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Exploratory analyses of migration timing and morphometrics of the Thrush Nightingale *(Luscinia luscinia)*

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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 seventh 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 (1984–2017). First, we give a concise description of foreign ring recoveries of the Thrush Nightingale in relation to Hungary. We then shift focus to data of 1138 ringed and 547 recaptured individuals with 1557 recaptures (several years recaptures in 76 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 present data only for the autumn migratory period since there were only 27 spring captures in the study period. We distinguish the age groups (i.e. juveniles and adults) in the analyses. 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, migratory connectivity, Sprosser

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 (1984–2017). A sorozat hetedik tagjaként szolgáló jelen cikkben először áttekintjük a nagy fülemüle magyar gyűrűs külföldi és külföldi gyűrűs magyarországi megkerüléseit, majd rátérünk a faj egy magyarországi, 1984 óta standard módszerekkel dolgozó gyűrűzőállomásról származó 1138 gyűrűzött és 547 visszafogott egyedétől (összesen 1557 visszafogási esemény, 76 esetben több éves) 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. Csak az őszi fogásokra közlünk elemzéseket, mivel összesen 27 tavaszi fogás volt a vizsgálati időszakban. A korcsoportokat (fiatal, öreg) megkülönböztetjük. 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, vonulási kapcsoltság

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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, 2017). 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).

The civil interest towards nature can be well matched with serious, scientific work. Many scientific research is based on the important work of volunteers, ”civilians” in data collection (citizen science, Miller-Rushing *et al.* 2008, Cooper *et al.* 2014).

Here we present exploratory and descriptive statistics on the migration timing and morphometrics of the Thrush Nightingale *(Luscinia luscinia)* between 1984–2017 from a Central European ringing station (Ócsa Bird Ringing Station, Hungary, see Csörgő *et al.* 2016 in English and Csörgő & Harnos 2018 in Hungarian for details).

The Thrush Nightingale is a sexually monomorphic, omnivorous, medium-sized species of the Muscicapidae family (Collar 2018). The upper parts are typically dark olivaceous grey-brown, the tail is dull rufus-brown, the breast is brown, almost invariably mottled grey. The great-covers and tertials of adults are uniform brown. The juveniles' feathers are spotted until the postjuvenile moult. Thrush Nightingales are typically darker than Nightingales *(L. megarhynchos)*. Post-moult juveniles are similar to adults, but tips of tertials and greater covers retain pale spots (Cramp 1988, Svensson 1992, Demongin 2016). The plumage of sexes are similar, but the males are slightly darker and larger than females, and have more prominent grey mottling on breast. The exact sexing is only possible in hand, using the incubation patch of breeding adults (Dittberner & Dittberner 1989, Svensson 1992, Demongin 2016).

The Thrush Nightingale is a monotypical species with an extensive breeding range from Norway, Denmark, Germany, Poland, to central Asia, covering the temperate and continental climate zones, complementing the more southerly and westerly distribution of the Nightingale (Cramp 1988, Tucker & Heath 1994, Bogucki & Sorjonen 1997, Collar 2018). The Thrush Nightingale and the Nightingale are two ecologically and morphologically similar, closely related sister species (Sorjonen 1986, Reifová *et al.* 2011a). In a narrow zone from Denmark to the Balkans the Thrush Nightingale is sympatric with the Nightingale (Storchová *et al.* 2010). Both species have similar ecological requirements but partial habitat segregation has been observed in sympatry (Ranoszek 2001). The divergence in bill size most likely reflects segregation of feeding niches between the species in sympatry (Reifová *et al.* 2011b). The two species diverged approximately during the Pleistocene (1.8 Mya) (Storchová *et al.* 2010). Despite the close relationship and similarities of the sister species, their migratory strategies are remarkably different (Hahn *et al.* 2016, Csörgő *et al.* 2017). The hybridisation of the two species is relatively common in the overlapping breeding areas (Reifová *et al.* 2011b). The hybrid males are fertile and can reproduce with either of the parental species (Becker 1995, Reifová *et al.* 2011a). The two species are isolated by incomplete prezygotic isolation and female hybrid sterility (Kverek *et al.* 2008, Reifová *et al.* 2011a). The F1 birds have intermediate wing formula (Becker 2007, Kováts *et al.* 2013, Demongin 2016).

The Thrush Nightingale is classified as Least Concern in the IUCN Red List (BirdLife International 2018). After a largely stable population between 1970–1990, it has increased in Denmark, Poland, Norway, Finland and Estonia, and some range expansion has occurred in Sweden. The species has occupied urban areas, parks and cemeteries. Warmer springs have allowed new breeders to increase density and range (Bogucki & Sorjonen 1997). These increases proved a longer-term spread to the west and north (Tucker & Heath 1994, Valkama *et al.* 2014). The Swedish population changed from cca. 15,000 breeding pairs in the 1970's to cca. 20,000–50,000 pairs in the 1980's (Bogucki & Sorjonen 1997). The Finnish population size was about 200 pairs during the early 1950's (Merikallio 1958) and increased to around 8000 pairs during the early 1980's (Hildén & Koskimies 1984), and to 15,000–20,000 pairs for the late 1990's (Bogucki & Sorjonen 1997). The number of breeding occurrences also increased in eastern Germany in the early 1990's (Becker 1995). The long-term Pan-European trend showed a 9% population increase between 1980–2009, which means a 0.3% mean annual rate of change (Vickery *et al.* 2014). Number of vagrants greatly increased in Britain during the twentieth century in association with changes in population size or distribution (Newton 2008). In the meantime, number of birds decreased in Sweden based on point count and ringing data between 1980 and 1999 (Karlsson *et al.* 2005) and in Denmark (point-count census data) between 1976 and 2005 (Heldbjerg & Fox 2008).

