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Research Article

Age and sex effects on spring migration timing in great reed warblers: early start allows older males to arrive first

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Long-distance migrants face numerous challenges during their migration, with the spring migration timing being particularly important, as early arrival at the breeding grounds often enhances breeding success. Both innate and environmental factors influence migration timing in birds, and the earlier arrival of males than females is common among songbirds breeding in temperate zones. The great reed warbler *Acrocephalus arundinaceus* males departed from the wintering grounds 10.5 days earlier than females. Interestingly, the oldest males (≥ 4-year-olds) departed significantly earlier than younger adult males (2- and 3-year-olds), suggesting that accumulated experience and/or age-related hormonal changes may underlie this pattern. No significant differences were observed among female age groups. In contrast, we found no significant age effect for the duration of spring migration in either males or females. Males arrived 9.9 days earlier than females at the breeding grounds. Similar to departure dates, the oldest males (≥ 4-year-olds) arrived significantly earlier than middle-aged males (3-year-olds), while no such age-dependent relationship was observed in females. In both males and females, we found positive relationships between the departure date from the wintering grounds and the arrival date at the breeding grounds with a slope of $\beta = 0.59$, showing that spring migration duration becomes shorter as the spring season progresses. In addition, for a given departure date from the wintering grounds, males arrived 3.9 days earlier than females, but no significant differences were observed between age groups either in males or females. Our findings have important implications for understanding how long-distance migratory birds might adjust their endogenous migration programs based on individual qualities, and highlight the potential role of learning and experience in these processes. This further emphasizes how adaptations to ongoing climate change might depend not only on individual quality, but also on plasticity and the age structure of the population.

Keywords: bird migration, geolocators, multisensor data loggers, songbirds, tracking

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Introduction

To maximize fitness, long-distance migratory birds must time their annual life cycle events accurately (Newton 2008). This is especially evident during spring migration, where the arrival order at the breeding grounds can be a key determinant of reproductive success. Typically, early arriving individuals can occupy better quality territories and thereby achieve higher pairing and reproductive success (Aebischer et al. 1996, Hasselquist 1998, Kokko 1999).

Protandry, i.e. when males arrive earlier at the breeding grounds than females, is the most common form of sex-biased migration timing, for which seven non-mutually exclusive ultimate hypotheses have been proposed to explain its evolution (Morbey and Ydenberg 2001). Among these, the three most prominent in explaining protandry in birds are the mate opportunity hypothesis, the rank advantage hypothesis and the susceptibility hypothesis (Morbey and Ydenberg 2001, Kokko et al. 2006, Morbey et al. 2012). However, rather than considering them separately, it has been proposed that a more integrated approach that combines all these three hypotheses may better explain the ultimate causes for protandry (Kokko et al. 2006, Morbey et al. 2012). In addition, three main hypotheses have also been proposed to explain proximate mechanisms for protandry in birds: 1) males could migrate faster than females, 2) males could migrate shorter distances by wintering closer to the breeding sites, and 3) males could initiate spring migration earlier than females (Coppack and Pulido 2009). The relative importance of these mechanisms can vary not only between species, but also between subspecies within a species (Schmaljohann et al. 2016).

The common view is that long-distance migrants mainly rely on their robust endogenous migration program, which is thought to be governed by the photoperiod, to correctly time their annual cycle events (Gwinner 1996a, 1996b, Åkesson and Helm 2020). Yet, other factors, e.g. habitat quality, climate change, weather and individual and social experience, can also modify annual cycle events including timing, distance and direction (Alerstam 1979, 2011, Norris et al. 2004, Balbontín et al. 2009, Sergio et al. 2014, Dhanjal-Adams et al. 2018). Long-distance migratory birds have been shown to be flexible to conditions experienced on the wintering grounds or en route during migration. For example, male American redstarts *Setophaga ruticilla* arrived earlier at the breeding grounds when wintering in higher-quality habitats (Norris et al. 2004). Similarly, pied flycatchers *Ficedula hypoleuca* departed from the wintering grounds 12 days earlier when provided with extra food compared to the control group (Ouwehand et al. 2023), while semi-collared flycatchers *F. semitorquata* delayed their spring arrival date when experiencing colder temperatures en route (Briedis et al. 2017). However, responses to similar conditions experienced on the wintering grounds or en route may also vary between populations within a species (Balbontín et al. 2009). How rigid or flexible annual cycle events are and the extent to which birds can adapt phenotypically, or even evolve genetically as a response to a changing environment, is currently a subject of great interest to many researchers (Knudsen et al. 2011, Radchuk et al. 2019).

Numerous studies have assessed the impact of age (and experience) on the migratory performance of birds. However, these studies have primarily been focused on differences between adult and young (first calendar year) birds (Ellegren 1993, Thorup et al. 2003, Mitchell et al. 2015). Some of these studies demonstrated that adult birds outperformed their young conspecifics in various aspects of migration. For example, adult birds coped better with wind drift (Thorup et al. 2003), departed with more favourable winds (Mitchell et al. 2015) or achieved higher migration speeds (Ellegren 1993). When tracking individual black kites *Milvus migrans* over their lifetime, Sergio et al. (2014) found that migratory performance followed a consistent developmental trajectory, where the improvement in migratory performance was more gradual and extended over a longer part of life than initially expected.

However, age-specific differences do not necessarily follow linear relationships, such that migratory traits would improve throughout an individual's lifetime. Senescence has been shown to affect the arrival date and reproductive success of barn swallows *Hirundo rustica*, with both traits increasing in early life, reaching a plateau and then decreasing in older individuals (Møller and De Lope 1999, Balbontín et al. 2007). Still, however, many questions remain regarding the effects of age and experience on migration.

