective descriptive statistics are presented in *Table 3*.

Third primary length *(Figure 6, Table 4)*, tail length *(Figure 7, Table 5)* and body mass *(Figure 8, Table 6)* are presented in a similar fashion. Body mass in relation to season and age and fat scores are visualized with boxplots in *Figure 9 a,c,e,g,i*. Finally, the distributions of fat and muscle scores grouped by season and age can be found in *Figure 9 b,d,f,h,j*, and *Figure 10*.

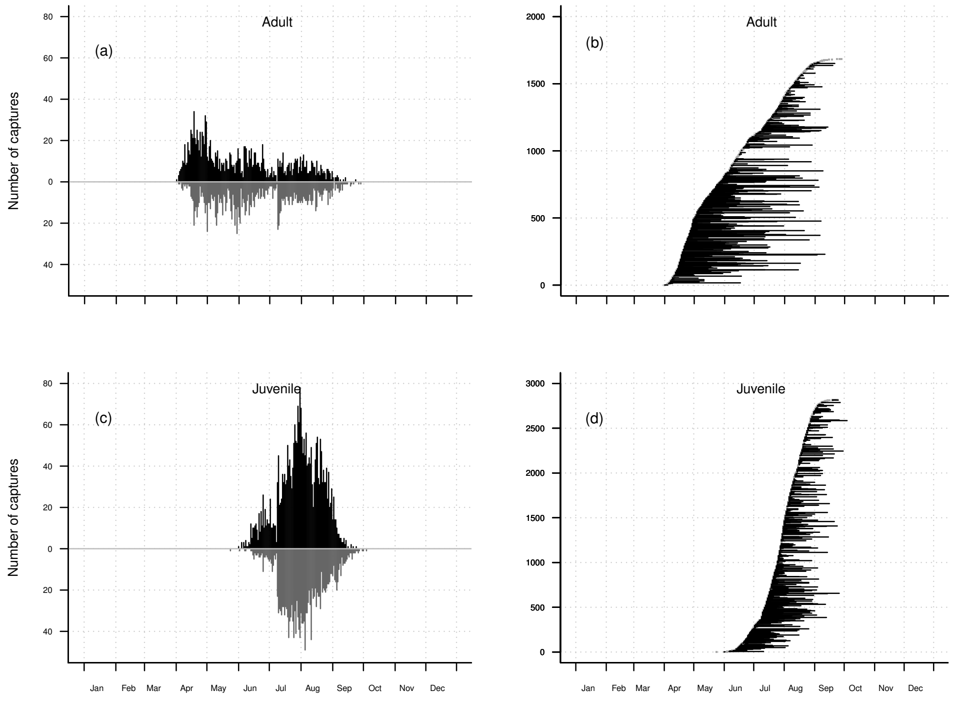


Figure 3. Within-year capture (black bars) and recapture (grey bars) frequencies (a,c) and cumulative distributions of individual first capture dates (b,d) according to age groups (horizontal lines: stopover durations)

3. ábra Éven belüli fogás (fekete oszlopok) és visszafogás (szürke oszlopok) gyakoriságok (a,c) és az egyedek első megfogási idejének kumulatív eloszlása (b,d) korcsoportonként (vízszintes vonalak: tartózkodási idők)

Table 1. Descriptive statistics of migration timing (day of the year)
1. táblázat A vonulás időzítés (év napja) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	115.1	114	11.8	91	140	508
breeding	adult	160.4	161	10.5	141	179	321
breeding	juvenile	171.2	172	5.9	152	179	212
autumn	adult	212.9	212	17.2	180	266	362
autumn	juvenile	216.1	215	16.9	180	267	2443

Table 2. Descriptive statistics of stopover duration (day)
2. táblázat A tartózkodási idő (nap) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	11.6	9	9.7	1	36	239
autumn	adult	21.2	16	18.1	1	65	95
autumn	juvenile	14.6	11	13.8	1	71	580

