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SHORT NOTE

Increasing protandry in the spring migration of the Pied Flycatcher (*Ficedula hypoleuca*) in Central Europe

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Abstract Sexual selection theory suggests that the degree of protandry in spring migration should increase when earlier males benefit from better mating opportunities. Western European studies failed to show differences in sex-specific arrival dates for the Pied Flycatcher. However, different climatic conditions and other constraints may affect its phenology in continental Europe. Here, we present evidence that sex-related phenological changes have occurred over the past 25 years (between 1989 and 2013) in Central Europe (Ócsa Bird Ringing Station, Hungary). The spring arrival of male flycatchers shifted to earlier dates whereas female arrival showed no change, implying an increasing degree of protandry.

Keywords Protandry · Spring migration · Local temperature · Carpathian Basin

Zusammenfassung

Zunehmende Protandrie beim Frühjahrszug des Trauerschnäppers (Ficedula hypoleuca) in Mitteleuropa

Der sexuellen Selektionstheorie zufolge sollte das Ausmaß der Protandrie beim Frühjahrszug zunehmen, wenn früher eintreffende Männchen von besseren Paarungsgelegenheiten profitieren. Studien in Westeuropa konnten keine Unterschiede in den geschlechtsspezifischen Ankunftsdaten bei Trauerschnäppern zeigen. Unterschiedliche klimatische Bedingungen und andere Zwänge könnten jedoch die Phänologie in Kontinentaleuropa beeinflussen. Hier liefern wir Hinweise darauf, dass in Mitteleuropa (Ungarn, Ócsa-Vogelberingungsstation) im Verlauf der letzten 25 Jahre (zwischen 1989 und 2013) mit dem Geschlecht verbundene phänologische Veränderungen aufgetreten sind. Die Ankunft männlicher Trauerschnäpper im Brutgebiet verfrühte sich, während sich die Ankunft der Weibchen nicht veränderte, was auf zunehmende Protandrie schließen lässt.

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Introduction

Avian migrants show large interspecific variability in the timing of migratory events. Moreover, phenology may vary between populations, age and sex groups within species, so detecting and inferring shifts in migratory decisions can be challenging. For instance, published results on changes in the phenology of a long-distance migrant, the Pied Flycatcher (*Ficedula hypoleuca*), are controversial. Both and Wisser (Both and Visser 2001) did not detect any changes in the first arrival dates of flycatchers between 1980 and 2000, and they failed to find any correlation with the

temperature just before the arrival of most birds in the Netherlands. Another analysis of first-arrival dates for Western European populations was also unable to detect changes in spring migration (Fischer 2002). However, Both et al. (2005) showed that the arrival dates of flycatchers in the Netherlands are correlated with the weather at their main North African stopover site. On the other hand, Sokolov et al. (1998) showed that the flycatchers advanced their spring migration between 1959 and 1990, and their arrival time depended on the temperature in April. Other studies indicate that climatic rather than endogenous factors influence spring migration and subsequent breeding (Ahola et al. 2004). Hüppopp and Winkel (2006) studied temperature trends along the migration route of Pied Flycatchers and found convincing correlations with first-arrival times. They hypothesise that, due to future climate change, different populations migrating along distinct routes will experience different effects because of the complexity of the weather systems in Europe. The sensitivity of individuals to environmental and climatic changes may vary among age and sex groups in a population, so temporal shifts in migratory decisions that are driven by climatic factors are likely to take place (Spottiswoode and Saino 2010).

Avian protandry, i.e. earlier arrival of males than females in spring, has been shown for several species along various migratory flyways. Males arriving earlier at breeding sites are hypothesised to have adaptive advantages over later-arriving conspecifics through better mating opportunities, so protandry may evolve as an indicator of individual male quality. The degree of protandry (i.e. the difference between the arrival dates of males and females) may also be influenced by climate change, as different selection pressures may act upon distinct populations. However, Bauböck et al. (2012) could not find any change in the magnitude of protandry over a period of 32 years for six protandrious American species. Moreover, Raino et al. (2007) did not find evidence for a temporal change in protandry in Pied Flycatchers at five ringing stations in the North Sea and the Baltic area over their 22-year (1976–1997) study period.

The populations migrating through the Carpathian Basin differ from the populations migrating further west. Based on band recoveries in Estonia and Russia, we can surmise that the migrating population in Hungary originates from the Baltic region, Russia and Belarus.