The species is protected on the breeding area, but the situation is different on its migratory route. For example, beyond the 3.3 million Quails *(Coturnix coturnix)*, 0.5 million other birds were captured and killed in North Sinai during the 45 days of peak migration in 2012 in autumn and near 50,000 of them were Thrush Nightingales (Eason *et al.* 2016). The ratio of killed birds among the recoveries is decreasing (Fransson & Hall-Karlsson 2008).

The Thrush Nightingale inhabits more continental areas complementing the distribution of the Nightingale. Its preferred habitat is dense, damp thickets, often riverine or swampy, forest-edges with good ground cover (nettles and bramble). They occupy variable, densely vegetated habitats from lowland riverine woodland, edges of broad-leaved woodlands to bushland, managed open woodlands (young deciduous trees), suburban habitats and gardens (Cramp 1988, Tucker & Heath 1994, Bogucki & Sorjonen 1997).

Their mating system is social monogamy. Only the females incubate, but both parents feed the offspring. The pair-bond breaks down at the end of breeding season (Cramp 1988).

The Thrush Nightingale – mainly males – has a high breeding site fidelity (Cramp 1988, Becker 2007). In Czech Republic only 2% out of 351 adults have been found more than 10 km away, and 91.2% of juveniles settled less than 10 km from the natal site (Kverek *et al.* 2008). The median dispersal distance for birds ringed as nestlings is 2 km (0–220) and for breeding adults 0 km (0–51) in Finland (Valkama *et al.* 2014).

After breeding the complete moult of adults takes around 30–35 days, which is faster than in case of Nightingales (cca. 45 days) (Ginn & Melville 1983, Svensson 1992, Jenni & Winkler 1994).

The Thrush Nightingale is a long distance migratory bird with a typical funnel-shaped migratory pattern. Birds from the whole breeding distribution converge to a relatively narrow wintering zone in East-Africa (Cramp 1988).

Despite the large European population (3,7000,000–6,900,000 breeding pairs) (BirdLife International 2004), the number of ringed birds is relatively small, and thus the number of recoveries is also small (3831 ringed birds with 15 foreign recoveries up to 2002 in Denmark, 14,245 ringed birds up to 2003 with a mean of cca. 400 in the recent years and 14 foreign recoveries in Sweden, 11,608 ringed birds with 14 foreign recoveries up to 2012 in Finland) (Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008, Valkama *et al.* 2014). Ringing work is intense only in the western edge of its distribution, most birds breed east to this area (BirdLife International 2018). Even though the Thrush Nightingale is one of the most common Palaearctic passerine on the north-eastern side of the Ngulia ridge, in the West Tsavo National Park in south-east Kenya during November and December on the narrowest part of the funnel, where several hundreds of birds are ringed daily (Pearson & Backhurst 1976), there were only one Swedish and one Finnish recoveries (Fransson & Hall-Karlsson 2008, Valkama *et al.* 2014).

From the western breeding areas the species migrates to south-east direction in autumn. It is very common in the Eastern Mediterranean in during the postbreeding migration (Cramp 1988, Alerstam 2006), also the Appenine Peninsula can be a refuelling site for them (Stach *et al.* 2012), but the more eastern sites (Balkan area) are probably more important, since there are a relatively small number of ringed birds in Italy during autumn migration (Spina & Volponi 2009).

Recoveries in Denmark indicate that migrants from Sweden and Finland pass Denmark (Bønløkke *et al.* 2006), and the Swedish birds pass Germany. Birds ringed in Germany were recovered in Hungary and in North-Italy (Bairlein *et al.* 2014). The Thrush Nightingale migrates with a strong concentration of recoveries in Egypt (Fransson *et al.* 2005, Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008, Bairlein *et al.* 2014).

The species leaves the breeding areas from early August to mid- or late September (Cramp 1988). The migration interval is quite wide, meanwhile the migration of individuals may be quick. For example, there were recoveries in Finland at the beginning of August, and in the meantime a bird with Finnish ring was found in on the 12th of August in Egypt (Valkama *et al.* 2014). While one Danish bird was recovered in Hungary in August, two others were recovered in Austria and in Egypt in September (Bønløkke *et al.* 2006).

The small set of ringing data has a peak in the second decade of August in Italy (Spina & Volponi 2009). Thrush Nightingales pass through Cyprus from mid-August to October with a peak in late August and September, through Egypt from mid-August to mid-October with a peak in late August to mid-September, through Ethiopia from the second week of September to early November and through central Sudan around the Nile system in August – November with a peak from late September. Movement into Kenya begins at the end of October peaking from 10th of November to 10th of December (Pearson & Backhurst 1976, Hogg *et al.* 1984, Cramp 1988, Yohannes *et al.* 2009b).

The Thrush Nightingale tracks vegetation greenness and the peaks of insect abundance occurring after rains throughout their annual cycle, adjusting the timing and direction of migratory movements with seasonal changes in resource availability over Europe and Africa. The species stops several times for longer time periods during autumn migration. The birds probably spend three-four weeks in southern Europe (Appenine and Balkan Peninsulas), then they spend up to 2 months (or a few of them even may stay for the whole winter) in green areas of eastern Sudan and western Ethiopia, then they break their journey in the east Kenyan bushland from late November to late December. They move between consecutive staging areas even within the wintering region in Africa to match seasonal variation in regional climate (Pearson & Lack 1992, Stach *et al.* 2012, Thorup *et al.* 2017).

