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Short Communication

Icelandic Whimbrel first migration: Non-stop until West Africa, yet later departure and slower travel than adults

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Migratory behaviour in young individuals is probably developed by using a complex suite of resources, from molecular information to social learning. Comparing the migration of adults and juveniles provides insights into the possible contribution of those developmental factors to the ontogeny of migration. We show that, like adults, juvenile Icelandic Whimbrel *Numenius phaeopus islandicus* fly non-stop to West Africa, but on average depart later, follow less straight paths and stop more after reaching land, resulting in slower travel speeds. We argue how the variation in departure dates, the geographical location of Iceland and the annual migration routine of this population make it a good model to study the ontogeny of migration.

Keywords: movement ecology, *Numenius phaeopus*, ontogeny, shorebird, social learning.

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Migration is a syndrome of complex behaviours that involves periods of fuelling and migratory movements (Alerstam & Lindström 1990, Piersma *et al.* 2005) and can vary in multiple aspects both within and among individuals. One particularly relevant trait underlying such variation and operating at both levels is age, with juveniles often migrating at different times than adults (e.g. Neto *et al.* 2008, Patchett *et al.* 2022, Verhoeven *et al.* 2022) and also in some cases following different routes (e.g. Handel & Gill 2010, Mellone *et al.* 2013, Crysler *et al.* 2015) and wintering at different destinations (e.g. Cristol *et al.* 1999, Nebel *et al.* 2002, Lok *et al.* 2011). While differential migration of inexperienced juveniles and experienced adults may be evident, understanding how migratory behaviour develops with age remains a knowledge frontier in the study of bird migration (Flack *et al.* 2022, Loonstra *et al.* 2023).

The ontogeny of migration is likely to be the result of interactions across various internal and external developmental resources, including molecular information and social and experiential learning (Oyama *et al.* 2001). In cases where juveniles start their migraton after their family members and many other experienced adults in the population (Vega *et al.* 2016, Verhoeven *et al.* 2022), the use of social and experiential information appears more problematic than for juveniles that migrate in family groups, together with adults. In the latter case, it is easy to envisage how they could learn the migration route, suitable stopover sites and destination locations (Rotics *et al.* 2016, Abrahms *et al.* 2021). Juvenile migratory behaviour can even be unequally linked to a progenitors' behaviour (Méndez *et al.* 2021, Byholm *et al.* 2022). Therefore, there is probably a range of developmental resources contributing to the ontogeny of migration across, and possibly within, species.

Recent findings suggest that in the course of life into adulthood, individuals refine their migratory behaviour (Thorup *et al.* 2003, Mueller *et al.* 2013, Sergio *et al.* 2014, Rotics *et al.* 2016, Vansteelant *et al.* 2017, Campioni *et al.* 2020, Verhoeven *et al.* 2022, Wynn *et al.* 2022). However, the size of available electronic tracking devices has limited the pool of possible species to track (Bridge *et al.* 2011) and therefore current knowledge mostly stems from studies on large-bodied species that migrate socially, in family groups or large flocks, possibly biasing current knowledge towards certain life-histories (but see Crysler *et al.* 2015, Evens *et al.* 2017, Patchett *et al.* 2022). Studies across a variety of taxa, encompassing species or populations with varying life-histories, are fundamental for a wider understanding of the ontogeny of migration (Flack *et al.* 2022).

Tracking individuals throughout their lives into adulthood, where the first and the subsequent migrations are recorded, allows direct observation of how individual migratory behaviour changes and develops, providing invaluable insight into the ontogeny of migration. However, obtaining such datasets has rarely been achieved (Abrahms *et al.* 2021), possibly due to high juvenile mortality and dispersal (Paradis *et al.* 1998, Oppel *et al.* 2015, Sergio *et al.* 2019, Verhoeven *et al.* 2022), which can considerably reduce numbers of individuals sampled continuously up to adulthood, and by technological limitations due to early failure of tracking devices (C. Carneiro pers. obs.). An alternative approach is to track different age-classes in the same population, allowing informative analysis among age-groups (Hake *et al.* 2003, Campioni *et al.* 2020). This approach reduces the issue of sample thinning among older individuals.

