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Sex and age dependent migration phenology of the Pied Flycatcher in a stopover site in the Carpathian Basin

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Abstract Very little is known about Pied Flycatchers crossing the Carpathian Basin. We give a comprehensive picture about its migration based on the data collected during the past 26 years (1989–2014) at a stopover site in Hungary: (1) sex and age related phenological changes over the years, (2) sex, age and size dependent migration patterns during and (3) between migration periods, (4) sex and age composition in spring and in autumn and their change over years.

The timing of spring migration shifted to earlier dates in the case of males, while that of females did not change implying an increasing rate of protandry. In autumn the timing did not change, but juveniles leave the area earlier than adults. The average wing length increased during the past decades in spring in the case of both sexes. In autumn, wing length did not change significantly during the years, but it increased during the seasons in all age and gender groups.

The proportion of males is about 60% in spring and among juveniles in autumn, and it is around 39% in the adult group in autumn. The male ratio diminishes during spring, but it does not change during the autumn season. The average wing of adults is shorter in spring than in autumn. Based on this fact and the different sex ratios in the two seasons we may hypothesize that Pied Flycatchers are loop migrants on this area, and even the sexes of the same population take different routes.

Keywords: protandry, migration timing, Carpathian Basin, wing length, sex ratio, loop migration

Összefoglalás Keveset tudunk a Kárpát-medencén átvonuló kormos légykapókról. Átfogó képet adunk vonulásáról egy magyarországi pihenőhelyen az elmúlt 26 évben (1989–2014) gyűjtött adatok alapján: (1) ivar- és korfüggő fenológiai változásokról az évek során, (2) ivar-, kor- és méretfüggő vonulási mintázatáról a vonulási időszakok alatt és (3) között, (4) valamint az ivar- és korösszetételéről a tavaszi és őszi időszakban, továbbá ezek változásáról az évek során.

Míg a hímek tavaszi vonulása korábbra tolódott, a tojóké nem változott, így nőtt a protandria mértéke. Ősszel nem változott az időzítés, de a fiatalok korábban hagyják el a területet, mint az öregek. A tavaszi átlagos szárnyhossz szignifikánsan nőtt az elmúlt évtizedekben mindkét ivar esetén. Ősszel nem változott szignifikánsan a szárnyhossz az évek során, de az évszakok során minden ivar- és korcsoportban nőtt.

A hímek aránya 60% tavasszal és az őszi fiatal korcsoportban, de csak 39% az őszi öregek között. A hímek aránya csökken a tavasz folyamán, de ősszel nem változik. Az öregek átlagos szárnyhossza rövidebb tavasszal, mint ősszel. A különböző szárnyhossz és ivararány alapján arra következtethetünk, hogy a kormos légykapó hurokvonuló ezen a területen. Valószínű, hogy még ugyanannak a populációnak a két ivara is más útvonalon repül a vonulás során.

Kulcsszavak: protandria, vonulás időzítés, Kárpát-medence, szárnyhossz, ivararány, hurokvonulás

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Introduction

Timing of large scale individual movements of avian migrants often shows considerable intra- and interspecific differences between sex and/or age groups due to the variations in migration and moult strategies, territoriality on the wintering area, feeding ecology and other needs (Stutchbury 1994, Woodrey & Moore 1997, Stewart *et al.* 2002). Within species often males migrate earlier than females in spring (protandry) (Ellengren 1991, Stewart *et al.* 2002, Catry *et al.* 2004, Mills 2005) and adults migrate earlier than juveniles (differential migration) (Terrill & Able 1988), but there are examples for the opposite sequences (Reynolds *et al.* 1986). The differential migration of sexes has been intensely studied in spring (Kokko 1999, Rubolini *et al.* 2004, Tøttrup & Thorup 2008), but less attention has been paid to this phenomenon in autumn (Mills 2005, Jakubas & Wojczulanis-Jakubas 2010). Moreover, less is known about the differential timing between age classes within each sex during autumn migration.