The migration speed is cca. 120 km/day in Europe, and 140 km/day while the birds cross the desert, only cca. 20 km/day in north-east and east Africa in autumn (Yohannes *et al.* 2009a).

Some of the individuals winter in southern Ethiopia, but most of them winter south of the Equator (Kenya, Tanzania, Malawi, Zimbabwe, Mozambique, Namibia, Botswana, South Africa (Cramp 1988). Main arrival in southern Africa starts at late November (Cramp 1988, Bønløkke *et al.* 2006).

The body mass of the species decreases continuously in autumn from Europe (cca. 28 g) to the Equator (cca. 22 g) (Yohannes *et al.* 2009a,b). The body mass of Thrush Nightingales killed at Bahig on the Egyptian coast in autumn was 24.4 g with 5.2 g fat mass on average (Moreau & Dolp 1970). The deposited tissue consisted of 82% fat and 18% wet protein (Klaassen *et al.* 1997).

The species leaves the winter quarter in March, early April. Passage through Kenya lasts from late March until the 3rd week of April. They are present in Jordan, Israel, Syria, Lebanon from mid-April to early May. The birds arrive to the breeding site from mid-April in Romania and in early May in Germany and Sweden (Cramp 1988). The migration period is quite wide, and individual birds move quite fast similarly to the autumn migration. For example, there were Finnish birds at the end of April in Egypt, and there were migrating birds in Finland at the beginning of May (Valkama *et al.* 2014).

The species has an anti-clockwise loop migration (Klvaňa *et al.* 2018). The autumn migration route leads on the eastern side of the Nile and the Victoria-lake in Kenya, but the spring migration follows an even more eastern route in Africa, associated with the more humid conditions on the eastern coast (Pearson & Lack 1992, Tøttrup *et al.* 2012). A bird ringed in Sweden was recovered in Yemen (Fransson & Hall-Karlsson 2008), other two birds ringed in Finland were recovered in Lebanon (Valkama *et al.* 2014), and one Hungarian bird was recovered in Israel in spring (BirdLife Hungary 2018). The species is very rare in spring in Italy indicating also the more eastern route back to the breeding area (Spina & Volponi 2009).

During spring, their speed is cca. 80 km/day in East Africa, 230 km/day above the desert, and 80 km/day in Europe (Yohannes *et al.* 2009a).

Probably due to climate change, the whole migration wave advanced on the island of Christiansø, in the Baltic Sea in spring from 1976 to 1997 (Tøttrup *et al.* 2006) and the first-arrival days advanced during 1950 to 2012 at Ottenby, Sweden (Tøttrup *et al.* 2012). The actual weather situation also influences the migration, for example the arrival time at Ottenby of the species was delayed in an exceptionally drought year in north-east Africa in 2011 (Tøttrup *et al.* 2012). Arrival to Vilnius (Estonia) is negatively correlated with precipitation and positively correlated with atmospheric pressure (Zalakevicius *et al.* 2006).

The species is protected in Hungary (BirdLife Hungary 2018). The Thrush Nightingale was formerly common breeder species in the north-eastern part of Hungary (Farkas 1954), but in the second half of 20th century it has became a rare breeder in remnant patches of willow-poplar groves and willow bushes (Schmidt 1973). Recently the species was extinct from the site of the Felső-Tisza (and probably from its surroundings) and only interspecific hybrids with the Common Nightingale can be found. A strong evidence for a new haplotype group of Szatmár-Bereg was found, which had *L. megarhynchos* morphology but of *L. luscinia*' mtDNA (Ács & Kováts 2013). Currently 7% of the population of Nightingale were interspecific hybrids. The morphological character displacements and the proportion of hybrids refer a stable hybrid population (Kováts *et al.* 2013, Kováts & Harnos 2015).

Some birds recovered in Hungary have been ringed at the most western part of the breeding area: in Sweden, Germany, Finland, and birds ringed in Hungary were recaptured on the breeding areas (Csörgő & Kováts 2009, BirdLife Hungary 2018). These birds mostly fly from north-east to south-west direction in autumn. Two individuals ringed in Hungary were recovered in the following years in North-East (Belarus) indicating that the Carpathian Basin is in connection with a much wider zone. Birds ringed westward have typically been recovered in the western area of the country *(Figure 2)*. There were more several-year recoveries (76 birds (6.7%) in the study period at Ócsa). The pattern of recaptures and the high number of several-year recoveries are also signs of strong connectivity, which is atypical in case of long distance migrants (Finch *et al.* 2017).

The Thrush Nightingale is a regular, but not common migrant from late April until mid-May in spring, the peak is at the end of April, early May. Much more birds use the Carpathian Basin in the post breeding migration. The first specimens are usually captured at the beginning of August and the last ones in late September, early October peaking in mid-August. (Csörgő & Lövei 1986, 1995, Hadarics & Zalai 2008, Csörgő & Kováts 2009).

Many birds caught in two ringing stations near Budapest (Budakeszi and Ócsa) showed intensive increase in body mass during migration. The average body mass is cca. 25 g before the 20th of August, and it is near 30 g in the third pentad of September (Csörgő & Lövei 1986). 40% of the birds are recaptured at site within season with increasing body masses proving that the Ócsa area is used for stopover and pre-migratory fattening, so the fattest birds (some of them were more than 30 g) are able to reach Egypt without stopover (Csörgő & Lövei 1995). Contrarily, only 1% of the birds were recaptured (without several-year recaptures) in Szalonna, on a third ringing station of East Hungary. Here the individuals were in a relatively poor condition, indicating that birds only rest at that site. Here, within the 22 years of study (1989–2010), the median date of autumn migration of Thrush Nightingales shifted 8 days earlier (Kováts 2012). In the same time period, the arrival times also shifted earlier at Ócsa (see later in this paper).