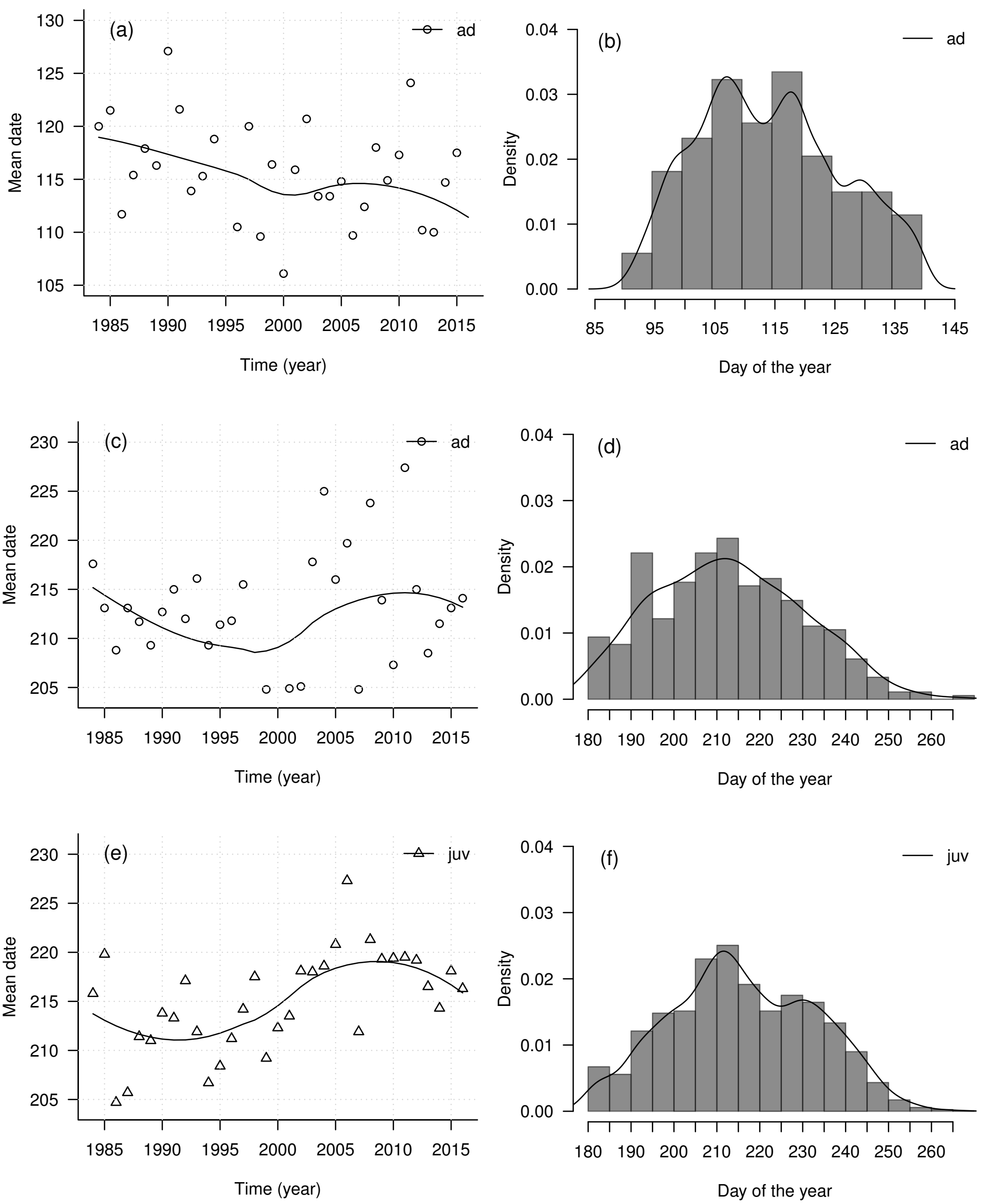
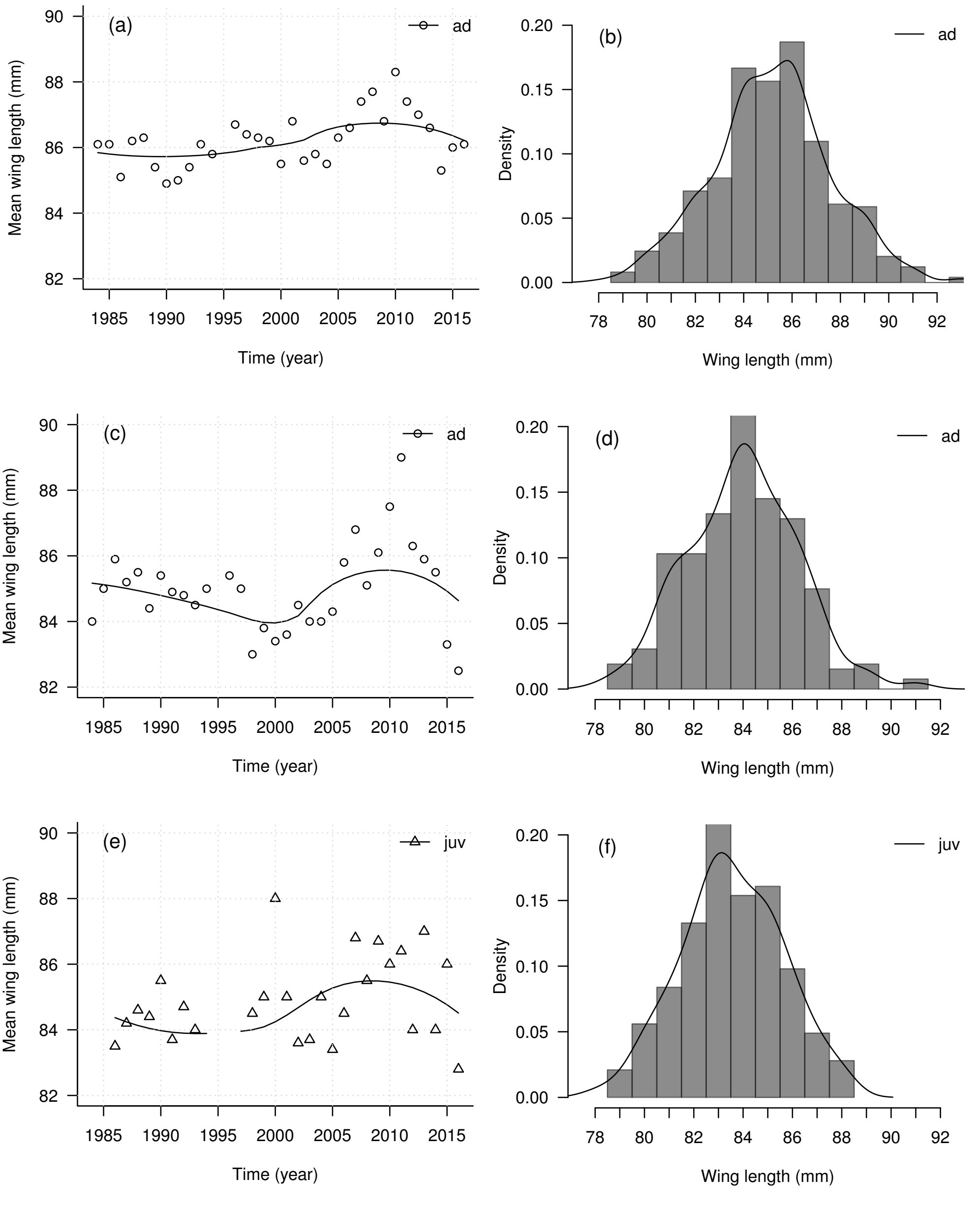


Figure 4. Annual mean migration timing (day of the year) throughout the study period and histograms/smoothed histograms of timing in spring (a–b) and in autumn (c–f)

4. ábra Az éves átlagos vonulás időzítés (év napja) a vizsgálati időszakban és az időzítés hisztogramja/simított hisztogramja tavasszal (a–b) és ősszel (c–f)