Although tracking technology has advanced rapidly and has resulted in a boom of detailed studies on adult migration, much less progress has been made for juveniles. This is the case for Whimbrel *Numenius phaeopus*, whose adult migrations have been tracked worldwide (e.g. Alves *et al.* 2016, Johnson *et al.* 2016, Li *et al.* 2020, Ruthrauff *et al.* 2021) but where information on juvenile migration is much scarcer, although observations prior their first migratory departure (Gunnarsson 2006) and of migratory flocks along the route (Skeel & Mallory 2020, Hines *et al.* 2023) suggest that many juveniles depart later than adults. For the Icelandic population *N. p. islandicus*, it is now well known that during post-breeding migration, adults virtually always make direct flights to the wintering sites (mostly located in West Africa; Carneiro *et al.* 2019a, 2023), departing starting from the second half of July until nearly the end of August (Carneiro *et al.* 2019b, 2023). During pre-breeding migration, adults move from the wintering to the breeding grounds between April and May, and make either a direct flight to Iceland (i.e. the same route as in autumn) or two flights with a stopover (usually in Ireland or the UK; Carneiro *et al.* 2019b). However, migration routes and phenology remain unknown for the juvenile stage, including the first migration.

Here, we (1) determine the migration phenology, routes and travel speed of juvenile Icelandic Whimbrels on their first migration, as well as their wintering region, and (2) compare these metrics with those of adults that have been published previously (Carneiro *et al.* 2019b, 2023).

We predict that juveniles depart on average later than adults, given that Whimbrels are observed in Iceland until early October (Gunnarsson 2006, eBird 2021), i.e. more than 1 month after the latest tracked adult has departed (Carneiro *et al.* 2023). Based on the relatively high number of Whimbrel records in Scotland and Ireland during August and September (BTO/RSPB/BirdWatch Ireland/SOC/WOS 2023), and knowing that adults almost always fly non-stop to the wintering grounds, we predict that juveniles may stop on their first autumn migration in this region, therefore following a different route than that of adults. Due to such stopover and route differences, we also expect that juveniles will travel at slower speeds than adults and show more tortuous tracks. By migrating later, juveniles may also settle at distinct wintering sites from adults.

METHODS

After monitoring Whimbrel broods throughout their development, we caught and tagged juveniles when they became able to fly at least 10 m (under ringing licence number 365 issued by the Icelandic Institute of Natural History). In total, we tagged 13 juveniles in South Iceland: 11 at 63°43'1.2"N, 20°6'46.8"W (six in 2021 and five in 2022), one at 63°55'51.6"N, 21°10'8.4"W (in 2021), and one at 63°46'19.2"N, 20°20'6"W (in 2022). To track their movements, we used two models of GPS/GSM devices manufactured by Hunan Global Messenger Technology Co., Ltd: HQBG0804 (mass: 4.5 g; $n = 4$ devices in 2021) and HQBG1206 (mass: 6 g; $n = 3$ and 6 devices in 2021 and 2022, respectively). These were modified by adding a layer of neoprene (*ca.* 3.5 mm thick) to make the solar panel protrude above the feathers' surface, to increase battery recharging ability and to cushion the devices' hard surface on the birds' back. The devices were attached using a leg-loop harness using ultra high molecular weight polyethylene (UHMW) straps, and the average mass (± se) added to the individuals (i.e. the mass of tag plus neoprene, straps, etc.) was 5.8 ± 0.1 and 8.2 ± 0. 1 g for HQBG0804 and HQBG1206 models, respectively. This represented 2.0 ± 0.1 and 2.7 ± 0.1% of the juveniles body mass at tagging age, and less than 2% of the breeding adult body mass in this population (mean ± se = 437.1 ± 4.6 g; Carneiro *et al.* 2023). Both models were programmed to collect a fix every 6 h, with geographical coordinates, timestamp (UTC) and associated accuracy (ranging from 5 to 2000 m). Data were transmitted via the GSM network. All geographical coordinates used in the analysis were accurate up to 10 m.

Departure date was determined as day of the last fix in Iceland. We assumed the wintering site to be location of the first fix at the lowest latitude site where individuals settled. We used the R package 'bcpa' (Gurarie 2022) to help identify these sites and associated arrival dates by running a behavioural changepoint analysis to find breakpoints of latitude along the tracking period. We then used these breakpoints to inspect each track visually and determine the *arrival date* as the day of the first fix at that site. *Travel duration* was defined as the period between *departure date* and *arrival date*, and *migration distance* was calculated as the cumulative distance of consecutive fixes between departure and arrival. We used these two metrics to calculate *travel speed* (i.e. *migration distance* divided by *travel duration*). The *straightness* of migration routes was calculated using the R package 'amt' (Signer *et al.* 2019). This metric is the Euclidian distance between the departure and wintering locations, divided by the total length of the movement.