Thrush Nightingales are regular, but not common passage migrants at the Ócsa Bird Ringing Station (regular in autumn, rare in spring as a sign of loop migration), 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 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 only for the autumn migratory season due to the almost total lack of spring migrants; birds caught after the 190th and before the 280th day of the year were considered to be autumn migrants. A total of 1138 Thrush Nightingales were captured and ringed between March and November; 27 adults in spring and 190 adults and 895 juveniles in autumn (the rest of the birds were not aged) in the study period of 1984–2017. This total value constitutes cca. 14.4% of the 3783 Thrush Nightingales ringed in Hungary in this period. Beyond the ringed individuals, there were 547 recaptured individuals with 1557 recaptures (76 several-year recaptures).

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). 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 distributions of the same variables were represented with histograms and overlaid smoothed histograms.

Figure 1. Foreign ring recoveries of Thrush 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 gyűrűzött és külföldön megkerült, illetve külföldön gyűrűzött és Magyarországon visszafogott nagy fülemülék

Boxplots were used to show the body mass distributions by fat score categories. Fat and muscle score frequencies are shown using barplots. We distinguished the 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).

Results

A total of 14 foreign recaptures were recorded between 1951 and 2017 in relation to Hungary *(Figure 1)*. Annual capture and recapture frequencies at the study site are shown in *Figure 2*. Within-year capture and recapture frequencies, together with cumulative distribution 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 distribution of wing length measurements according to 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 age and fat scores are visualized with boxplots in *Figure 9*. Finally, the distribution of fat and muscle scores grouped by age can be found in *Figure 9 b,d* and *Figure 10*.

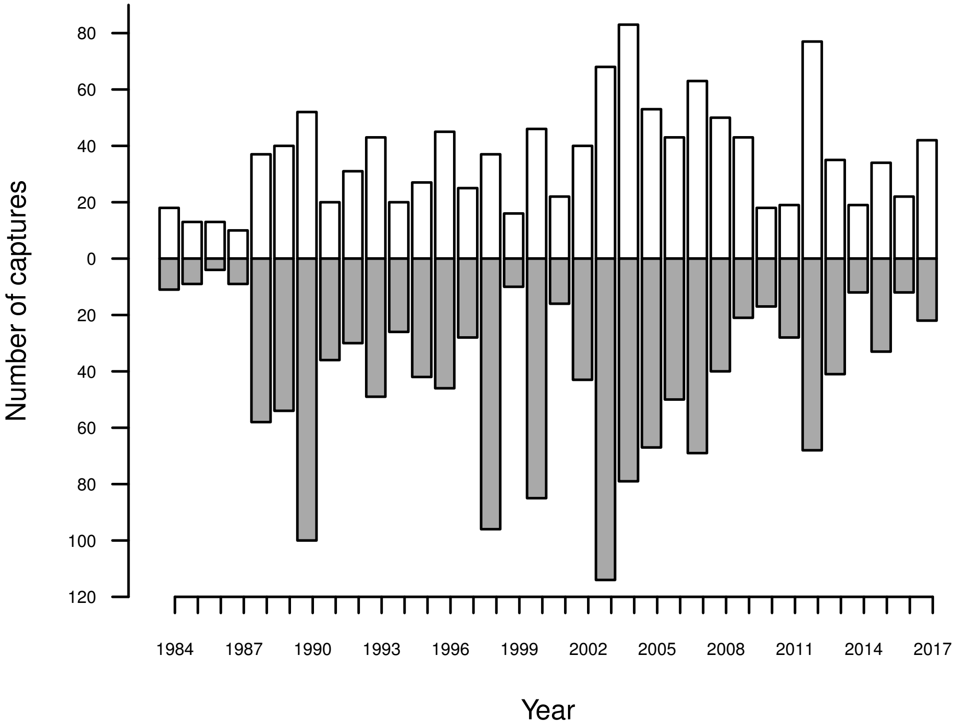

Figure 2. Annual capture (white bars) and recapture (grey bars) frequencies in autumn
2. ábra Éves fogás (fehér oszlopok) és visszafogás (szürke oszlopok) gyakoriságok ősszel