(a)
ad
Mean wing length (mm)
Time (year)
(b)
ad
Density
Wing length (mm)
(c)
ad
Mean wing length (mm)
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(d)
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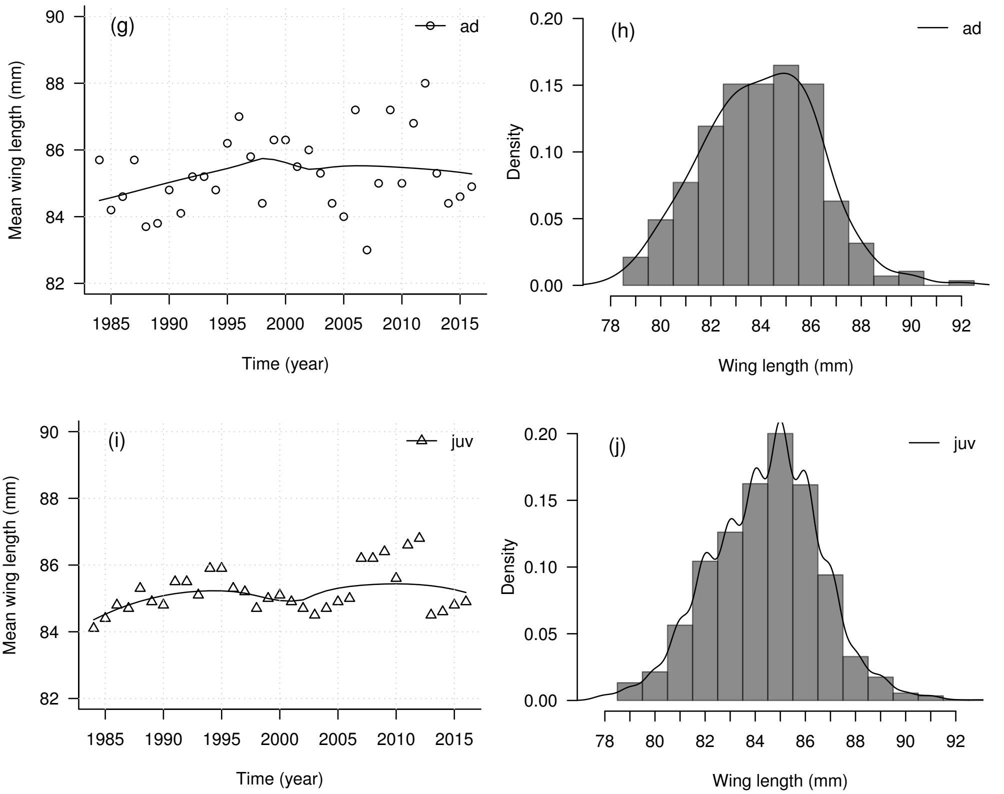


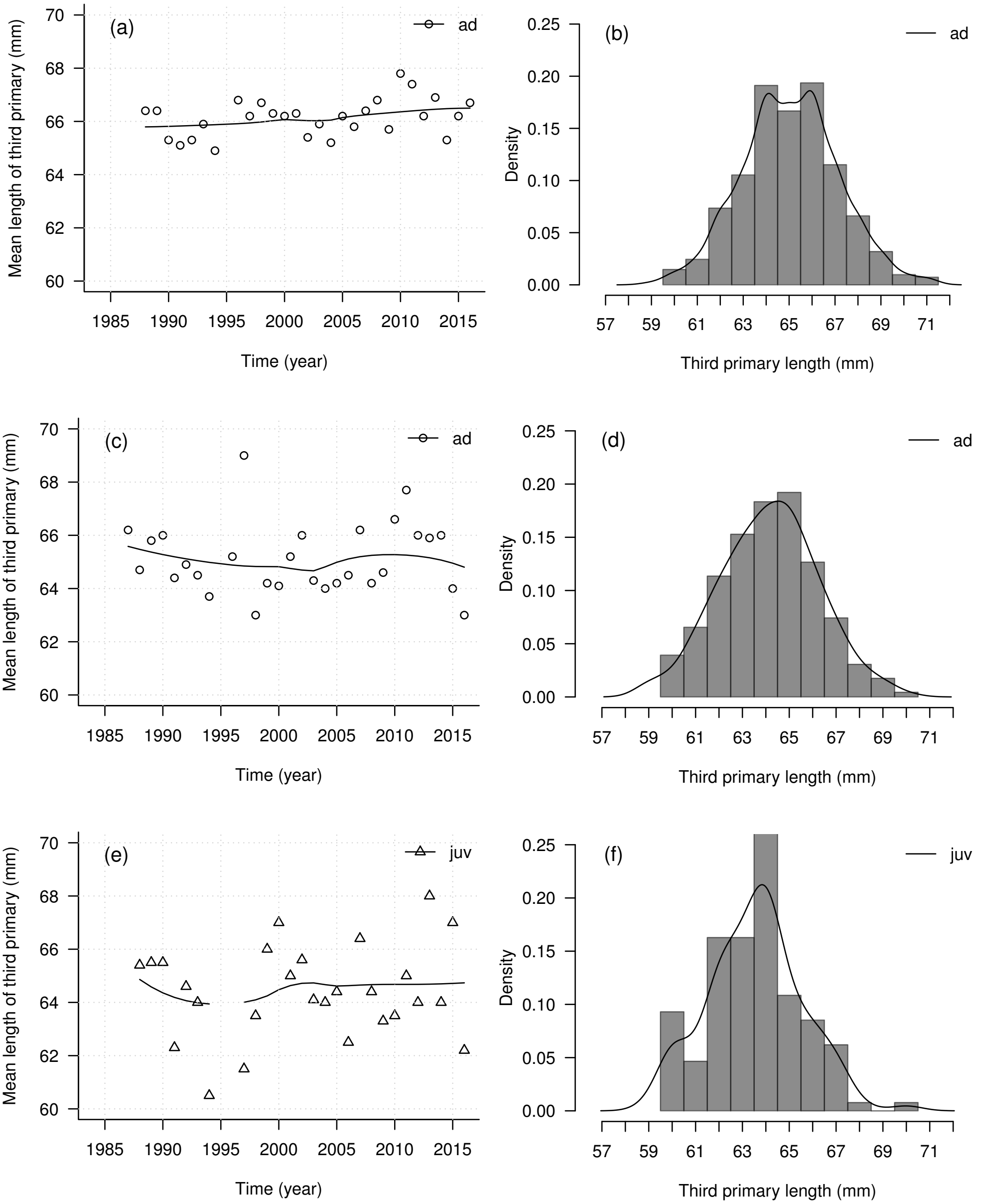
Figure 5. Annual mean wing length (mm) throughout the study period and histograms/smoothed histograms of wing length in spring (a–b) in the breeding period (c–f) and in autumn (g–j)