The Pied Flycatcher *(Ficedula hypoleuca)* is a small passerine bird which is distributed in the North-Western part of the Western Palaearctic (Cramp & Simmons 1983). Their breeding population in Europe is large (which means approximately 12 million pairs) and it was stable until the last quarter of the 20th century (BirdLife International 2004). It is a sporadic to rare breeder in Hungary (predominantly in the Southern Great Plain, Alpine Foothills and Zala Hills) (Hadarics & Zalai 2008, Török 2009).

Ring recoveries related to the British Isles shows that birds from this region move south, the most important stopover (refuelling) site areas are: Southwest France, Northwest Spain and Northern Portugal (Jones 2002). However, the main direction of the continental birds in autumn migration is southwest. The birds ringed in Scandinavia and North-Western Europe are concentrated along the Atlantic coasts of France, Spain and Portugal (Fransson & Hall-Karlsson 2008). The most important stopover sites during the autumn migration are located on the Iberian Peninsula, from where they cross the Mediterranean region and the Sahara with a direct non-stop flight to reach their wintering grounds. Their wintering grounds are in tropical West Africa ranging from Guinea to Ghana (Cramp & Simmons 1983, Salewski *et al.* 2004). The spring migration route probably leads further east over the Northern part of Apennine Peninsula and Central Europe as it is indicated by recoveries (Zink 1985, Fransson & Hall-Karlsson 2008).

Sporadic ring recoveries suggest that the migrant population flying across Hungary originates from the Baltic region and western Russia (based on the two recoveries ringed in Estonia and Russia) (Török 2009). Two birds ringed in Hungary were recovered in South France and South Portugal (Török 2009), thus it is plausible that the Pied Flycatchers fly over the Carpathian Basin and continue their way towards the Iberian Peninsula.

The Pied Flycatchers arrive back to their breeding grounds between April and May. Their autumn migration lasts between August and September (Cramp & Simmons 1983). It is a common migrant from mid-April to mid-May in spring and from late August until mid-September in autumn in Hungary (Hadarics & Zalai 2008, Török 2009). Precise wintering grounds and ecology is yet to be described for this species, furthermore little is known on its migration phenology in Western (Jones 2002, Fransson &

Hall-Karlsson 2008, Spina & Volponi 2008) and East-Central Europe (Török 2009).

Pied Flycatchers are prime candidates to serve as model species to study the complexity of migration phenology as individuals can be easily sexed and aged on site (Svensson 1992). In a previous study (Harnos *et al.* 2015), we have already showed how the timing of spring migration changed in case of this species. In the current study, we describe: (1) the sex and age related phenological changes over the years (2) sex, age and size dependent migration patterns during and (3) between the migration periods, (4) sex and age composition in spring and in autumn and their changes during the past 26 years (1989–2014) at a stopover site in Hungary.

Materials and Methods

The data was collected in Central Hungary (47°15'N, 19°15'E) at the Ócsa Bird Ringing Station, in the Danube-Ipoly National Park. This site is at the edge of a postglacial peatbog. The surrounding area comprises all habitat types from reed-beds to mature forests. Mist-nettings were conducted at the same locations throughout the whole study period during 1989–2014.

We used the records of 2323 Pied Flycatchers trapped and ringed between April and September (241 males and 162 females in spring, 121 adult males and 182 adult females, 967 juvenile males and 650 juvenile females in autumn).

The daily ringing work was carried out with 100 mist nets in standard places covering completely both migration periods of Pied Flycatchers. Every newly trapped bird was ringed and its age and sex were determined based on plumage. First calendar year birds (juveniles) were distinguished from adults (Svensson 1992). All birds were measured according to the same methodology. The wing length was measured with 1 mm accuracy, using a ruler in the case of birds where feather abrasion was low.

Linear mixed effects (LME) models were used to detect the changes in the timing of migration. Sex, age and their interaction were included in the models. We put year as a random factor in all models. Wing length and timing were also analysed by linear mixed models. To analyse sex and age ratios and their dependence on year and season, generalized linear mixed models with binomial error distribution and logit link were fitted. We gave 95% confidence intervals (CI) for the estimated sex ratios based on the models. We used the 'nlme' (Pinherio *et al.* 2014) and 'lme4' R packages (Bates *et al.* 2014).