Pied Flycatchers arrive back at their breeding territories between April and May (Cramp and Simmons 1983). They are very common migrants from mid-April until mid-May in spring and from late August until mid-September in autumn in Hungary (Török 2009). They are also very rare and sporadic breeders in Hungary at various sites (the southern Great Plain, Alpine Foothills, Zala Hills) (Török 2009), so they have two distinct migration periods per year in Hungary, meaning that the usual difficulties associated with separating the migration and breeding periods in the analysis of the data were not present. In the work reported in the present paper, we analysed the spring migration trends of Pied Flycatchers during the past 25 years (1989–2013) at a stopover site in Hungary. We describe the sex-related phenological changes over that time period and show their temperature dependence.

Materials and methods

The bird ringing data for this species were 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 peat bog. The surrounding area comprises all habitat types, from reed beds to mature forests. Mist-netting was conducted with 100 mist nets in standard places throughout the whole study period (1989–2013). We used the records of 398 (238 male and 160 female) Pied Flycatchers that were trapped and ringed during the spring migration period. Every newly trapped bird was ringed and sexed based on plumage characteristics. Daily meteorological data (minimum, maximum and mean temperatures) of the nearest (approx. 20 km) weather station (Pestszentlőrinc) were downloaded from ftp://ftp.ncdc.noaa.gov/pub/data/gsod/, and monthly averages were calculated.

We used linear mixed effects (LME) models to detect changes in the timing of migration. In addition to year, we included sex, age and their interaction in the models. We analysed the effects of weather parameters in separate models that did not include year as a fixed factor; year was a random factor in all models. We used the "nlme" (Pinheiro et al. 2014) R package. All statistical analyses were done in R 3.02 (R Core Team 2013).

Results

While we found a 11.3-day shift (slope (s) = 0.45, SE = 0.12, $p < 0.0001$) to earlier days in the timing of male arrival during spring migration, the timing of female arrival did not change significantly ($s = -0.03$, SE = 0.15, $p = 0.83$) (Fig. 1). At the beginning of the time period, there was no significant difference between the arrival times of the sexes ($p = 0.63$), but the estimated difference has been 11.3 (SE = 1.74, $p < 0.0001$) days in recent years.

For males, the arrival time depended significantly on the mean ($s = -1.63$, SE = 0.67, $p = 0.0166$) and maximum ($s = -1.39$, SE = 0.52, $p = 0.008$) local temperatures in

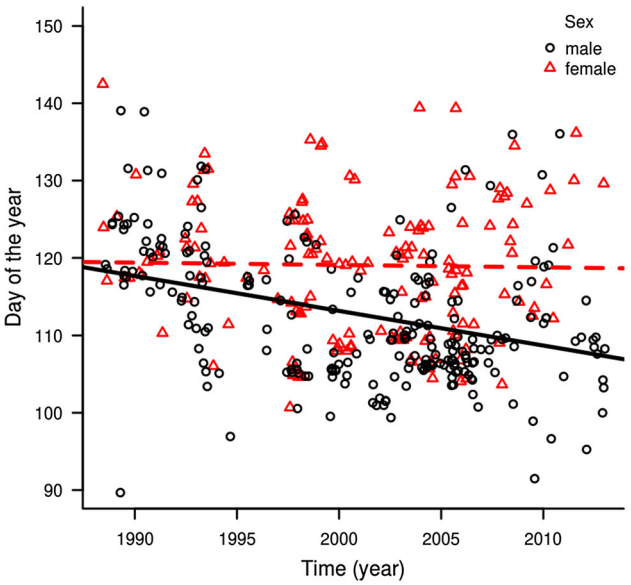

Fig. 1 Spring arrival times of male and female Pied Flycatchers between 1989 and 2013. The *continuous line* highlights the significant advancement in arrival time over the years for males, while the *dashed line* corresponds to the nonsignificant advancement in arrival time over the years for females. Note that a small amount of noise was added to the data in order to prevent overplotting