5. ábra Az éves átlagos szárnyhossz (mm) a vizsgálati időszakban és a szárnyhossz hisztogramja/simított hisztogramja tavasszal (a–b), a költési időszakban (c–f) és ősszel (g–j)

Table 3. Descriptive statistics of wing length (mm)

3. táblázat A szárnyhossz (mm) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	86.2	86	2.4	79	94	492
breeding	adult	85.0	85	2.2	79	92	262
breeding	juvenile	84.5	84	2.1	79	89	143
autumn	adult	85.0	85	2.3	79	93	285
autumn	juvenile	85.4	86	2.2	79	94	2339


(a)
ad
Mean length of third primary (mm)
Time (year)
(b)
ad
Density
Third primary length (mm)
(c)
ad
Mean length of third primary (mm)
Time (year)
(d)
ad
Density
Third primary length (mm)
(e)
juv
Mean length of third primary (mm)
Time (year)
(f)
juv
Density
Third primary length (mm)

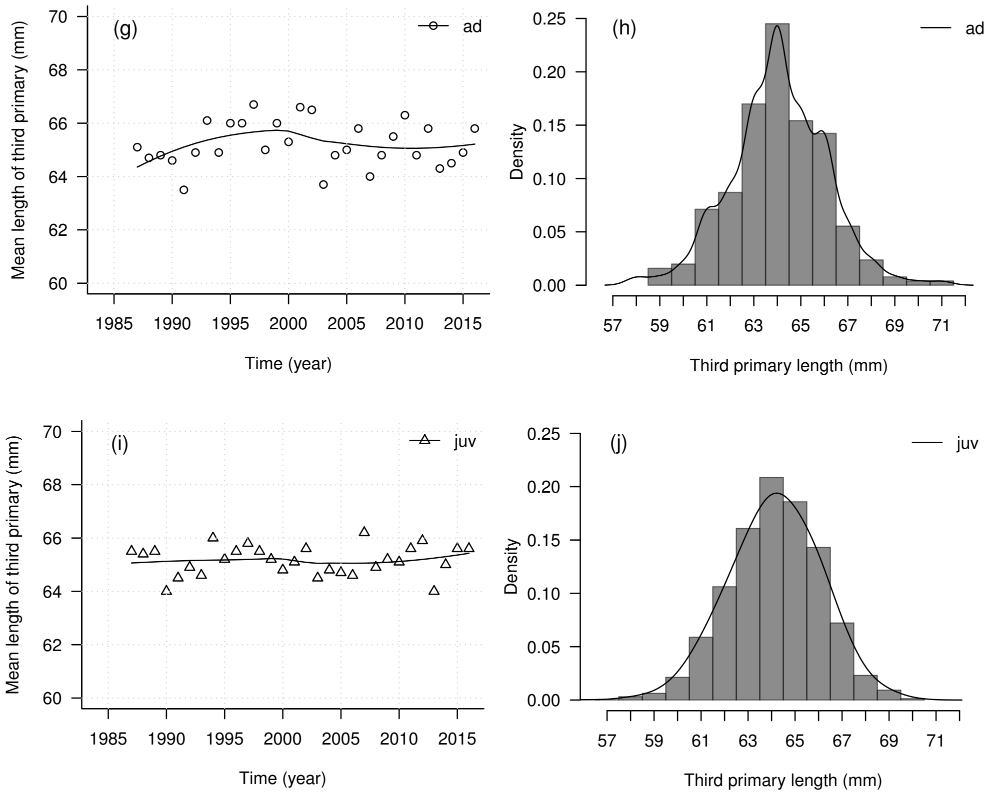


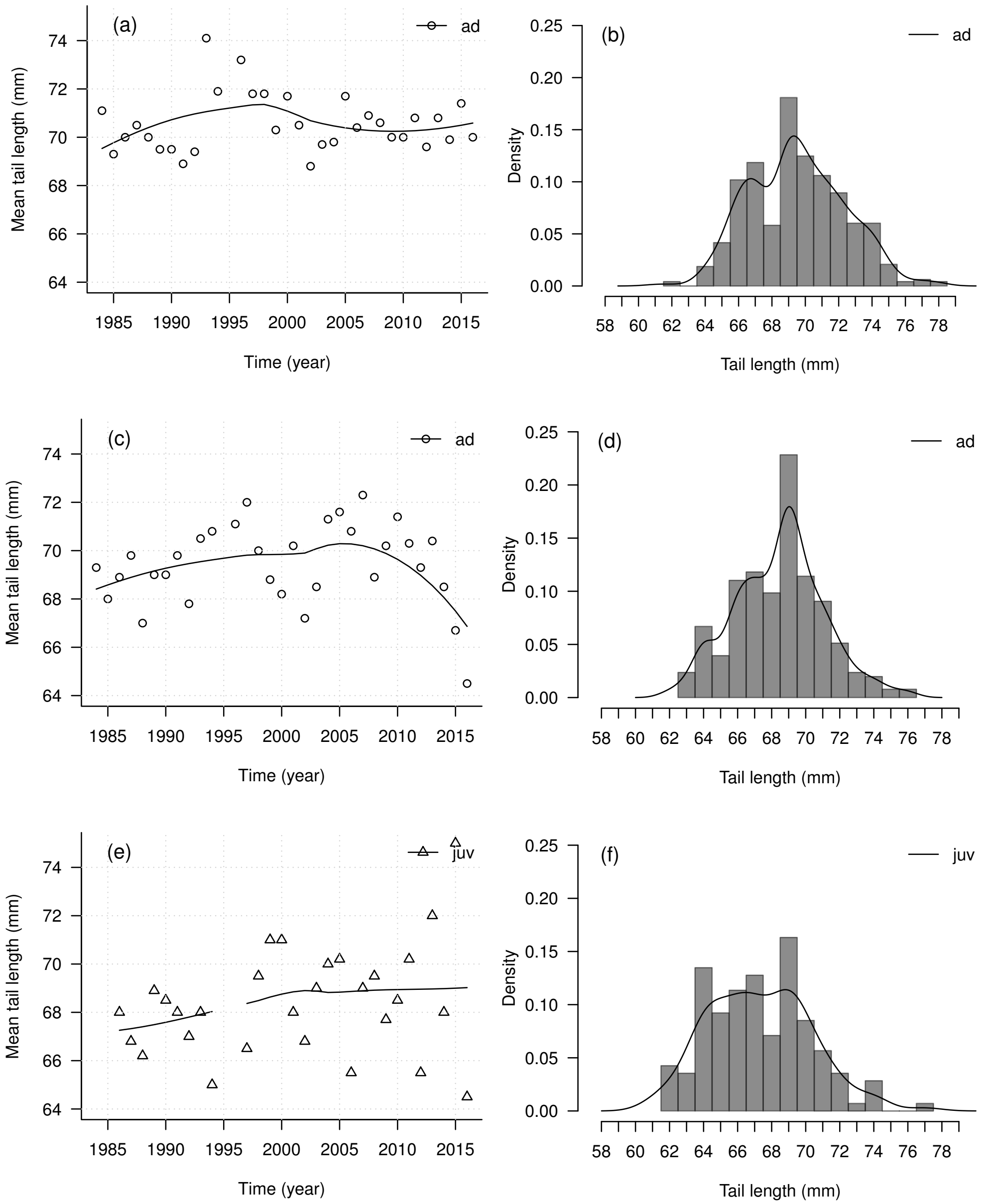
Figure 6. Annual mean length of third primary (mm) throughout the study period and histograms/smoothed histograms of third primary length in spring (a–b) in the breeding period (c–f) and in autumn (g–j)