To compare the migratory behaviour of juveniles with that of adults, we collated adult migration data from Carneiro *et al.* (2019b) and added arrival and departure dates from Carneiro *et al.* (2023). In brief, adult data were collected with geolocators between 2012 and 2018, from which two fixes per day were determined, and timings of departure and arrival were further refined using temperature, conductivity and wet contacts data collected at 4-h intervals (Battley & Conklin 2017). The wintering site for adults was determined as the average location across all the winter fixes. For further details see the methods in Carneiro *et al.* (2019b). The data provided by the devices used to track adults (geolocators) and juveniles (GPS) differ, and therefore may influence the metrics obtained, as geolocators can have considerable associated spatial uncertainty, much higher than the GPS devices (Phillips *et al.* 2004, Fudickar *et al.* 2012). The smaller longitudinal than latitudinal uncertainty associated with geolocator data (Phillips *et al.* 2004, Fudickar *et al.* 2012) means that our estimates of straightness may be less influenced than the wintering latitude. Regarding travel timings, data recorded by the two types of devices are comparable (every 4 h for geolocators and every 6 h for GPS).

We tested for differences in migration metrics between juveniles and adults using the appropriate Student's *t*-test or Mann–Whitney test with the R package 'ggstatsplot' (Patil 2021), after testing the data for normality and homogeneity of variance. Because the two age groups were tracked in distinct periods, we could not account for year effects, as these would be confounded with age effects. To investigate whether structural annual differences exist that could impair our comparison between ages, we tested for potential annual differences in adult departure dates, but we did not find differences ($\chi^2_{\text{Kruskal-Wallis}}$ (6) = 10.49, $P = 0.11$; see SOM Fig. S1), and hence the comparisons between age groups should reflect age differences.

Unless otherwise noted, means are followed by standard error. Significant statistical differences were considered for an alpha level of 0.05.

RESULTS

We gathered full first migration data from 11 juvenile Whimbrels, of the 13 tagged. We did not receive data from one individual outside of Iceland, but it may have departed and never reached a location with GSM coverage. The tag on another bird failed to record fixes around the departure date (due to low battery levels), so we decided to exclude it from the analysis. This individual's first fix after departure was close to the Madeira archipelago (Portugal), on 2 September 2021. It then landed on Madeira Island and no data were received after 16 September 2021. Of the remaining 11 birds, six tags provided data for an average of 185 days before stopping (range: 71–378 days), whereas five (deployed in July 2022) were still working by July 2023 (see SOM Table S1 for details on tag longevity).

Juveniles departed between 4 August and 2 September (mean = 22 August ± 8 days, $n = 11$), significantly later than adults (t_{Student} (86) = −6.95, $P < 0.001$; Fig. 1b), although departure dates partially overlapped with those of adults (adults range from 24 July to 21 August; mean = 7 August ± 7 days, $n = 77$). Similarly, juveniles arrived at the wintering sites later than adults ($W_{\text{Mann-Whitney}} = 44.5$, $P < 0.001$; Fig. 1c), between 11 August and 14 October (mean = 3 September ± 16 days), whereas adults arrived between 28 July and 26 August (mean = 21 August ± 7 days).

Juvenile migration routes were less straight than those of adults (juveniles: mean straightness = 0.86 ± 0.18; adults: mean straightness = 0.96 ± 0.00; $W_{\text{Mann-Whitney}} = 315.0$, $P < 0.001$; Fig. 1f), nevertheless following an overall N–S direction towards West Africa over the Atlantic Ocean, where they tended to make stops along the African coast before reaching the wintering sites (Fig. 1b). Such behaviour, not detected in adults (Carneiro *et al.* 2019b), inevitably increased juvenile travel duration and consequently resulted in a significantly lower travel speed (juveniles: mean = 35.3 ± 3.4 km/h, $n = 11$; adults: mean = 53.5 ± 0.8, $n = 30$; t_{Student} (86) = 7.39, $P < 0.001$, Fig. 1d).