We have monitored a population of great reed warblers *Acrocephalus arundinaceus* that breeds in southern central Sweden and winters in a large area from sub-Saharan West Africa to north-east of the Congo Basin (Lemke et al. 2013, Koleček et al. 2016, Brlík et al. 2020b). From previous studies, we know that male great reed warblers of our study population are usually first observed at the breeding site about 11 days earlier than females (Hasselquist 1998, Tarka et al. 2015). Over a two-decade study period spanning from 1985 to 2004, the mean arrival date to our study site was advanced by 6 days. This advancement was interpreted as likely a result of phenotypic plasticity rather than microevolution, although the latter might also contribute (Tarka et al. 2015). It is worth noting that both sexes benefit from earlier arrival, as evidenced by negative directional selection for earlier arrival date acting through increased reproductive success in both sexes (Tarka et al. 2015). Males benefit from early spring arrival by being able to occupy more attractive territories, resulting in higher pairing and reproductive success (Hasselquist 1998). Females benefit from early spring arrival by occupying the primary position in the harem of socially polygynous males (Bensch and Hasselquist 1992, Bensch 1996). In addition, both sexes benefit from earlier spring arrival because this increases opportunities for initiating replacement clutches in case of predation, as well as providing more time to prepare for autumn migration (Hansson et al. 2000, Hemborg et al. 2001). These similar selection patterns between the sexes lead to the question of how differences in male and female migratory timing arise, and how age contributes to this variation.

In this study, we investigated the timing of spring migration in our population of great reed warblers, accounting for age and sex. We used two types of data loggers – light-level geolocators and multisensor data loggers – to acquire detailed data on the timing of spring migration. Our previous research showed that older great reed warbler males, at least three years old, tend to show earlier territory occupation dates at the breeding grounds than younger males (Hasselquist 1998). However, the mechanism behind this earlier territory occupation date, whether it comes from earlier departure from the wintering grounds or faster overall spring migration, is still unknown. A third possible explanation, that older males winter farther north, closer to the breeding grounds, is unlikely since great reed warbler males show high spatial repeatability of their wintering sites (Hasselquist et al. 2017). Similarly, our previous research has shown that both sexes from our breeding population have overlapping wintering grounds (Lemke et al. 2013, Brlík et al. 2020b, Malmiga et al. 2021). Therefore, we aim to investigate whether the proximate reasons for the (considerably) earlier arrival dates at the breeding grounds of males, compared to females, are earlier spring departure, shorter duration of spring migration or both. Specifically, we investigate whether changes in timing and duration of spring migration are dependent on age in great reed warblers that already have experience of spring migration (i.e. adults at ages from 2 to ≥ 4 years), and if such patterns differ between males and females.

Material and methods

We studied a population of great reed warblers breeding in reed marshes within the Kvismaren nature reserve (59°10′41″N, 15°22′37″E) and in the nearby Segersjö marshes (12 km away) in southern central Sweden. For our study, we used two types of data loggers: 1) light-level geolocators, which measure light intensity or both light intensity and temperature, and 2) multisensor data loggers, which measure barometric pressure (altitude), temperature, light intensity and acceleration (i.e. movement activity, allowing differentiation of e.g. migratory flights from movement in vegetation at ground level; Sjöberg et al. 2018, 2023). From 2008 to 2019, we attached 241 geolocators (147 on males and 94 on females) and 134 multisensor data loggers (89 on males and 45 on females) on adult great reed warblers (including repeatedly tracked individuals) at our two study sites. In the following years, we retrieved 44 geolocators from males (30%) and 21 from females (22.3%), as well as 30 multisensor data loggers from males (33.7%) and 21 from females (46.7%). Four males and two females had lost their data loggers. In addition, one male that arrived late to our study site (2 August) was excluded from the analyses that year and the following year as something might have compromised his migration, causing him to arrive at the breeding grounds at a time of the year when adult males usually leave the breeding grounds to begin autumn migration. Due to various issues, including data logger failures, and uncertainties in the age categorization of tracked birds, data from 47 geolocators (30 males and 17 females) and 28 multisensor data loggers (14 males and 14 females) are included in this study. Hence, we had a total of 75 data loggers that contained data (males per age group: 2-year-olds n = 6, 3-year-olds n = 16, ≥ 4-year-olds n = 22; females per age group: 2-year-olds n = 6, 3-year-olds n = 12, ≥ 4-year-olds n = 13) that could be used in the current study.

From 2008 to 2009, we used the geolocator model Mk10S and from 2010 to 2011 the model Mk12-SAD (British Antarctic Survey; www.birdtracker.co.uk). In 2012, we used the geolocator model Intigeo-P65C2J; in 2014–2019, we used Intigeo-P65C2-7; while in 2013 we used both types of geolocators (Migrate Technologies Ltd). From 2015 to 2019, we also used multisensor data loggers (Bäckman et al. 2017, Sjöberg et al. 2018). We attached the data loggers to the great reed warblers using leg-loop harnesses made of non-elastic nylon strings. Geolocators, including attaching material, weighed approximately 1.0 g and multisensor data loggers weighed approximately 1.1 g, resulting in a mean increase of 3.2% (range: 2.7–4.0%; n = 69) of the body mass of a great reed warbler by attaching the data logger. Our previous study found no significant difference in the body mass of returning great reed warblers with or without data loggers (Malmiga et al. 2021), a result consistent with a broader meta-analysis showing weak or no negative effect of geolocators on tagged small birds (Brlík et al. 2020a).