6. ábra Az éves átlagos harmadik evező hossz (mm) a vizsgálati időszakban és a harmadik evező hosszának hisztogramja/simított hisztogramja tavasszal (a–b), a költési időszakban (c–f) és ősszel (g–j)

Table 4. Descriptive statistics of third primary length (mm)

4. táblázat A harmadik evező hosszának (mm) leíró statisztikái

Season	**Age**	**Mean**	**Median**	**SD**	**Min**	**Max**	**N**
spring	adult	66.0	66	2.1	60	72	408
breeding	adult	65.2	65	2.1	60	71	229
breeding	juvenile	64.5	65	2.0	60	71	129
autumn	adult	65.1	65	2.0	59	72	253
autumn	juvenile	65.1	65	1.9	57	71	2259


(a)
ad
Mean tail length (mm)
Time (year)
(b)
ad
Density
Tail length (mm)
(c)
ad
Mean tail length (mm)
Time (year)
(d)
ad
Density
Tail length (mm)
(e)
juv
Mean tail length (mm)
Time (year)
(f)
juv
Density
Tail length (mm)

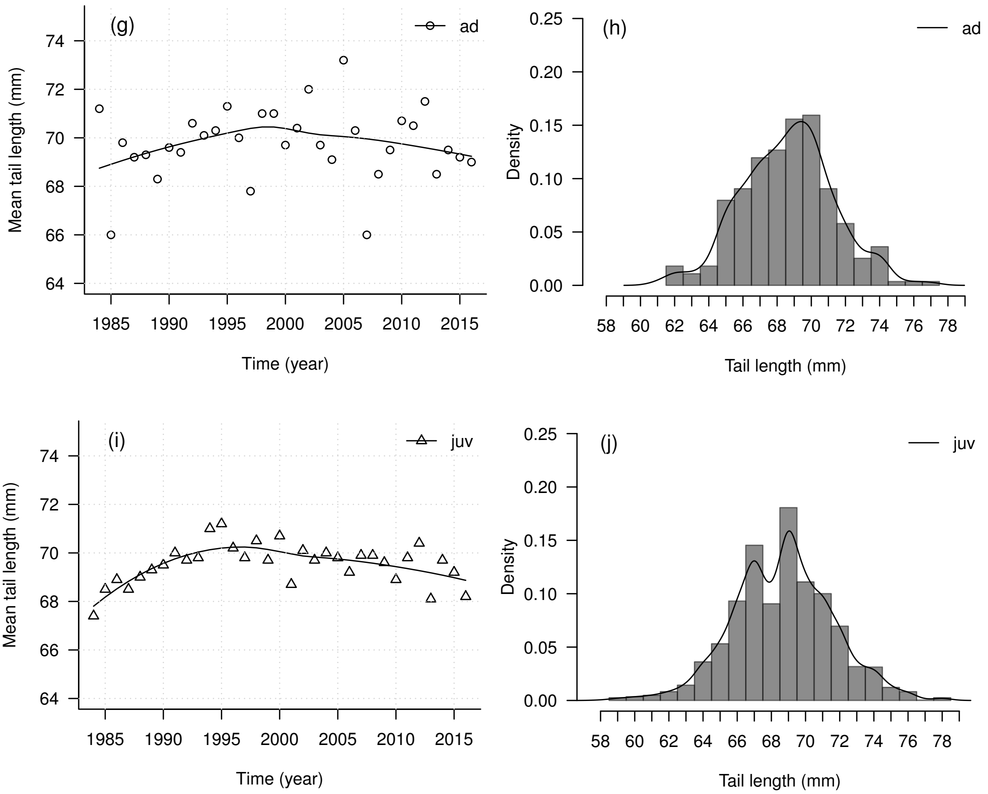


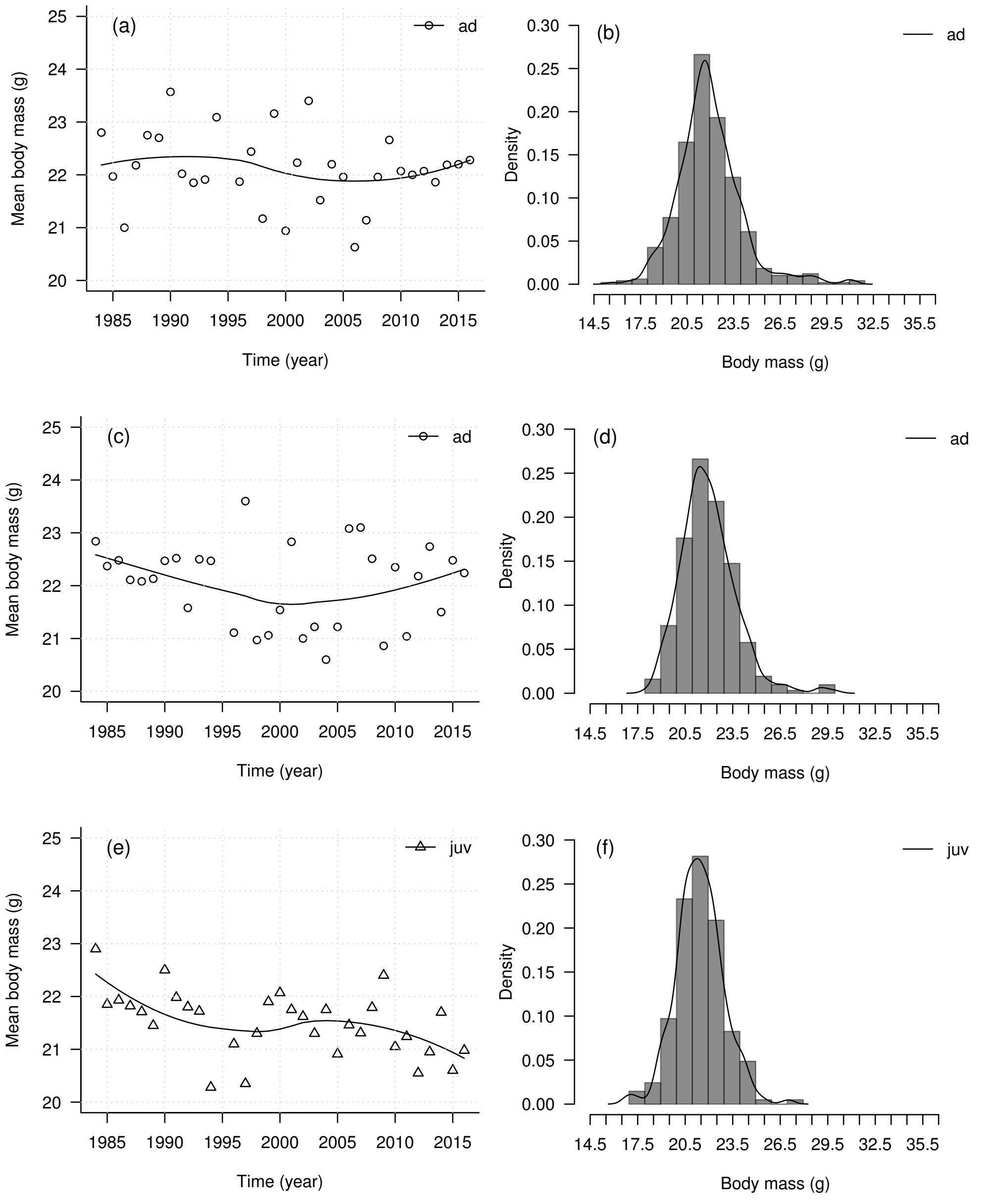
Figure 7. Annual mean tail length (mm) throughout the study period and histograms/smoothed histograms of tail length in spring (a–b) in the breeding period (c–f) and in autumn (g–j)

7. ábra Az éves átlagos farokhossz (mm) a vizsgálati időszakban és a farokhossz hisztogramja/simított hisztogramja tavasszal (a–b), a költési időszakban (c–f) és ősszel (g–j)

Table 5. Descriptive statistics of tail length (mm)

5. táblázat A farokhossz (mm) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	70.5	70	2.8	62	79	481
breeding	adult	69.4	70	2.6	63	77	254
breeding	juvenile	68.3	68	3.0	62	78	141
autumn	adult	69.6	70	2.7	62	78	276
autumn	juvenile	69.7	70	2.9	59	79	2297


(a)
ad
Mean body mass (g)
Time (year)
(b)
ad
Density
Body mass (g)
(c)
ad
Mean body mass (g)
Time (year)
(d)
ad
Density
Body mass (g)
(e)
juv
Mean body mass (g)
Time (year)
(f)
juv
Density
Body mass (g)