We compared the wing length and the proportion of males and females, the proportion of adults and juveniles and the seasons by calculating contrasts and least squares means for the fitted models ('lsmeans' package, Russell 2014). A small amount of noise was added to the data on the figures in order to prevent over plotting. The significance level was set to 0.05. All statistical analyses were done in R 3.2.2 (R Core Team 2015).

Results

Timing

Two distinct migration waves can be observed, so the determination of the beginning of the autumn season is very easy and precise *(Figure 1)*.

While we found a 11.3 day shift (slope (s)=0.48, SE=0.12, p<0.0001) to earlier days in the timing of males during spring

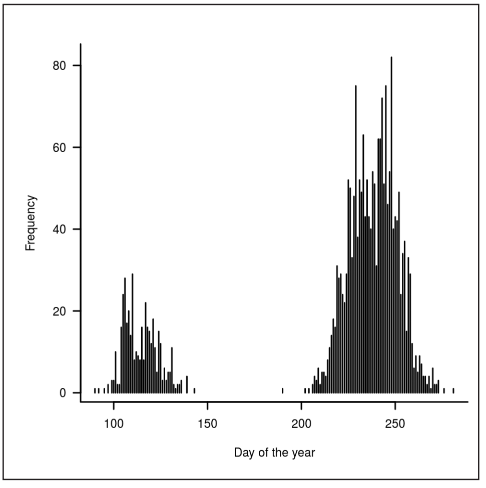

Figure 1. The daily number of mist-netted Pied Flycatchers caught between 1989 and 2014. The two distinct migration waves can be observed

1. ábra A kormos légykapó gyakorisága az év napjain az 1989 és 2014 közötti összesített adatok alapján. Jól megfigyelhető a két elkülönülő vonulási hullám

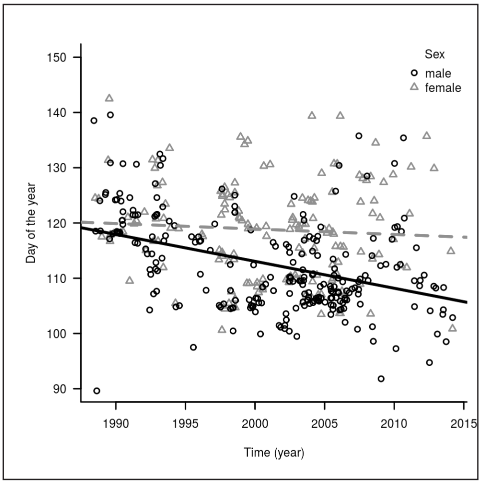

Figure 2. Spring arrival times of male and female Pied Flycatchers between 1989 and 2014. The continuous line highlights the significant advancement in arrival time over the years for males, while the dashed line corresponds to the non-significant advancement in arrival time over the years for females

2. ábra A kormos légykapó egyedeinek tavaszi érkezési ideje 1989 és 2014 között. A folytonos vonal mutatja a hímek érkezési idejének szignifikáns korábbra tolódását. A szaggatott vonal a tojók adataira illesztett nem szignifikáns trendet mutatja

migration, the timing of females did not change significantly (s=-0.09, SE=0.14, p=0.48) *(Figure 2)*. At the beginning of the time period, there was no significant difference between the timing of the sexes (p=0.3577), but the estimated difference is 11.3 (SE=1.79, p<0.0001) days, recently.

In autumn, no significant change could be detected in the timing of any sex or age groups (s=0.15, SE=0.11, p=0.1816) and the migration timing of sexes did not differ significantly (p=0.0630), but juvenile birds migrated 4 days (SE=0.75, p<0.0001) earlier on average than adult birds.