We analysed geolocator data using the packages 'Geolight' ver. 2.0 (Lisovski and Hahn 2012) and 'TwGeos' ver. 0.0-1 (Lisovski et al. 2015). We log-transformed the data and identified sunset and sunrise events with 'TwGeos'. We then analysed the data with 'Geolight'. For a more detailed description of the geolocator data analyses, see Malmiga et al. (2021). When analysing departure and arrival dates from multisensor data loggers, we only used accelerometer (i.e. movement activity) data. For a more detailed description of the multisensor data logger and the accelerometer data, see Bäckman et al. (2017). For a more detailed description on analyses from multisensor data loggers and identification of flights in great reed warblers, see Sjöberg et al. (2018).

While the sole source of information about departure dates came from our data loggers, we occasionally (16 cases) used direct observations of birds to determine dates of arrival. The reasons for this was that either data from data loggers were not available (9 cases) or that field observations indicated an earlier arrival than the data logger (7 cases). In the latter case, field observations were used, because due to various environmental factors that can cause shading (e.g. vegetation, cloud cover) the departure and arrival dates estimated by geolocators have an error margin of ± a few days (Lisovski et al. 2012, Rakhimberdiev et al. 2016). In our study, the arrival dates estimated from geolocators compared with those from field observations (n = 27) were quite similar as they on average only differed by two days**.** In addition, there was a highly significant positive relationship between arrival dates estimated from field observations and geolocator data ($F_{1,20} = 145.5$, $p < 0.001$, $\beta = 0.89$), with no significant interaction between the sexes ($F_{1,20} = 0.6$, $p = 0.45$). We calculated the total duration of spring migration by subtracting the departure date from the arrival date.

We assigned the adult great reed warblers into age groups based on two methods: 1) individuals for which the true age was known with certainty, and 2) birds whose age we estimated at first capture based on body appearance (three criteria that when considered together give reliable age estimates in both great reed warblers and reed warblers; see below and Bensch et al. 1998).

In total, 38 (50.7%) of the great reed warblers in this study were of known age as they were either ringed as nestlings at one of our two study sites, ringed as juveniles (1CY birds) during their first summer, or adults that immigrated into the study area and were caught, ringed and followed until they reached a minimum age of 4 years (5CY), at which point they were included in the ≥ 4-year-old group. The other 37 (49.3%) great reed warblers had their ages estimated based on body characters, because these had immigrated into our two study sites as adults after hatching elsewhere. In the great reed warbler, it is possible to categorize adult birds during the breeding season into four age groups: juveniles, 1-year-old birds, 2-year-old birds and 3-year-old or older birds (Bensch et al. 1998, Hasselquist 1998, Hansson et al. 2002). We estimated the ages of immigrant great reed warblers based on the following criteria: 1) the colour of the iris of the eyes, with dark grey iris in juveniles, becoming more greenish in 1-year-old birds; partly reddish-brown in 2-year-old birds; and more warmly reddish-brown all over the iris in 3-year-old birds, 2) the presence of two tongue spots (large ~ 2 × 1 mm, black-dark and easily visible) at the back of the tongue in juveniles, which gradually diminish and bleach out to become more like shadows of 50–100% of their original size in 1-year-old birds; just a small dot or thin crescent line at the inner part of the original tongue spot in 2-year-old birds; and then finally no sign left of the tongue spot on a shining orange tongue in 3-year-old or older birds, and 3) the colour of the outside of the tarsus, with dark grey tarsus (a dark graphite colour) in juveniles; evenly greyish (a light graphite colour) in 1-year-olds; mottled greyish and pale brown in 2-year-olds; and evenly light yellowish brown (straw-coloured) in 3-year-olds or older birds. These criteria for ageing have been developed within the Kvismaren long-term study (40 years) project and are based on annual scores of these criteria when studying the same individuals of known age over their whole lives up to an age of 5–9 years (6CY–10CY). If two of these traits suggested a particular age group, we assigned the bird to this age group. However, if the traits used to age an individual provided conflicting information (e.g. all body parts suggested different age groups), this individual was excluded from further analysis (2 cases).

The three age groups used for adult great reed warblers when attaching the data loggers during the summer of year_x (1-year-olds, 2-year-olds and 3-year-olds or older) correspond to the age groups of 2-year-olds (i.e. birds in their 3rd calendar year (3CY); see Demongin 2016); 3-year-olds (i.e. birds in their 4th calendar year (4CY)); and ≥ 4-year-olds (i.e. birds in their 5th calendar year or older (≥ 5CY)) during the spring migration in $\text{year}_{x+1,}$ which generated the dataset used in this study. Consequently, all birds included in this study were adults that had conducted at least one spring migration (and two autumn migrations) before being included in the analyses.