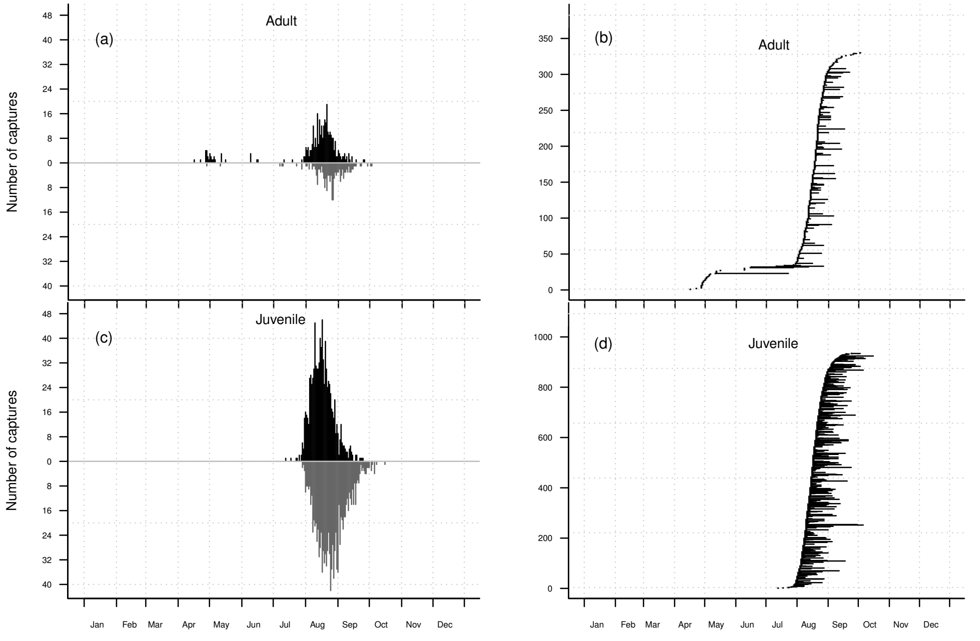

Figure 3. Within-year capture (black bars) and recapture (grey bars) frequencies (a, c) and cumulative distributions of individual first capture dates (b, d) according to age groups (horizontal lines: stopover durations)

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 stopover duration (day)
1. táblázat A tartózkodási idő (nap) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
autumn	adult	12.6	11	9.4	1	47	97
autumn	juvenile	12.0	10	9.4	1	57	395

Migration timing

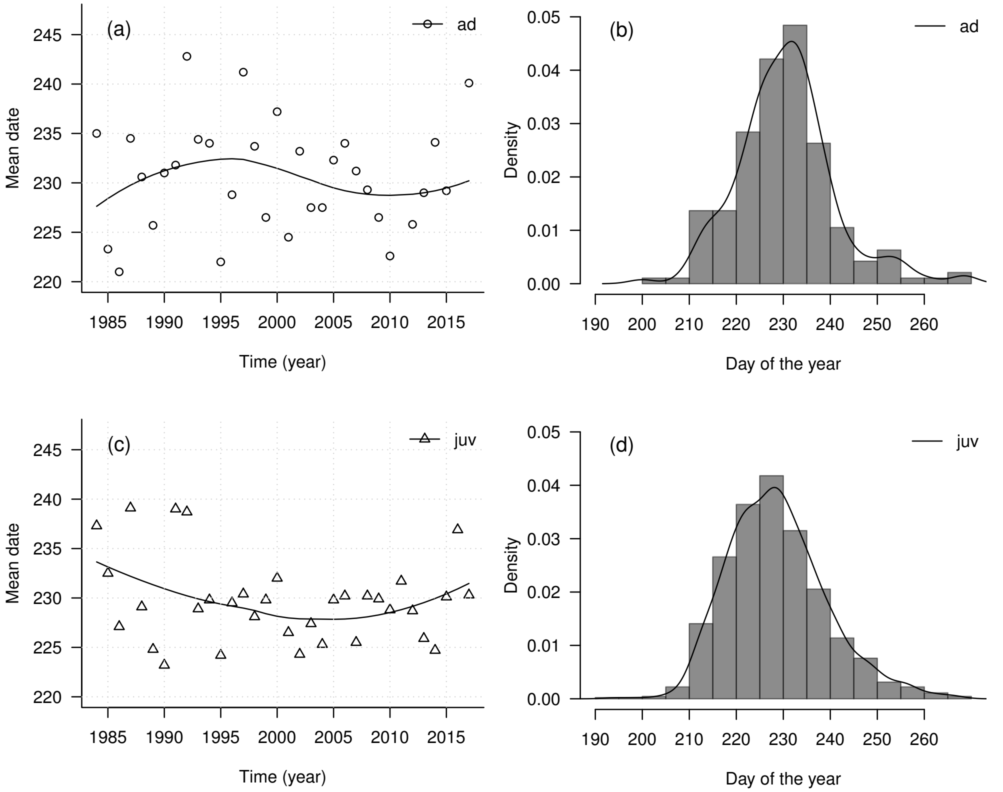

Figure 4. Annual mean migration timing (day of the year) throughout the study period and histograms/smoothed histograms of timing in autumn

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

Table 2. Descriptive statistics of migration timing (day of the year)

2. táblázat A vonulás időzítés (év napja) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
autumn	adult	230.7	230.5	10.4	200	269	190
autumn	juvenile	228.7	228.0	10.5	194	267	895