Juveniles' wintering sites were on average further north (mean = 12°18'0" ± 0°18'0"N, $n = 11$) than those of adults (mean = 10°36'0" ± 0°24'0"N, $n = 29$; $W_{\text{Mann-Whitney}} = 38.0$, $P < 0.001$). However, there was a complete overlap of wintering latitudes (juveniles' range: 11°0'0"–13°54'0"N; adults' range: 5°54'0"–24°18'0"N; Fig. 1f).

DISCUSSION

This study contributes to the growing field of ontogeny of migration (Flack *et al.* 2022). Our results show that, similar to adults, juvenile Icelandic Whimbrels migrate non-stop to West Africa during their first migration, while departing on average later, exhibiting less straight routes with more frequent stopovers, and slower travel speeds.

The observed differences in departure date between the age-classes is not uncommon among birds (Newton 2008), including waders (e.g. Gunnarsson 2006, Verhoeven *et al.* 2022). Later timings by juveniles were also detected in a recent study where age ratios of Hudsonian Whimbrels *N. p. hudsonicus* were calculated at

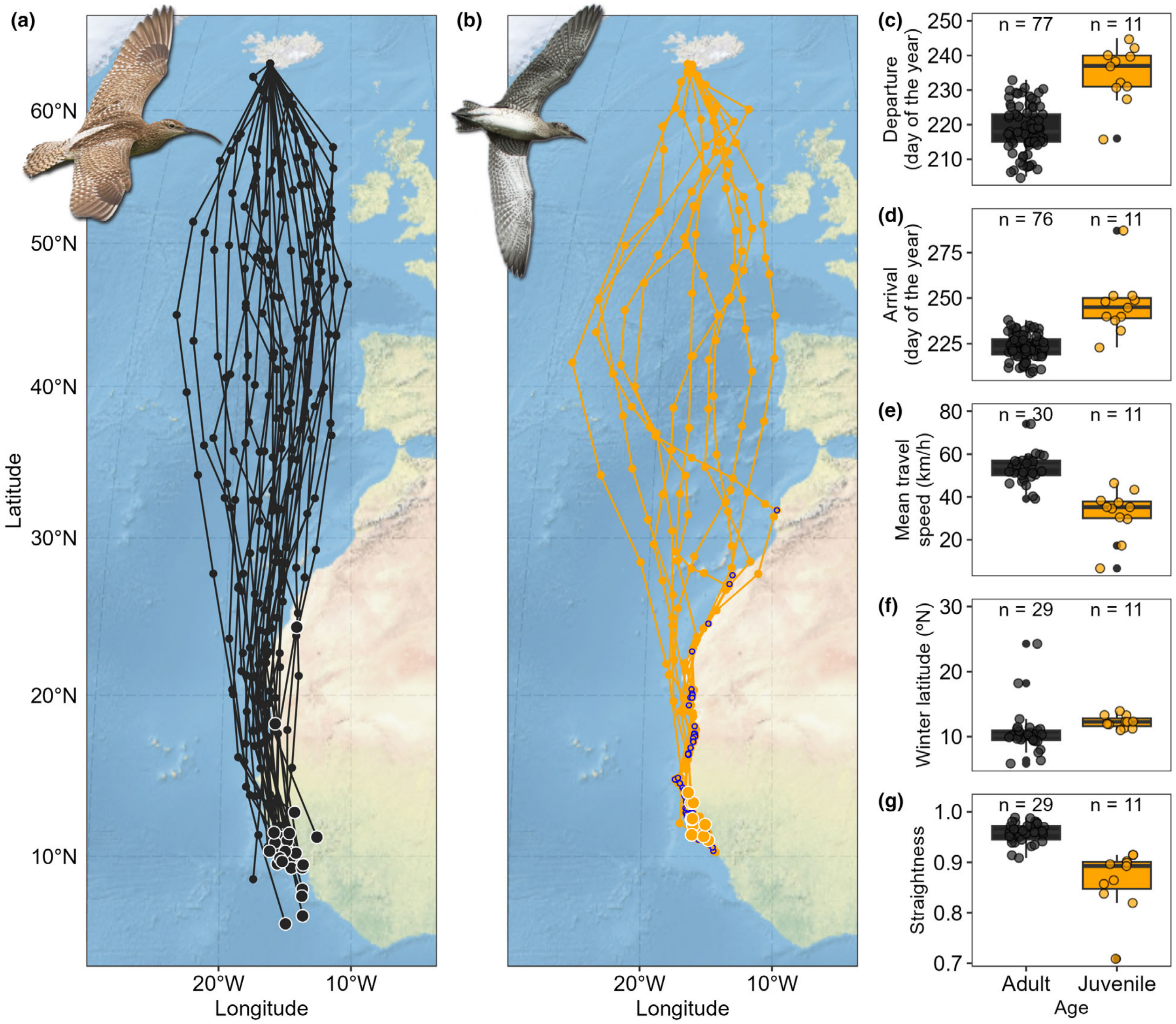

Figure 1. (a,b) Migration routes of adult (*n* = 76) and juvenile Whimbrels (*n* = 11), respectively; the larger filled circles with a white outline represent the wintering sites. Blue circles in (b) represent the juvenile stopover locations (defined by fixes with zero ground speed). (c–g) Boxplots summarizing adult and juvenile migratory parameters: day of the year of autumn departure (c) and arrival dates (d), mean travel speed (e), winter site latitude (f) and straightness of route (g; higher values = straighter route). Boxes show the median and 25% and 75% quartiles, whiskers extend up to 1.5 times the interquartile range from the median and points beyond that are individually marked in black. Individual data points overlap the box plots. Sample size is shown above each boxplot. Adult data were collated from Carneiro *et al.* (2019b, 2023). Photos by Tómas G. Gunnarsson ((a), adult) and Triin Kaasiku ((b), juvenile).

stopover sites in the West Atlantic Flyway (Hines *et al.* 2023). Hines *et al.* (2023) observed an overlap in timings between juveniles and adults at stopover sites, similar to what we observed in the departure dates, with a few early juveniles departing during the same period as late adults. This raises a relevant contrast between early and late departing juveniles: whereas early juveniles may be able to join departing Whimbrel flocks with experienced adults and culturally inherit the migration route, late departing juveniles may lack this opportunity. Nonetheless, we cannot rule out the possibility of other information cues that may be gathered by late juveniles in the weeks preceding departure, including heterospecific ones, such as observing departing flocks and learning the direction of departure (Piersma 2022).