We used linear mixed-effect models to analyse age and sex effects on the timing of spring migration with 'lme4' R package (ver. 1.1–21; Bates et al. 2015). To estimate p-values and degrees of freedom, we used 'lmerTest' R package (ver. 3.0-1), using Satterthwaite's method (Kuznetsova et al. 2017). We used 'emmeans' R package (ver. 1.4.1; Lenth 2019) to estimate marginal means and perform pairwise post hoc multiple comparisons with Tukey adjustments, with degrees of freedom estimated with the Kenward–Roger method. We used day of year (DOY) as a time variable, with 1 January corresponding to DOY 1, to perform statistical analyses. All linear mixed models included individual ID and the year the data logger was attached as random intercepts. The final model that applied to all response variables (departure from the wintering grounds and arrival at the breeding grounds) was – response variable ~ sex + age_group + sex × age_group + (1 |bird_ID) + (1 | year_deployed) fitted with the restricted maximum likelihood (REML) method. When analysing the relationship between departure date from the wintering grounds and arrival date at the breeding grounds, we first computed the full model (arrival ~ departure + sex + age_group + sex × age_group + age_group × departure + sex × departure + (1 |bird_ID) + (1 | year_deployed)). We then used the *dredge* function in the R package 'MuMIn' (ver. 1.48.11), which ranks all possible models by AICc (Akaike's information criterion) (Bartoń 2025). From the two top ranked models (ΔAICc ≤ 2) we selected the one with the lowest AICc and the most parsimonious structure (with the fewest parameters: arrival ~ departure + sex + (1 |bird_ID) + (1 |year_deployed); Supporting information). Additionally, to test whether age had a significant effect, we compared the final model with a model that also included age group and its interaction with sex using a likelihood ratio test based on maximum likelihood (ML). All statistics were performed in R ver. 4.2.2 (www.r-project.org).

Results

Departure date from the wintering grounds for males ($n = 44$) ranged from 27 March to 3 May, and for females ($n = 31$) from 8 April to 11 May. The estimated marginal mean departure date for males was 16 April (marginal mean ± SE = 16 ± 1.6), which was 10.5 days earlier than the estimated marginal mean of females – 26 April (26 ± 1.7). This difference was statistically significant ($F_{1,61.9} = 23.1$, $p < 0.001$, $R^2_{\text{marginal}} = 0.4$, $R^2_{\text{conditional}} = 0.63$; Fig. 1). The overall age effect was also significant ($F_{2,65.7} = 4.3$, $p = 0.018$), but not the interaction between sex and age ($F_{2,65.7} = 1.4$, $p = 0.26$). A post hoc test revealed that, among males, there were significant differences between the 2-year-old and ≥ 4-year-old age groups

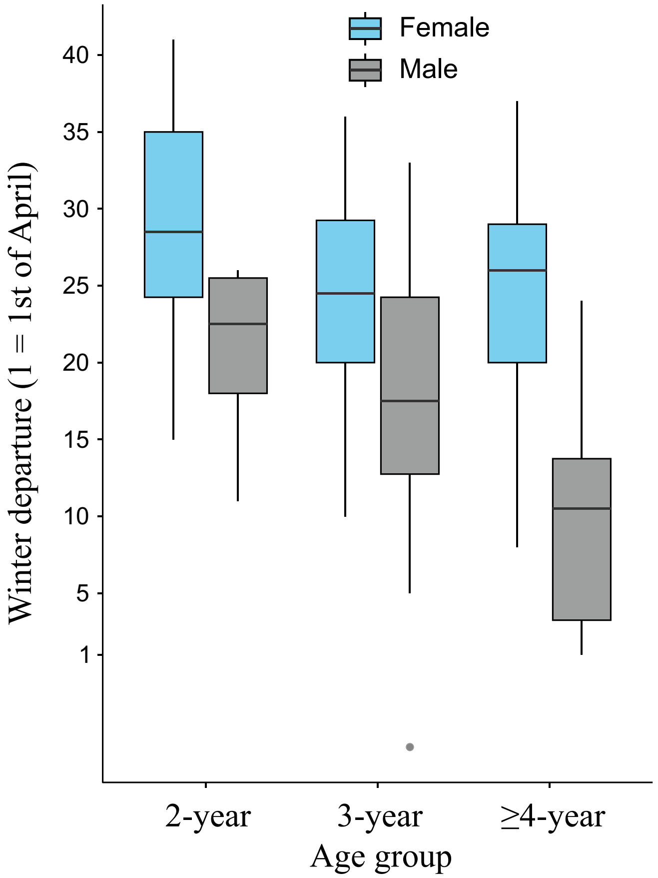

Figure 1. Departure dates from the wintering grounds (1 = 1 April) for adult great reed warblers divided into three age groups for males and females separately. Boxplots show median values (horizontal lines) with 25 and 75 percentiles, whiskers represent a 1.5 interquartile range and the dot represents an outlier.

(mean difference = 9.5 days earlier in ≥ 4-year-olds, SE = 3.9, df = 64.9, t = 2.5, $p = 0.042$), as well as between the 3-year-old and ≥ 4-year-old age groups (mean difference = 7.1 days earlier in ≥ 4-year-olds, SE = 2.8, df = 66, t = 2.6, $p = 0.032$), but not between the 2-year-old and 3-year-old age groups (t = 0.7, $p = 0.8$; Fig. 1; Supporting information). In contrast, there were no significant differences among the three age groups of adult females (all $p > 0.36$; Supporting information). Qualitatively similar results were found in the sub-sample of birds whose age group was known with certainty (Supporting information).

The arrival date on the breeding grounds for males (n = 44) ranged from 2 May to 1 June, and for females (n = 31) from 6 May to 2 June. The estimated marginal mean arrival date for males was 14 May (14 ± 1.4) which was an estimated 9.9 days earlier than the estimated marginal mean arrival date of females – 24 May (24 ± 1.5; Fig. 2). This difference was highly significant ($F_{1,62} = 29.6$, $p < 0.001$, $R^2_{marginal} = 0.43$, $R^2_{conditional} = 0.78$). In addition, the overall age effect on the arrival date to the breeding grounds was also significant ($F_{2,59.4} = 3.6$, $p = 0.034$), but not the interaction between sex and age ($F_{2,57.2} = 2$, $p = 0.14$).