Wing length

The mean wing length increased by 0.08 mm/year (2.1 mm altogether) during the 26 years (SE=0.019, p=0.0003) in spring *(Figure 3)*. We found a significant relationship between wing length and timing within season *(Figure 4)*. The individuals arriving earlier have longer wings on average (s=-0.024, SE=0.012, p=0.0421) and the estimated difference is 1.3 mm between the beginning (90^{th} day) and the end of the season (143^{rd} day). The rate of change during the 26 years and along the season does not differ significantly between sexes, but there is a 1.4 mm (SE=0.22, p<0.0001) significant difference in their average wing length (the females' average wing length is smaller).

The autumn wing length did not change significantly (p=0.1918) during the 26 years in any age and sex groups.

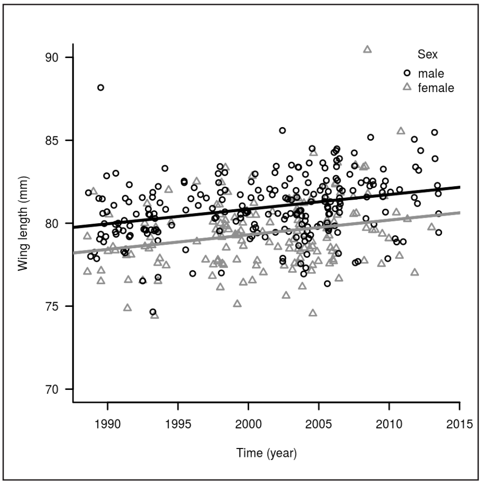

Figure 3. Spring wing length of male and female Pied Flycatchers between 1989 and 2014. The continuous lines highlights the significant increase of average wing length over the years

3. ábra A kormos légykapó tavaszi egyedeinek szárnyhossza 1989 és 2014 között. A folytonos vonalak az átlagos szárnyhossz növekedést mutatják az évek során

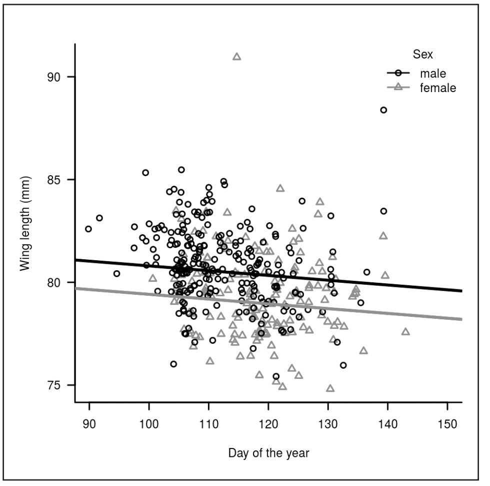

Figure 4. Wing length of male and female Pied Flycatchers during the spring season. The continuous lines highlights the significant decrease of average wing length over the season

4. ábra A kormos légykapó egyedeinek szárnyhossza tavaszi időszakban. A folytonos vonalak a szignifikáns átlagos szárnyhossz csökkenést mutatják a szezon során

In autumn, the birds arrived earlier had shorter wing on average (s= 0.015, SE=0.004, p=0.0001), meaning that there was 1.2 mm mean difference between the beginning (200th) and the end (280th) of the season. The rate of change is independent of sex and age groups, but the wing of female birds is 1.7 mm (SE=0.22, p<0.0001) and 1 mm (SE=0.09, p<0.0001) shorter on average than that of the males in case of adults and juveniles, respectively. Juveniles have 0.6 mm shorter wings than the adults (SE=0.16, p=0.0003) in case of females, and the difference is 1.2 mm (SE=0.18, p<0.0001) in case of males (*Figure 5a* and *b*).

The average (±SE) wing length (according to an LME model) of adult female and male birds are 79.4±0.21 mm and 81±0.19 mm in spring, 79.9±0.19 mm and 81.5±0.21 mm in autumn and 79.2±0.14 mm and 80.25±0.14 mm in case of juveniles in autumn. There is a 0.44 mm (SE=0.17, p=0.0099) significant difference between the average wing lengths in the two seasons in the case of both sexes.