All tracked juvenile Whimbrels undertook a non-stop flight to West Africa, following a comparable route to adults. This finding contrasts with our initial prediction based upon observations in the western UK and Ireland during autumn migration, where Whimbrels are often recorded between August and September. It is therefore possible that those records belong to individuals of the nominate subspecies, breeding in north-east Europe (Delany *et al.* 2009); however, our sample of juveniles is limited and some may stop in that region. It is also possible that individuals that stop originate from other regions in Iceland, although early tracking of adult birds from north-west Iceland indicates non-stop flights to West Africa ($n = 3$ individuals, C. Carneiro pers. obs.), similarly to those reported here.

Compared with adults, juveniles showed less straight autumn migration routes, which could have been shaped by different wind conditions experienced en route (Vansteelant *et al.* 2017). Although tracking device differences may have an influence (see Methods), differences in straightness also result from juveniles tending to stop at several sites along the West African coast before settling at their wintering site, in contrast to adults. Such behaviour resembles what was observed in Eleonora's Falcon *Falco eleonorae*, where juveniles showed similar migration routes to adults only until they reached the Sahel region, presumably because there they could meet favourable foraging conditions and needed to restore energy reserves (Mellone *et al.* 2013). Juveniles may have lower flight efficiency than adults (Rotics *et al.* 2016), which could explain why they need to stop more frequently or sooner than adults. If juveniles simply fly in a flock with adults until the wintering site, then early juveniles would be more likely to achieve higher travel speeds (i.e. similar to those of adults), but we found no trend of mean travel speed in relation to departure date among juveniles (linear regression: $R^2 = 0.027$, $F_{(1,9)} = 0.025$, $P = 0.63$). Although not conclusive, this suggests that juvenile Whimbrel may be limited in their ability to reach the wintering site in a single flight, contrary to adults. Furthermore, hopping along the West African coast may allow naïve and uninformed juveniles to explore and sample potential wintering sites before settling, while possibly following other individuals (Whimbrels or other waders) southwards.