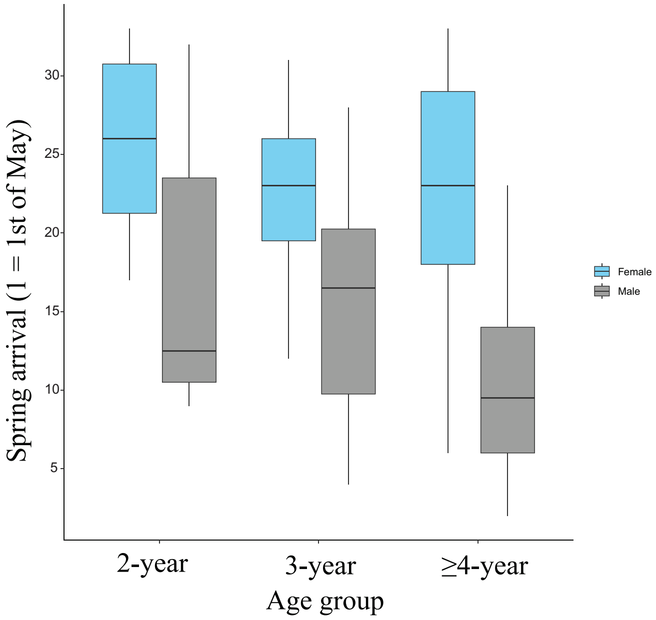

Figure 2. Arrival dates at the breeding grounds (1 = 1 May) for adult great reed warblers divided into three age groups for males and females separately. Boxplots show median values (horizontal lines) with 25 and 75 percentiles, whiskers represent the 1.5 interquartile range.

Post hoc tests between the age groups in males revealed that there were significant differences in arrival dates between 3-year-olds and ≥ 4-year-olds (mean difference = 5.7 days earlier in ≥ 4-year-olds, SE = 2.1, df = 59, t = 2.7, $p = 0.024$), but not significantly so between 2-year-olds and ≥ 4-year-olds (mean difference = 6.7 days, SE = 3, t = 2.3, $p = 0.07$) nor between 2-year-olds and 3-year-olds (mean difference = 0.98 days, SE = 2.8, t = 0.4, $p = 0.9$; Fig. 2; Supporting information). None of the three age groups of adult females differed significantly from one another (all $p > 0.36$; Supporting information). Qualitatively similar results were found in the sub-sample of birds whose age group was known with certainty (Supporting information).

The duration of spring migration for males ranged between 15 and 43 days (27.5 ± 1.5), and for females it ranged between 22 and 42 days (27.9 ± 1.5) (Supporting information). We found a significant positive relationship between departure date from the wintering grounds and arrival date at the breeding grounds ($F_{1,63,3} = 92.6$, $p < 0.001$, $R^2_{marginal} = 0.69$, $R^2_{conditional} = 0.83$, $\beta = 0.59 \pm 0.06$; Fig. 3), with males arriving significantly earlier than females by almost four days (3.9, SE = 1.4, df = 56.2, t = 2.8, $p = 0.006$; Fig. 3). There was no significant improvement in model fit when comparing the final model (arrival ~ departure + sex + (1 |bird_ID) + (1 |year_deployed)) with a model that also included age group and the interaction between sex and age group ($\chi^2 = 2.4$, df = 4, $p = 0.66$). Qualitatively similar results were found in the sub-sample of birds whose age group was known with certainty (Supporting information). In Fig. 3, it can be observed that the later the date of spring departure from the wintering

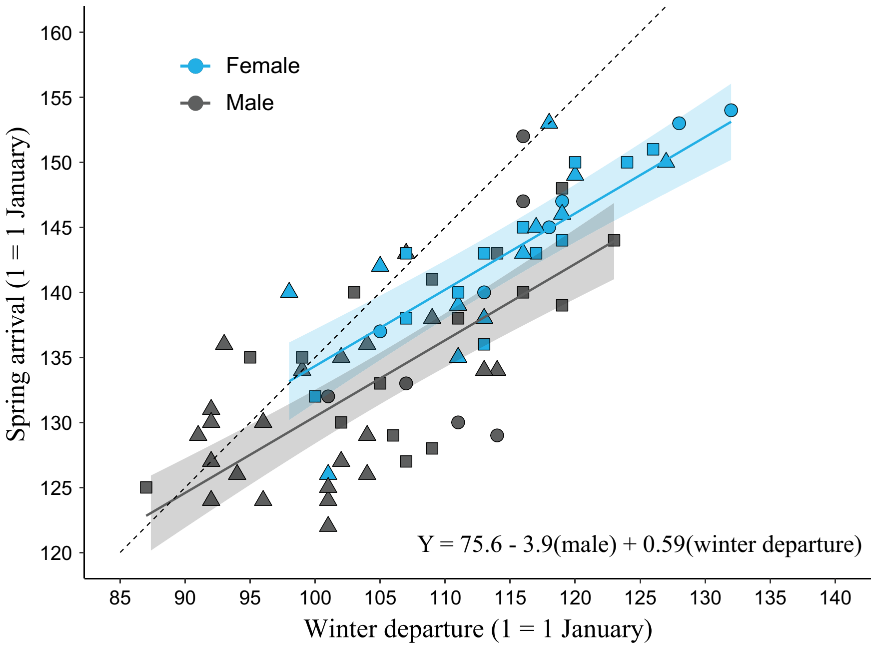

Figure 3. Relationship between departure date from the wintering grounds and arrival date at the breeding grounds for male and female great reed warblers (1 = 1 January). Circles represent 2-year-old age group, squares – 3-year-old age group and triangles – ≥ 4-year-old age group. The dashed line represents the 1:1 relationship. The blue and grey lines are estimated from the model and coloured areas indicate 95% confidence intervals. Note that for each specific departure date males arrived on average 3.9 days earlier to the breeding grounds than females, i.e. males had on average 3.9 days shorter duration of migration compared to simultaneously migrating females.