Sex ratio

According to a generalized linear mixed model, the estimated ratio of males in spring is 60.1% (CI: 54.7% to 65.3%). In autumn, the proportion of adult males is 39.8% (CI: 33.7%, 46.2%) and the proportion of juvenile males is 58.8% (CI: 53.3%, 64%) and these ratios did not change significantly during the 26 years (p=0.6289).

In spring the male ratio diminishes during the season from 89.5% to 3% (s=0.098, p<0.0001). Contrary, in autumn it does not change significantly during the season

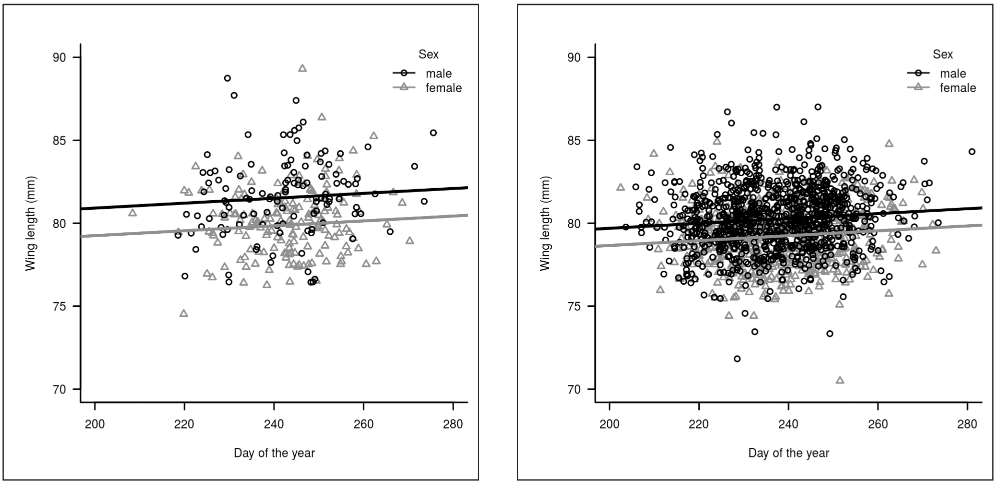

Figure 5a and *b* Wing length of adult (a) and juvenile (b) male and female Pied Flycatchers during the autumn season. The continuous lines highlights the significant increase of average wing length over the season

5a és *b ábra* Az öreg (a) és fiatal (b) hím és tojó szárnyhosszak az őszi vonulási időszakban. A folytonos vonalak a szignifikáns átlagos szárnyhossz növekedést mutatják a szezon során

(p=0.0827) but depends on the age group (s=-0.786, p<0.0001), the male ratio is lower in the adult group (40.9% vs. 60.1%).

Discussion

Environmental factors do not necessarily influence the migration of the sexes uniformly. Sexual selection has been supposed to affect the evolution of protandry, because early arriving males enjoy a mating advantage (Møller 1994, 2004). Temporal trend in the size of protandry was only found in three case studies until now. In the case of Chiffchaffs *(Phylloscopus collybita)* protandry increased (Csörgő & Harnos 2011). In the case of Barn Swallows *(Hirundo rustica)* the males arrived earlier, but the females did not between 1971 and 2003 in Denmark (Møller 2004), and in our previous study (Harnos *et al.* 2014), Pied Flycatchers also showed sex dependent migration strategies with increasing protandry in spring.

The onset of fall migration did not change during the past decades on our study site, consequently the timing of breeding and successive events probably did not change either, as in a similar study from South-West Finland. Aloha *et al.* (2004) showed that climate warming along the migration route and earlier arrival does not influence the breeding dates of Pied Flycatchers. Breeding is constrained by the arrival of both sexes, therefore increased protandry is unlikely to cause advancements in breeding dates.