Our tracked juvenile Whimbrels settled on wintering sites that were on average at higher latitudes than those of adults, even though all juvenile wintering sites were within the range of wintering sites of adults, and most were located close to the Guinea-Bissau region, where wintering conditions are known to be favourable for Whimbrels (Carneiro *et al.* 2021). These differences may also be partially explained by the different spatial accuracy of the tracking devices used on juveniles and adults (see Methods). Nonetheless, as wintering locations are known to vary between age groups in other species (Nebel *et al.* 2002, Lok *et al.* 2011), further research where both age groups are tracked with the same technology is necessary to determine the age differences accurately.

Icelandic Whimbrel as a model to study ontogeny of migration

The role for in-flight social information can be studied in Icelandic Whimbrel, as juveniles may be departing on their first migration with and without experienced adults. Early juveniles are likely to encounter multi-age departing flocks (Gunnarsson 2006) and can acquire knowledge en route, whereas late juveniles have no such opportunity. Simultaneous tracking of adults and juveniles, while observing departures in the field to determine age proportions in flocks, can shed light on the role of social learning in the first migration.

The geographical characteristics of Iceland also provide an advantage when studying the importance of knowledge transfer in the ontogeny of migration. Together with our findings that juveniles fly non-stop to West Africa, in this system juveniles have only one chance to gather social information for most of the migratory route (i.e. before departure). This is different from most migratory species that fly over land, allowing juveniles the opportunity to stop, join new flocks and gather knowledge from them (Németh & Moore 2014, Loonstra *et al.* 2023).

Furthermore, the Icelandic Whimbrel allows for a particular investigation of migration development once individuals are tracked to their first pre-breeding migration and in subsequent years. After departing the wintering sites in spring, adults typically take one of two routes: a direct flight to Iceland (i.e. the same route as in autumn) or two flights with a stopover (usually Ireland or the UK; Carneiro *et al.* 2019b). From repeated individual tracking of 12 adult Whimbrels over 2–5 years, it has been possible to observe three individuals changing their spring route between years. Interestingly, such change was only detected in one direction: individuals switched from a direct route to a stopover one; the opposite was not observed (Carneiro *et al.* 2019a). These findings stem from a reduced sample size but they support the idea that the locations of stopovers and the route between them are probably learnt. A successful juvenile may migrate to the breeding area, for the first time, following the route it knows (i.e. a direct one) and continue to do so until, in a given spring, it joins and follows a flock making a stopover, the pattern most commonly found in the population (Carneiro *et al.* 2019b). There may be advantages in making stopovers in spring, such as improved prediction of weather conditions at breeding sites by being closer to them (Winkler *et al.* 2014, Bauer *et al.* 2020, Carneiro *et al.* 2020). Once individuals learn the route with a stopover, they may be expected to follow it in subsequent years (Lok *et al.* 2011, Verhoeven *et al.* 2022) simply by being able to better time their arrival into Iceland given weather conditions at stopover sites. The Icelandic Whimbrel thus presents an exceptional 'developmental system' (*sensu* Oyama *et al.* 2001) to investigate the roles of various developmental factors on the ontogeny of migration.

AUTHOR CONTRIBUTIONS

Camilo Carneiro: Conceptualization; methodology; data curation; formal analysis; funding acquisition; visualization; writing – original draft; writing – review and editing; project administration. **Tómas G. Gunnarsson:** Conceptualization; funding acquisition; writing – review and editing; methodology; writing – original draft; project administration. **Triin Kaasiku:** Writing – review and editing; writing – original draft; methodology. **Theunis Piersma:** Writing – review and editing; funding acquisition; writing – original draft; conceptualization. **José A. Alves:** Writing – review and editing; funding acquisition; writing – original draft; conceptualization; project administration.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

Data Availability Statement

Adult data were collated from Carneiro *et al.* (2019b, 2023) and can be accessed in the Dryad Digital Repository at https://doi.org/10.5061/dryad.3kf35s5 (Carneiro *et al.* 2018) and at https://doi.org/10.5061/dryad.vt4b8gtv9 (Carneiro *et al.* 2022). Juvenile data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICAL NOTE

None.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Annual variation in autumn departure date for adults and juveniles.

Table S1. Longevity of the tags used, and probable reason for failure, per tag model.