grounds, the shorter the duration of spring migration, as indicated by the shallower slopes ($\beta = 0.59$) that differed significantly from a slope of 1 ($t = -6.6$, $df = 63.7$, $p < 0.0001$).

Discussion

Departure from the wintering grounds

Here we investigated the proximate mechanisms in males and females of different age groups that lead to earlier arrival at the breeding grounds during spring migration, which in turn also could improve our understanding of the ultimate causes of protandry in the great reed warblers. Our study revealed that among adult male great reed warblers (i.e. migration-experienced individuals), those in the oldest age group (≥ 4-year-olds) departed earlier from the wintering grounds than 2- and 3-year-old males. In contrast, there was no such clear age-dependent pattern among adult females (Fig. 1; Supporting information). We can envision three potential explanations for this age-dependent advancement in spring departure dates for adult males.

First, birds may accumulate experience over multiple spring migration events, improving their capabilities to, for example, select their (final) wintering ground. A good choice could improve the ability to accumulate fuel (fat) for the first and particularly demanding leg of spring migration across the Sahara Desert. Additionally, their previous experience may help them make better decisions in preparation for migration, as well as during migration itself, ultimately enabling earlier departure from the wintering grounds. Early spring is usually characterized by harsher environmental conditions, including a lack of rain in sub-Saharan Africa, lower ambient temperatures and shorter daylight hours in Europe, which result in lower food availability and thus reduced fuel deposition rates (Newton 2008). For example, earlier-migrating white storks *Ciconia ciconia* experience weaker thermals and expend more energy during flight (Rotics et al. 2018), whereas more hostile environmental conditions en route, such as drought or cold spells, have been found to delay arrival at the breeding grounds in some songbird species (Tøttrup et al. 2012, Briedis et al. 2017). So far, only a few studies have investigated age effects on migration performance, aside from comparing young (juvenile/1-year-old) to adult (≥ 2-year-old) birds. In the two studies we are aware of, there was a gradual improvement in migration performance with age in black kites and white storks, i.e. in large-sized, long-lived species (Sergio et al. 2014, Aikens et al. 2024). In songbirds, to our knowledge, there has so far been no study reporting data on initiation of spring migration flights among adult age groups (i.e. beyond 1 year of age). However, we predict that in small-sized, short-lived species, there is likely less room for learning and experience to influence migration performance as compared to long-lived species, such as storks and kites.

Second, in addition to experience gained from previous migrations, for migratory birds, mortality rates are highest during migration periods (Sillett and Holmes 2002, Klaassen et al. 2014). Therefore, selective disappearance effects caused by higher mortality of poor performers at younger and middle age stages could result in a higher proportion of the ≥ 4-year-old age group being of higher quality with superior performance during the pre-migratory period, allowing them to depart earlier from the wintering grounds. In line with this reasoning, selective mortality in black kites, mainly acting in early life, contributed significantly to shaping the pattern of improved migratory capabilities with age (Sergio et al. 2014). However, in the current study, even though we only analysed data from successful migrants, we did not investigate any individuals that were inexperienced in spring migration (i.e. 1-year-old birds) and they had therefore all survived the strongest culling effect that is thought to occur during the first spring migration (Klaassen et al. 2014). Hence, we believe it is less likely that selective mortality had a strong influence on our results. This is further supported by the lack of an age-dependent pattern in timing of spring migration in females – something that we would have expected if selective disappearance of the poor performers at earlier age stages was the explanation for the age-dependent pattern on timing of migration we found in males.

Third, age-related changes in the secretion of the endocrine system might affect departure decisions in males. Hormones, such as testosterone, have been shown to mediate migratory behaviour and performance in birds (Tonra et al. 2011, Becker and Watts 2025). Elevated levels of testosterone in the dark-eyed juncos *Junco hyemalis* advanced their migratory preparation by approximately ten days compared to the control group (Tonra et al. 2011), whereas exogenous testosterone stimulated migratory restlessness in otherwise nomadic pine siskin *Spinus pinus* (Becker and Watts 2025). Furthermore, Těšický et al. (2022) observed a significant quadratic relationship between testosterone levels and age, peaking in midlife, in male but not female great tits *Parus major*. Although direct evidence linking age-related hormonal changes to migration timing is lacking, these findings suggest that changes in the secretion of the endocrine system could contribute to age-related variation in timing of departure in songbird migrants. Future research integrating hormonal profiling with multi-year individual tracking is needed to investigate the potential effects of the endocrine system on migration phenology.