Morphological distinction of birds entering Europe through the Iberian Peninsula and those entering further East is impossible (Winkel & Hudde 1993), but the contradicting trends found in Central and Southern Europe last decades (Hüppop & Winkel 2006) suggest population specific reactions to the changing climate (Menzel *et al.* 2006, Rubolini *et al.* 2007). For instance, at a

Mediterranean stopover site (Island of Capri, Italy), according to a 19-yearlong study (between 1980–2004) the time of arrival shifted to 4.4 days later (Jonzén *et al.* 2006). Similar trends were recorded at medium latitudes: on the Heligoland Islands (Germany) and Courish Spit (Russia) (Sokolov & Kosarev 2003, Sparks *et al.* 2005). In the case of the cross migrants of Germany – mostly originating from Scandinavia – the Pied Flycatcher started arriving earlier between 1960 and 2000: the shift was 6.4 days (Hüppop & Hüppop 2002). In Sweden there was no shift after a 50 year long period between 1952 and 2002 (Stervander *et al.* 2005). In South-West Finland the early migrants (5th percentile of the sample) advanced their arrival date, by approximately 8 days, while the late migrants (95th percentile) did not (Ahola *et al.* 2004). Our results complement these findings, as advancement in arrival dates was detected at least for males. However, the differences in direction and rate of phenology amongst various studied locations further suggest that distinct populations migrate through these sites and/or that responses to altered environment are location specific.

The average wing length increased during our study period, which can be explained in two – not mutually exclusive, but possibly reinforcing – ways: (1) The wings of northern breeding populations of other species with longer migration routes to their wintering grounds are longer and more pointed than that of southern breeders with shorter migration routes (Tiainen & Hanski 1985, Lockwood *et al.* 1998) and this phenomenon probably also applies to Pied Flycatchers. In the background of increased average wing length could be the changes in cross migrating populations: the ratio of northern originated birds could increase. One of the effects of the climate change is that the species' range is shifting northward (Parmesan & Yohe 2003, Root *et al.* 2003). Some assessments suggest that the European range of Pied Flycatchers will extend from Norway to the Ural Mountains by the end of the 21st century (Huntley *et al.* 2007). (2) The size of the Sahara desert is increasing continuously (Le Houérou 1996), resulting in selection forces toward longer-winged individuals. In this case, the capture ratio of longer winged individuals at the Hungarian stopover site may increase, producing the observed pattern.

The average wing length is shorter in spring than in autumn. Pied Flycatchers have a post-nuptial moult, thus the difference may be attributed as the result of feather abrasion, however, individuals with observable feather wear were not measured. More likely this pattern is caused by the different composition of the trans-migrant populations, namely there are more birds with shorter wing in spring than in autumn. This observation is supported by studies in Denmark and in Italy: according to these Western European studies the species has a loop migration strategy (Bønløkke *et al.* 2006, Spina & Volponi 2008).

Based on our results, in spring the longer winged individuals of both sexes arrive earlier, like in Italy (Spina & Volponi 2008) while in the autumn the situation is reversed: longer winged birds leave the area later. It is possible that the birds of northern populations arrived earlier in spring and later in autumn.

The male ratio is higher (60%) at our study site in spring, and lower among the adults in autumn (39%), but 59% among juveniles. In the case of autumn migration, at Heligoland, off the coast of Northwest Germany, 46% were males out of 463 sexed individuals

(Bub 1981 in Lundberg & Alatalo 1992). In the south-western part of Finland, the male ratio was 45% (von Hartman 1985). The sex ratio was skewed in the opposite direction near Berlin, in Germany, 58% were males out of 406 sexed individuals (Curio 1959). Based on these facts and because the capture probabilities of the two sexes do not bias the estimated sex ratios in the migration periods in case of passerines (Amrhein *et al.* 2012), we hypothesize that even the sexes of the same breeding population use different routes during their migration, not only whole populations and thus sexes may react independently to environmental changes. In spring the males probably migrate on a shorter, easterly route, where spring temperatures increased from the second half of April (Hüppop & Winkel 2006), since the climatic trend has south-west to north-east direction. This is also supported by the differential timing of the sexes in spring.

In conclusion, we showed that the trans-migrant population of Pied Flycatcher in the Carpathian Basin behaved somewhat differently from those noted in Western European indicating that there is substantial geographic variation in migratory behaviour for this species. We recommend that future predictions of changes in demography and range extent consider these differences.

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