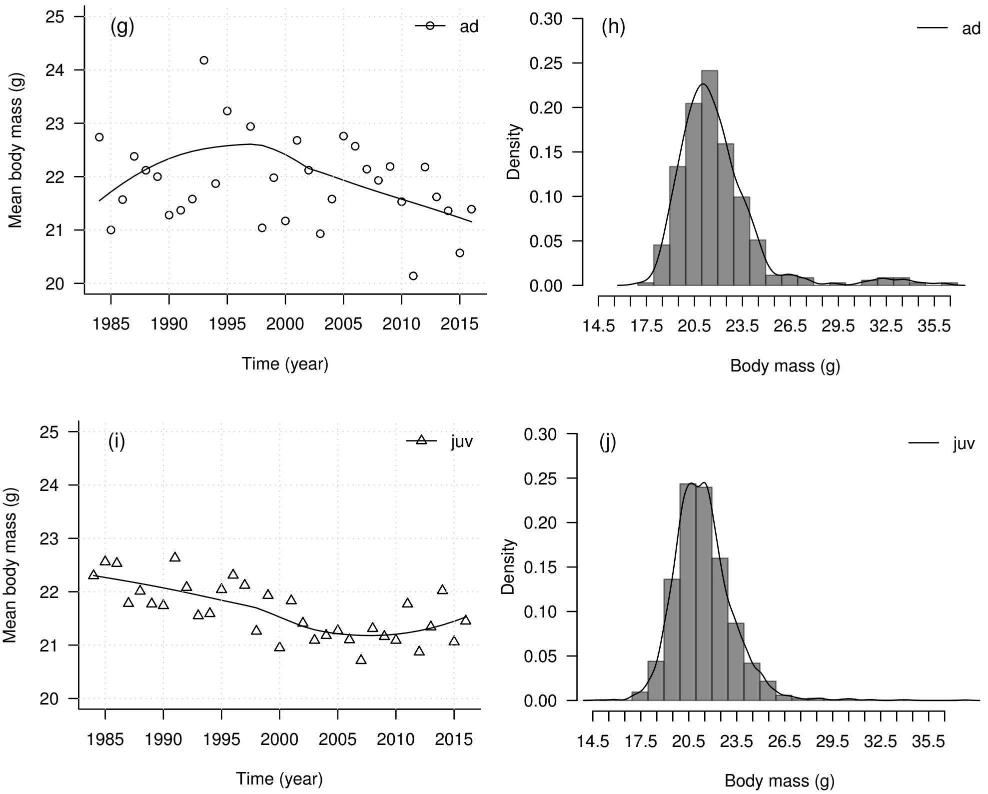
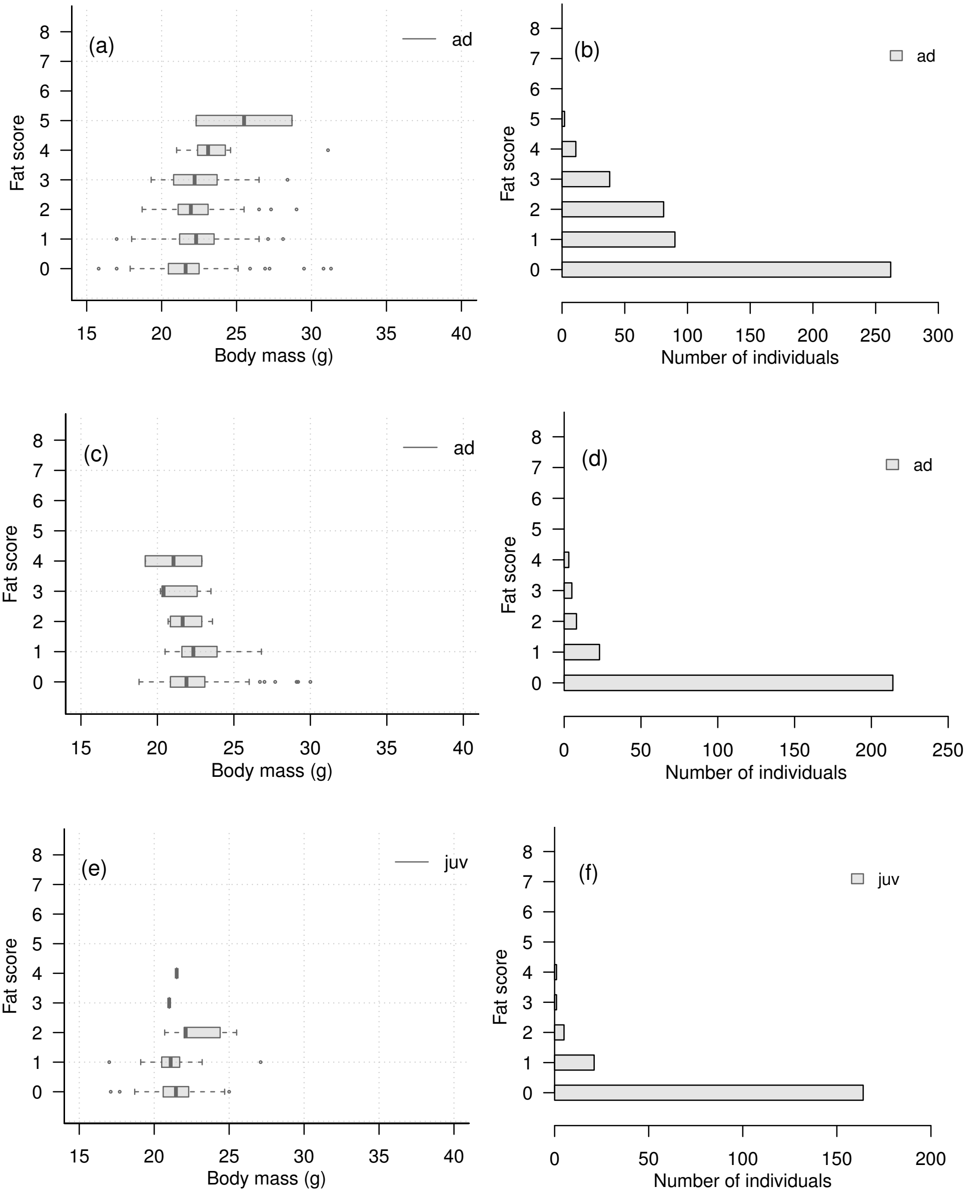


Figure 8. Annual mean body mass (g) throughout the study period and histograms/smoothed histograms of body mass in spring (a–b) in the breeding period (c–f) and in autumn (g–j)

8. ábra Az éves átlagos testtömeg (g) a vizsgálati időszakban és a testtömeg hisztogramja/simított hisztogramja tavasszal (a–b), a költési időszakban (c–f) és ősszel (g–j)

Table 6. Descriptive statistics of body mass (g)
6. táblázat A testtömeg (g) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
spring	adult	22.0	21.9	2.1	15.8	31.3	492
breeding	adult	22.1	21.9	1.8	18.2	30.0	312
breeding	juvenile	21.5	21.5	1.5	17.0	27.1	206
autumn	adult	21.9	21.5	2.6	17.2	36.1	352
autumn	juvenile	21.5	21.3	1.9	14.9	37.9	2407


(a)
ad
Fat score
Body mass (g)
(b)
ad
Fat score
Number of individuals
(c)
ad
Fat score
Body mass (g)
(d)
ad
Fat score
Number of individuals
(e)
juv
Fat score
Body mass (g)
(f)
juv
Fat score
Number of individuals