Hormones could partly explain differences in departure dates between sexes, although both sexes should gain experience with age. Selection may be more relaxed in females, since they do not share the same urgency to reach the breeding grounds as the males, who need to establish territories. This could explain the lack of age-related differences in female departure timing. Since females depart later than males, they migrate during a period with more benign weather and higher food availability than males, as suggested by our finding of a significant decrease in total duration of migration as spring progresses, independent of sex and age group. However, we have previously shown that females also benefit in terms of reproductive output by arriving earlier and that the strength of this selection pressure does not differ from the males (Tarka et al. 2015). This suggests that the selection on female departure timing is not relaxed, rather it seems canalized due to selection pushing females to arrive later than males, but earlier than the other females. This canalization may be reflected in the seemingly lower variance in the departure time in the females compared to males (Fig. 1).

When analysing overall differences between the sexes, male great reed warblers, on average, departed approximately 11 days earlier from the wintering grounds than females. This result agrees with the general pattern of sex-biased timing of spring migration observed in other protandrous species (Ouwehand and Both 2017, Briedis et al. 2019, Pedersen et al. 2019). The proximate reason for such sex-related differences seems to be endogenously controlled timing, for example, manifested by an earlier start of migratory restlessness in males compared to females (Maggini and Bairlein 2012, Deakin et al. 2019). In addition, local environmental conditions and habitat quality can influence the departure decisions of migrating birds, for example, via time spent on fuelling before migration (Alerstam and Lindström 1990). However, in the great reed warblers Brlík et al. (2020b) found no sex-specific differences in the non-breeding habitat quality, suggesting no sex-specific habitat quality segregation in this species.

Duration of spring migration

In terms of the duration of spring migration, we observed no significant difference between age groups in either sex (Fig. 3; Supporting information). This contrasts with findings in black kites and white storks, where duration of spring migration decreased up until six and seven years of age, respectively (Sergio et al. 2014, Aikens et al. 2024). Such disparities could potentially stem from differences in migration flight modes or due to social effects. Nocturnally migrating songbirds like the great reed warbler use flapping flight and migrate solitarily, while large, diurnal migrants like black kites and white storks use soaring flight and migrate more often in groups, where the ability to use and locate thermals likely improves with experience and social information, which may lead to age-related decreases in migration duration (Sergio et al. 2014, Aikens et al. 2024).

Fuel deposition rate is one of the main factors affecting the duration of migration (Alerstam and Lindström 1990, Hedenström and Alerstam 1997, Lindström et al. 2019). While some studies found significant differences in fuel deposition rates between young (i.e. inexperienced migrants) and adult (experienced migrants) birds (Jones et al. 2002, Neto et al. 2008), others failed to find such relationships (Seewagen et al. 2013, Schmaljohann et al. 2018). In our current study, the absence of significant age effects on the duration of spring migration in both sexes indicates similar fuel deposition rates en route. However, we did not analyse data from 1-year-old, inexperienced birds, for which it has been shown that fuel deposition rates can vary within a season, depending on the time of migration (Stępniewska et al. 2020).

When examining the sex-specific patterns, it can be noted that no females were migrating as early as the earliest males, and no male was migrating as late as the latest females (Fig. 1, 3; Supporting information). Furthermore, when controlling for the departure date from the wintering grounds, we found that males arrived at the breeding grounds approximately four days earlier than females (i.e. when comparing simultaneously departing males and females; cf. Fig. 3). Since both male and female great reed warblers overwinter at similar latitudes in western sub-Saharan Africa (Lemke et al. 2013, Koleček et al. 2016, Brlík et al. 2020b, Malmiga et al. 2021), a shorter duration of spring migration in males could be a result of either higher fuel deposition rates or more efficient and faster migration flights. Indeed, on a stopover site in Crete, it has been observed that male great reed warblers had higher fuel deposition rates than females (Fransson et al. 2017). Differences in fuel deposition rates between the sexes have been found in other species, where it was a contributing factor to protandry (Seewagen et al. 2013). Moreover, Schmaljohann et al. (2016) showed that such sex differences in fuel deposition rates can vary between subspecies, affecting the sex-specific timing of migration. In addition, male great reed warblers have longer and more pointed wings that could allow for faster flight speeds and lower energy expenditure during flight than females (Bowlin and Wikelski 2008, Tarka et al. 2014). Alternatively, male and female great reed warblers could adopt different migration strategies, such as time and energy minimization, respectively. In such cases, males might consider fuel deposition rates in their decision-making process, leaving a stopover site when these rates decrease below a certain threshold, whereas females might show less concern about fuel deposition rates when deciding whether to stay or depart (Alerstam and Lindström 1990, Hedenström and Alerstam 1997). Such disparity has been observed in northern wheatears *Oenanthe oenanthe* migrating to Greenland/Iceland, with males showing a positive correlation between departure fuel load and fuel deposition rates (indicating time minimizing strategy), while females departed with constant fuel stores, irrespective of fuel deposition rates (Dierschke et al. 2005). We think that this possibility deserves more attention and can be investigated in future studies, using data loggers collecting detailed information about activity that can separate time spent resting from time spent being active and moving (indicating feeding activity) during daytime on stopover sites (Macías-Torres et al. 2022).

Arrival at the breeding grounds

Males, on average, arrived at the breeding grounds 10 days earlier than females, which is consistent with previous results based on field observations showing an average male arrival of 11 days earlier than females in our study population (Tarka et al. 2015). Based on the reasoning that protandry is driven by stronger selection pressure in favour of earlier arrival at breeding grounds in males than females, we would expect (fierce) competition between males over the most favourable breeding sites, a key factor determining mating and reproductive success. This would be even stronger in a socially polygynous species such as the great reed warbler, where territory attractiveness is a key factor determining pairing success and harem size (Hasselquist 1998). For female great reed warblers, the main benefits of early spring arrival could be the improved possibility of laying replacement clutches (and possibly also true second clutches) after nest failure, slightly larger clutch size if laying early in the season, and an increased likelihood of securing primary female status in the harem (Bensch 1996, Hansson et al. 2000). However, females will generally not be able to form a social pair bond with more than one male in a season, and they may be able to settle in a breeding territory of relatively high quality even if they do not take the risk of earlier wintering ground departure and/or higher spring migration speed (Bensch 1996, Hasselquist 1998, Hansson et al. 2000).