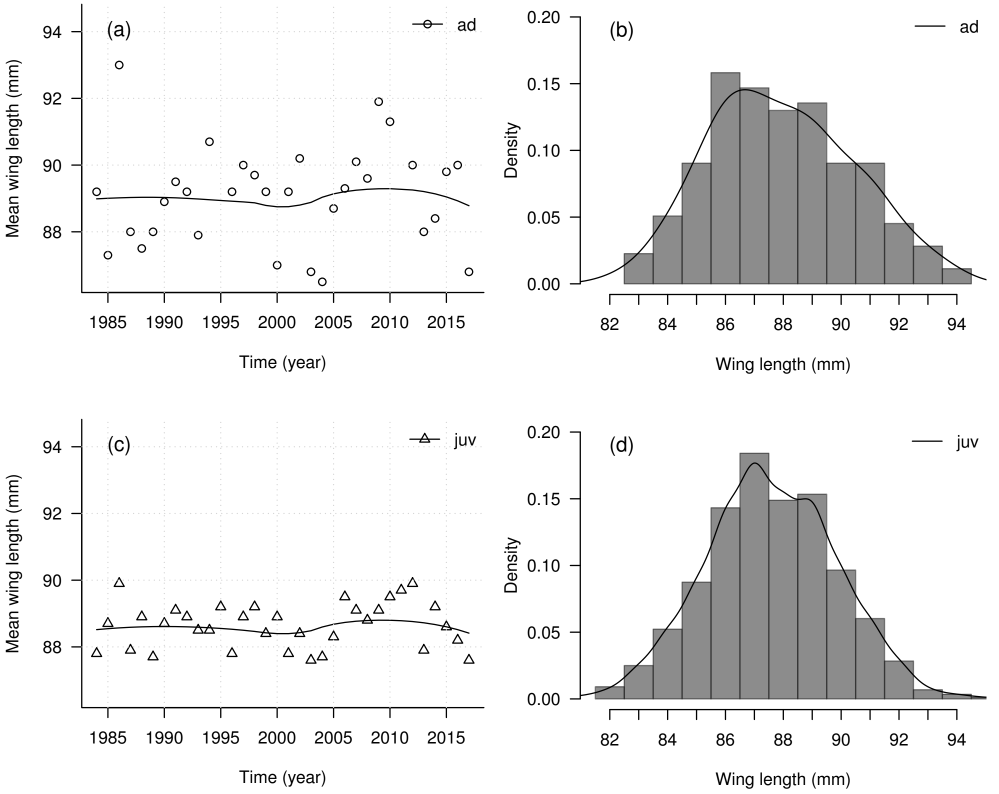

Figure 5. Annual mean wing length (mm) throughout the study period and histograms/smoothed histograms of wing length in autumn

5. ábra Az éves átlagos szárnyhossz (mm) a vizsgálati időszakban és a szárnyhossz hisztogramja/simított hisztogramja ősszel

Table 3. Descriptive statistics of wing length (mm)

3. táblázat A szárnyhossz (mm) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
autumn	adult	88.9	89.0	2.5	83	95	177
autumn	juvenile	88.6	88.0	2.3	82	96	880

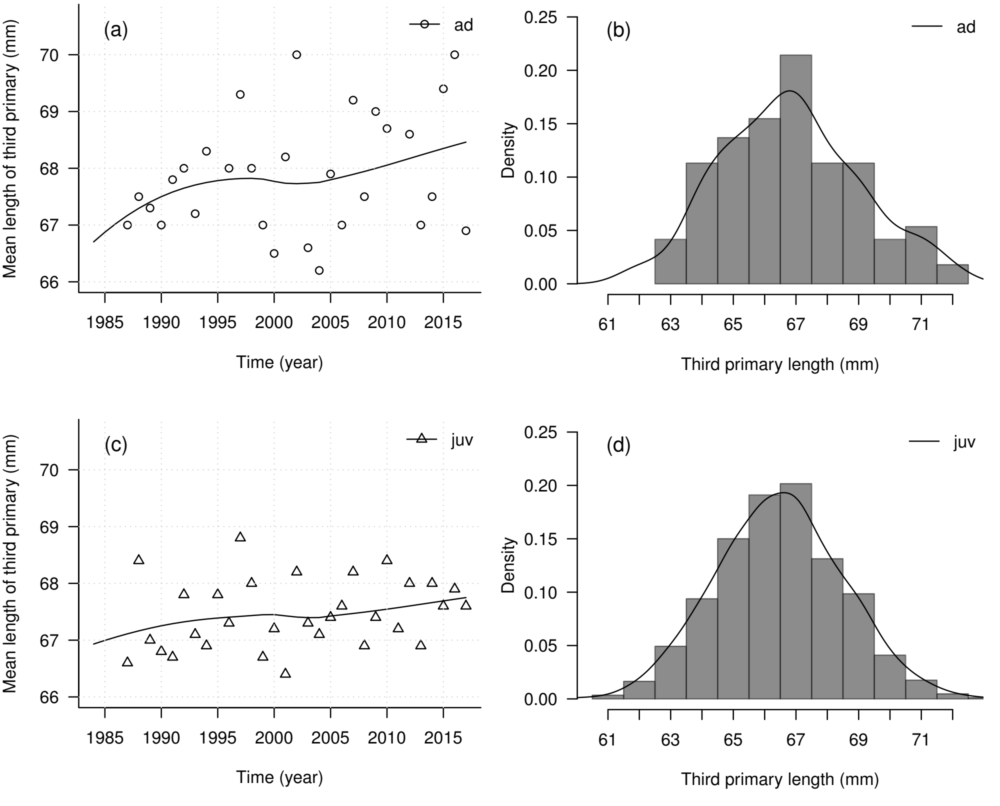

Figure 6. Annual mean third primary length (mm) throughout the study period and histograms/smoothed histograms of third primary length in autumn

6. ábra Az éves átlagos harmadik evező hossz (mm) a vizsgálati időszakban és a harmadik evező hosszának hisztogramja/simított hisztogramja ősszel

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**
autumn	adult	67.8	68.0	2.2	63	73	168
autumn	juvenile	67.5	67.0	2.0	61	74	853