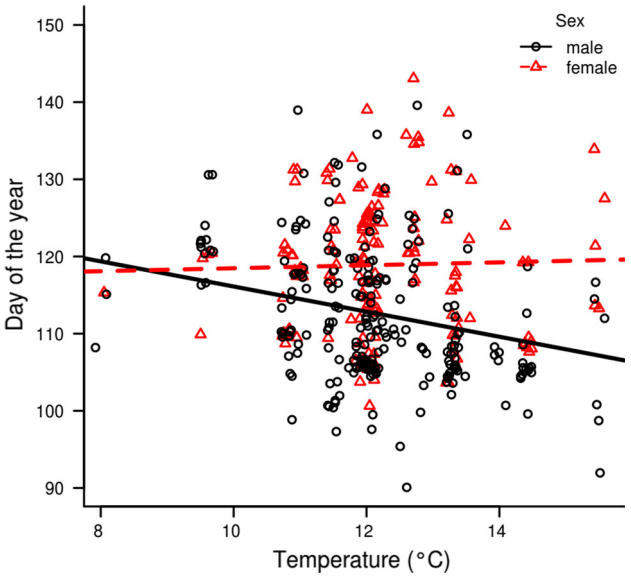

Fig. 2 Spring arrival times of males and females versus mean temperature in April. The *continuous line* highlights the significant relationship between arrival time and temperature for males, while the *dashed line* corresponds to the nonsignificant relationship between arrival time and temperature for females. Note that a small amount of noise was added to the data in order to prevent overplotting

April (Fig. 2). For females, we did not detect any significant relationship between arrival time and weather variables.

Discussion

We have shown that Pied Flycatchers migrating through a Central European ringing station present marked protandry, and that the rate of protandry changed over the study period. Moreover, we have provided evidence that the arrival times of passage migrant males correlate with local weather parameters. This result contradicts previously published results that analysed data derived from other distinct populations.

Weather in itself is unlikely to cause protandry, as it affects both sexes (unless the wintering grounds of the two sexes are not very distinct). It is more probable that there are effects due to interactions between weather and the different roles of the sexes.

For instance, barn swallows (*Hirundo rustica*) show similar phenology patterns to our results, since males of this species advanced their spring arrival whereas females did not between 1971 and 2003 in Denmark (Møller 2004). Moreover, male arrival dates were correlated with the mean temperature in April. In a previous study, we showed that male Chiffchaffs (*Phylloscopus collybita*) arrived earlier than females in spring, and that their annual arrival times showed a positive relationship with mean minimum temperature in March (Csörgő and Harnos 2011).

According to our recent study, Pied Flycatchers show sex-dependent migration strategies with protandry in spring, and this protandry has gradually increased since 1989. Males alter the timing of their migration according to local environmental factors, while females do not show such behavioural plasticity. In that respect, there are more extreme weather conditions in the probable breeding area (in the north-east) of the Pied Flycatchers migrating through the Carpathian Basin, and the mean temperature in April there has not increased significantly over the past 30 years (probably because the influence of the North Atlantic Oscillation is more pronounced on the edge of the continent than in its interior; Hüppop and Hüppop 2002), so there is no point in arriving early for females. In addition, females probably migrate further to the west, on a longer route.

It is highly probable that variations in the trends in the timing of the birds' arrival at the breeding areas in spring reflect the unevenness of warming in Europe (Rubolini et al. 2007). However, direct comparisons of our results with those from other studies are not easy due to differences in time intervals and migration routes. For instance, the study of Raino et al. (2007) analysed data from 1976 to 1997, while our study runs from 1989 to 2013, allowing for less than a decade of overlap. Moreover, we could not detect protandry at the beginning of our study period ($\sim$1990).

As the rate of protandry increased due to the advancement in the timing of males during our study period, only male specific direct or indirect hypotheses may explain our results (Morbey and Ydenberg 2001). The mechanisms behind these hypotheses entail (1) wintering more to the north, (2) initiating migration earlier, (3) flying faster, (4) taking different routes or (5) direct selection acting on better mating oppurtunities for earlier males. Thus, early arrival may evolve as an indicator of male quality. Since the arrival times of the sexes overlap, individual females can easily assess which males arrived earlier than themselves, and can also see this from the impacts of the males on their territories (i.e., the stage of building or refurbishing nests, etc.). We lack evidence suggesting sex-specific wintering ranges (1) or differences in the onset of migration (2). However, faster flight (3) of males due to longer wings is a possibility that should be considered, as well as the idea that males are more likely to be loop migrants than females are, so they shorten their spring route back to the breeding area (4). We think that the latter (5) possibility is the most likely explanation for the increasing protandry observed in our study.

In conclusion, we observed changes in the migration arrival times of a long-distance migrant over a period of several decades. These changes were found to be sex dependent and differed from those noted in Western European studies, thus supplementing our knowledge about this species.

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