Our analysis of arrival dates to the breeding grounds revealed that the oldest male age group arrived earlier than middle-aged males and tended to do so also compared to 2-year-old males. We did not observe a similar age-dependent pattern among females (Fig. 2; Supporting information). Our findings are consistent with previous research from our study population, which demonstrated that older male age groups arrive earlier at the breeding grounds, allowing them to occupy more attractive territories (Hasselquist 1998).

We found that with each day of delayed departure from the wintering grounds great reed warblers of both sexes arrived 0.59 days later (see also Schmaljohann 2019 for similar results in other songbirds). This is also consistent with the results of previous research on great reed warblers from Kvismaren, although analysed on a smaller dataset and only in males (Lemke et al. 2013). This suggests that conditions for migration over the Sahara Desert and/or through Europe improve considerably as the spring season progresses (see also Newton 2008).

The proximate cause of earlier arrival date at the breeding grounds for older compared to younger adult male great reed warblers is their earlier departure from the wintering grounds. Whereas protandry in the great reed warblers also mainly stems from earlier male departure from the wintering grounds, it is additionally complemented by a shorter spring migration duration in males. Similar patterns, with both earlier departure and shorter duration in males leading to protandry, have been observed previously (Briedis et al. 2019). However, in some other cases differences in departure timing alone have explained the occurrence of protandry during spring migration (Ouwehand and Both 2017, Pedersen et al. 2019).

It is unlikely that our results were biased by the use of two types of data loggers. Both data loggers were of similar weight, though their shapes differed slightly. Additionally, we used ‘year’ as a random intercept in the linear mixed models, which further accounted for the uneven use of the two types of data loggers across years. Future studies should explore possible age-related changes in hormones, behaviour, genetics, and individual quality, to see how these may contribute to the variation in migration timing in males and females.

Conclusions

Our study of adult great reed warblers revealed intriguing and unexpected results regarding the timing of spring migration in a long-distance nocturnal migrant songbird. We found that even among migration-experienced adult males, those belonging to the oldest age group departed earlier from the wintering grounds compared to younger adult males. However, we did not observe a similar pattern in adult females. This age-dependent improvement in wintering ground departure date in adult males could be explained by proximate factors such as: 1) accumulated experience leading to better resource access or refined internal time schedule allowing them to leave earlier than younger adult males, 2) selective mortality of poor performers, resulting in a bias towards high-quality individuals in the oldest age group, 3) age-related hormonal changes, or a combination of these factors. Irrespective of the underlying proximate mechanism, our findings show that long-distance migrant songbirds can modify their 'migration program', otherwise often thought to be strictly endogenously controlled. This was, however, only clearly demonstrated in males. Further studies need to examine this in more detail.

A key take-home message from the current study is that early departure date from the wintering grounds is a decisive proximate cause for the observed patterns of earlier spring arrival at the breeding grounds with increasing age in adult males. Similarly, protandry in the great reed warbler mainly stems from earlier departure from the wintering grounds by males, complemented by their shorter duration of spring migration. This is an important observation to help understand the proximate mechanisms that contribute to shaping patterns of protandry and age-dependent differences in timing of migration and spring arrival at the breeding grounds. However, it also puts the focus on an unresolved key question in migration research: what sets the limit to earlier departure from the wintering grounds? In fact, the first fuelling period before spring departure from the tropical wintering grounds has previously been pointed out as an important period for long-distance migrants that to some extent has been neglected (Lindström et al. 2019). Our current study further highlights this point, and we encourage further studies of this apparently critical period for flapping flight migrant birds wintering in sub-Saharan Africa.

Different patterns in males and females in terms of age-dependent advancement of both wintering ground departure and breeding ground arrival during spring migration can have important implications for the ability to cope with changing environmental conditions, including climate change. The successive advancement of wintering ground departure and breeding ground arrival in the oldest age group of adult males implies strong selection on earlier spring arrival, where any phenotypic improvement in physiological quality/condition, cognitive ability and memory-based improvements may result in earlier departure and higher migration speed to reach the breeding grounds as early as possible. However, earlier spring migration may be riskier if weather conditions become more variable and extreme due to ongoing climate change conditions, increasing the mortality risk for the oldest (and possibly highest-quality) males. This may in turn have negative implications for the viability of the breeding populations in Europe, as a larger fraction of the most potent males of each local population may be lost during migration, possibly lowering the total reproductive success and thus viability of local populations.

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Author contributions

Gintaras Malmiga: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Thomas Alerstam**: Conceptualization (equal); Formal analysis (equal); Investigation (supporting); Writing – review and editing (equal). **Bengt Hansson**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Writing – review and editing (equal). **Sissel Sjöberg**: Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Maja Tarka**: Funding acquisition (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Helena Westerdahl**: Funding acquisition (equal); Investigation (equal); Writing – review and editing (equal). **Dennis Hasselquist**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Writing – original draft (supporting); Writing – review and editing (lead).

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Data availability statement

The data files for light and activity can be downloaded from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.15507411 (Malmiga et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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