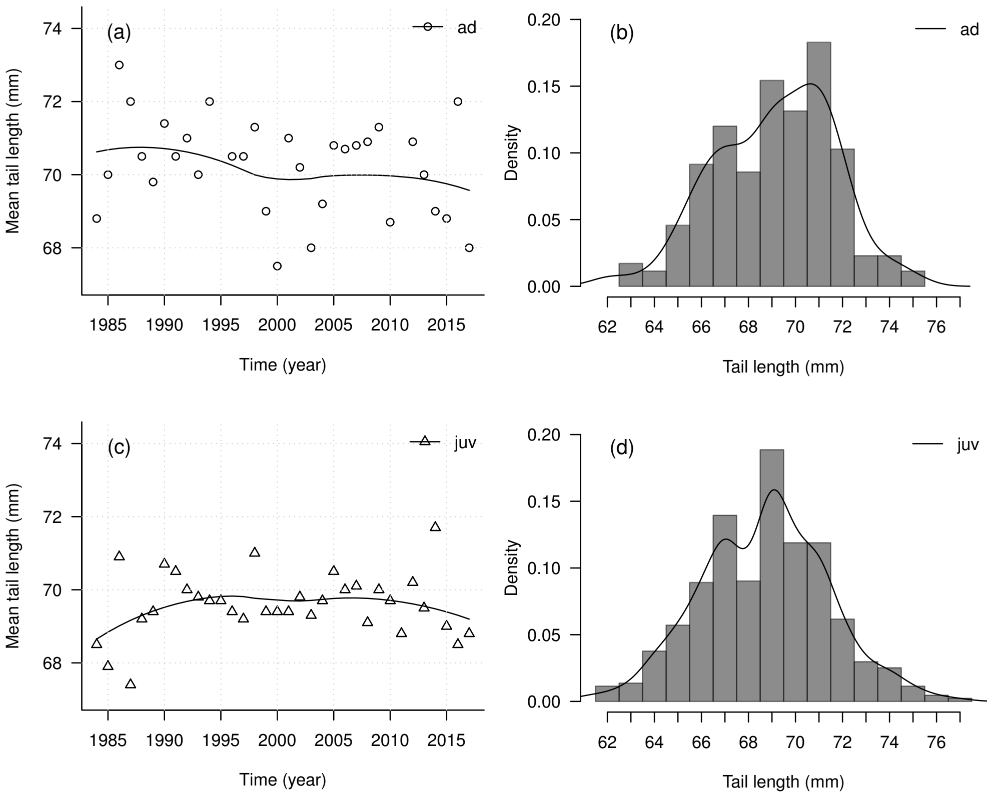

Figure 7. Annual mean tail length (mm) throughout the study period and histograms/smoothed histograms of third primary length in autumn

7. ábra Az éves átlagos farokhossz (mm) a vizsgálati időszakban és a farokhossz hisztogramja/simított hisztogramja tavasszal ősszel

Table 5. Descriptive statistics of tail length (mm)

5. táblázat A farokhossz (mm) leíró statisztikái

Season	**Age**	**Mean**	**Median**	**SD**	**Min**	**Max**	**N**
autumn	adult	70.1	70.0	2.5	63	76	175
autumn	juvenile	69.7	70.0	2.7	62	78	875

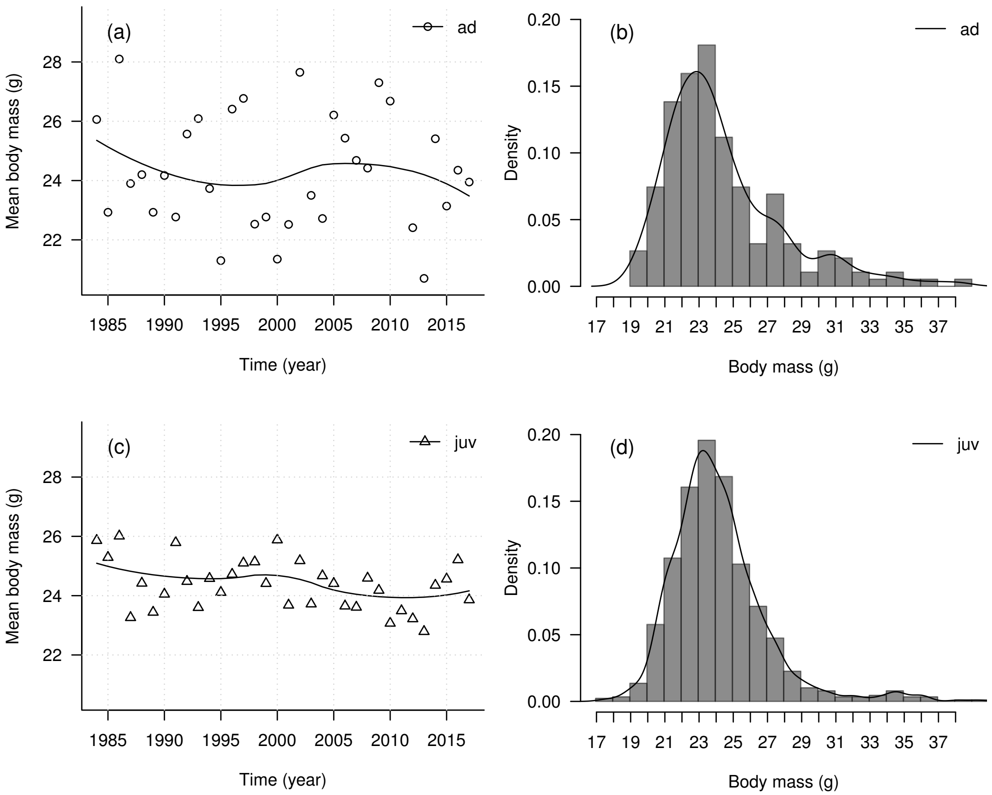

Figure 8. Annual mean body mass (g) throughout the study period and histograms/smoothed histograms of body mass in autumn

8. ábra Az éves átlagos testtömeg (g) a vizsgálati időszakban és a testtömeg hisztogramja/simított hisztogramja ősszel

Table 6. Descriptive statistics of body mass (g)

6. táblázat A testtömeg (g) leíró statisztikái

Season	Age	Mean	Median	SD	Min	Max	N
autumn	adult	24.5	23.6	3.4	19.4	38.3	188
autumn	juvenile	24.2	23.8	2.8	17.5	39.4	884