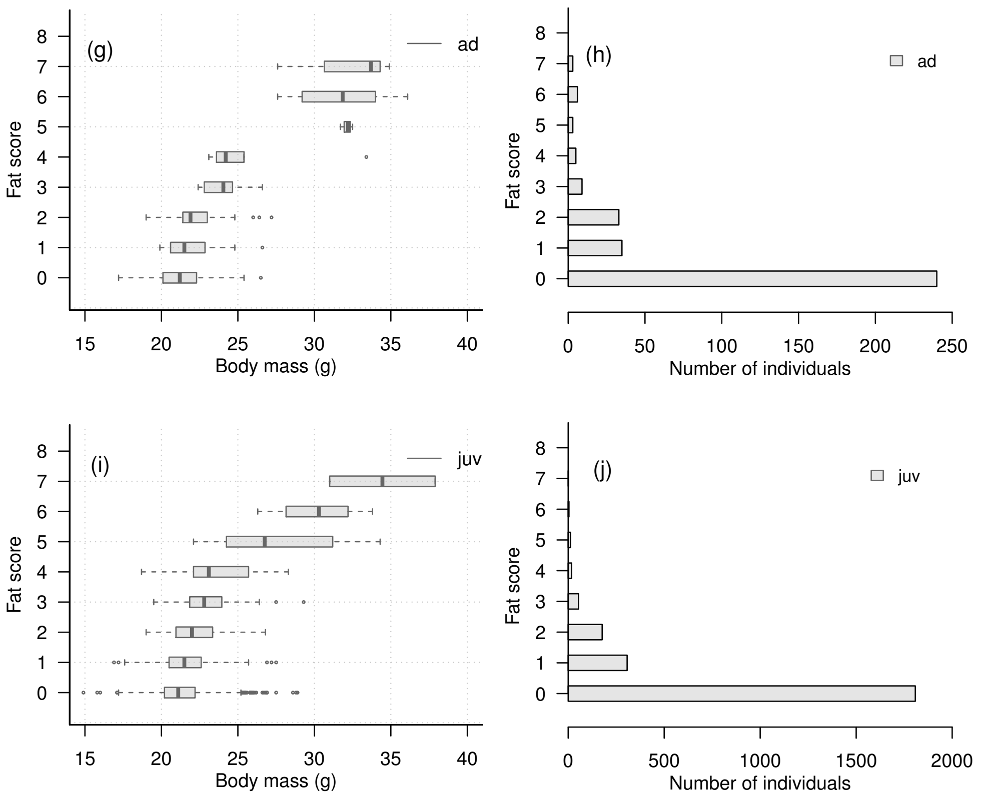


Figure 9. Boxplots of body mass according to fat score, and fat score frequencies in spring (a–b) in the breeding period (c–f) and in autumn (g–j)

9. ábra A testtömeg boxplot-ja zsírkategóriánként és a zsírkategóriák gyakoriságai tavasszal (a–b), a költési időszakban (c–f) és ősszel (g–j)

Discussion

Our exploratory and descriptive statistics of 33 years of Nightingale ringing data show several intriguing patterns. The very few foreign capture-recapture patterns indicate that the orientation of large scale movement patterns are generally south-southwest. Although the species breeds north of the Carpathians, birds migrate towards south-west from this area resulting the lack of northern recaptures in Hungary (only a single Slovakian recapture ringed close to the border, inside the Carpathian Basin) *(Figure 1)* (Kováts & Csörgő 2009). Apparently, there is considerable variation in inter-annual capture frequencies during migratory seasons *(Figure 2 a,c)*. In general, more adult birds were captured per season before 1995 and more juvenile in the second half of the study period *(Figure 2 a,b,c)*.

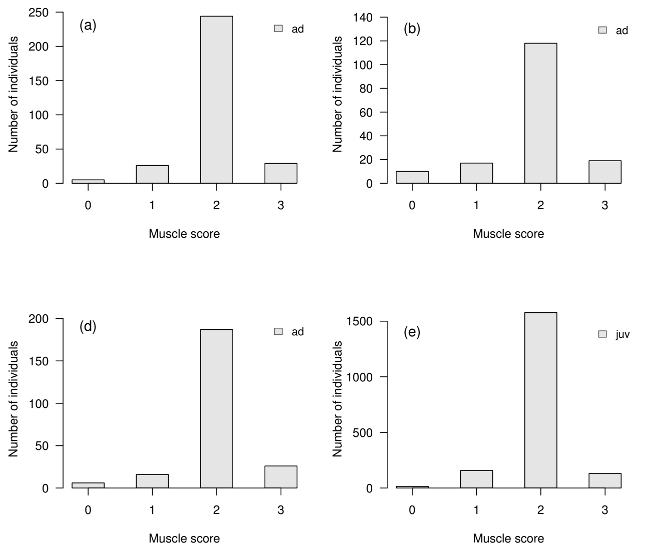


Figure 10. Muscle score frequencies in spring (a) in the breeding period (b–c) and in autumn (e–f)
10. ábra Izom kategória gyakoriságok tavasszal (a), a költési időszakban (b–c) és ősszel (e–f)

Overall, more adult birds are captured in spring than in autumn suggesting loop migration of the trans-migrant population at the Ócsa Bird Ringing Station *(Figure 3 a)*. In autumn the number of captured juveniles is remarkably high *(Figure 3 c, Table 1)*, far over the proportion of juveniles expected from the local reproductive output.

The stopover duration of adults is shorter in spring than in autumn indicating faster spring migration. The stopover duration of juveniles is seemingly shorter than that of the adults' in autumn *(Figure 3 b,d, Table 2)*.

While the spring migration timing of the adults appears to be advancing in the study period *(Figure 4 a)*, the autumn timing does not show a clear trend *(Figure 4 c)*. Timing of the adults and the juveniles in autumn are rather similar *(Figure 4 c–f)*. The distributions of arrival timing in both seasons are extended with multiple waves *(Figure 4 b,d,f)*.

Considering morphometrics, there is no indication of sexual dimorphism *(Figures 5–8 b,h,j)*, and no indication of changes in these parameters within the study period *(Figures 5–8 a,g,i)*. However, adult birds in spring apparently tend to have longer mean wing, third primary, tail lengths and body mass compared to autumn values of both age groups *(Tables 3–6)* futher indicating possible loop migration. Morphometric measures are similar in the age groups in autumn *(Tables 3–6)*, but there are more birds with fat stores in spring than in the other seasons *(Figures 9 b,h,j)*.

Our results show that comprehensive exploratory analyses may reveal intriguing patterns, which may be investigated in more detail in the future. However, we emphasize that although the temporal extent of the data reported here is considerably large, all information presented here derives from a single location and thus has to be interpreted accordingly. Nonetheless, we hope that our results will help researchers conducting comparative or meta-analyses with baseline data and may also encourage others to report their data in a similar fashion. We also seek cooperation with interested parties and are willing to share all data reported here. Please contact the corresponding author for details.

Acknowledgements

The authors express their gratitude for the work of all the volunteers who collected data at the Ócsa Bird Ringing Station. We are grateful for our colleagues – especially for Márton Demeter – who helped us develop the codes and for Bianka Jónás and János Kis, who helped us improve the manuscript. This work was supported by the National Scientific Research Fund of Hungary (OTKA under Grant No. 108571).

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