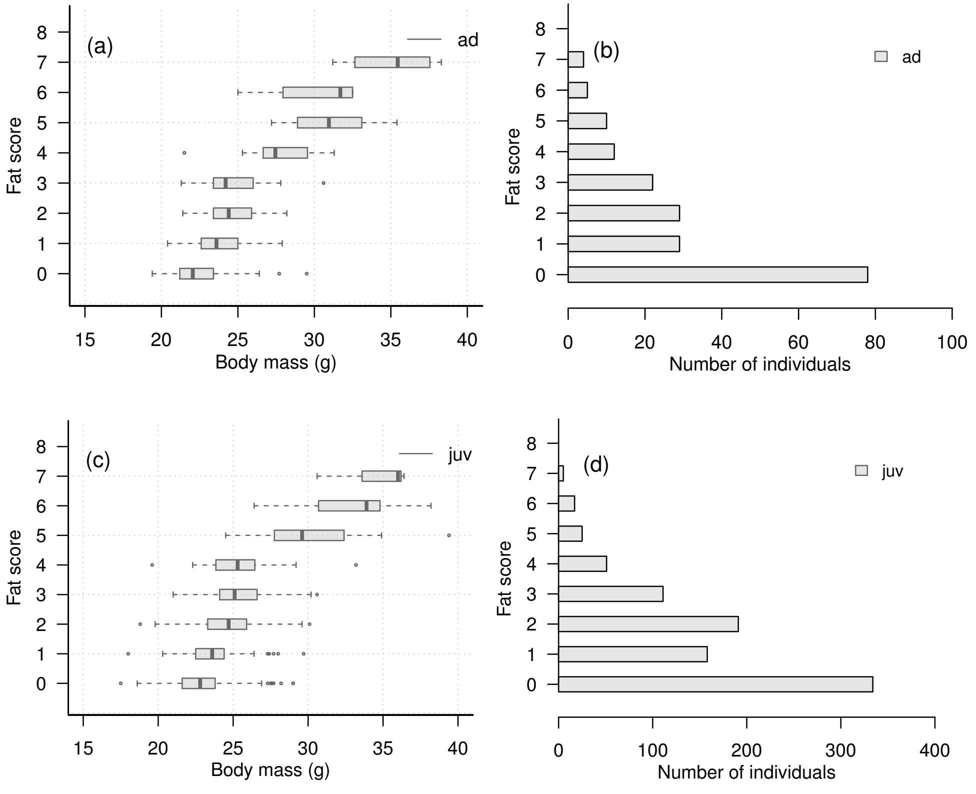

Figure 9. Boxplots of body mass according to fat score, and fat score frequencies in autumn
9. ábra A testtömeg boxplot-ja zsírkategóriánként és a zsírkategóriák gyakoriságai ősszel

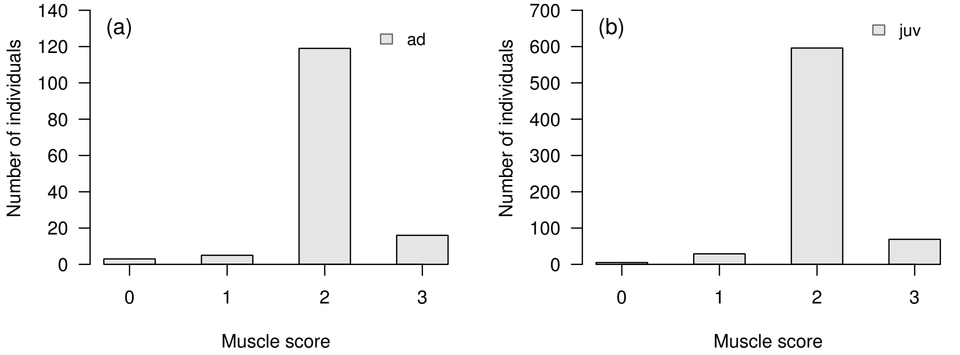

Figure 10. Muscle score frequencies in autumn
10. ábra Izom kategória gyakoriságok ősszel

Discussion

The exploratory analyses of timing and morphometrics of the Thrush Nightingale revealed several patterns of interest. Apparently, there is considerable variation (the maximum is cca. four times the minimum) annual capture and recapture frequencies in autumn *(Figure 2)*. During the last two decades of the previous century, when the number of birds was lower in Sweden, the numbers were also lower at the study site. Only 27 birds were captured in spring suggesting loop migration. The stopover durations are similar in all age groups *(Figure 3 b,d, Table 1)*.

The amount of juveniles greatly exceeds the amount of the adults *(Figure 3 a,c)*.

The autumn migration timing advanced in the first half and then delayed in the second half of the study period in case of the juveniles *(Figure 4 c)*. Timing of the adults is a bit delayed compared to that of the juveniles *(Figure 4 a,c, Table 2)*. The distribution of arrival timings are similar in the two age groups *(Figure 4 b,d)*. While there is no apparent trend over the years in wing length, there is a slight increasing trend in the third primary length *(Figures 5–6 a,c,e)*.

Tail length seems to be decreasing in case of adults although with a considerable inter-annual variation *(Figure 7 a)*, which can be caused by the low number of birds annually. This trend cannot be observed in case of juveniles *(Figure 7 c)*. The mean body mass seems to be constant over the years *(Figure 8 a)*, however a slight decreasing trend can be observed during the autumn season in case of the juvenile birds *(Figure 8 c)*.

The wing and tail distributions are slightly bimodal indicating some dimorphism between the sexes *(Figure 5–8 a,c,e)*.

The fat score distributions suggest that the birds can accumulate fat reserves *(Figure 9)*. Muscle score distributions suggest that the birds also build their muscles *(Figure 10)*.

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.

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