RESEARCH ARTICLE

Age-dependent timing and routes demonstrate developmental plasticity in a long-distance migratory bird

Mo A. Verhoeven[1] | A. H. Jelle Loonstra[1] | Alice D. McBride[1] | Wiebe Kaspersma[1] | Jos C. E. W. Hooijmeijer[1] | Christiaan Both[1] | Nathan R. Senner[1] | Theunis Piersma[1,2]

[1]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

[2]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands

Correspondence
Mo A. Verhoeven
Email: m.a.verhoeven@rug.nl

Present address
Nathan R. Senner, Department of Biological Sciences, University of South Carolina, 715 Sumter Street, Columbia, SC 29208, USA

Funding information
Ubbo Emmius Fund; Gieskes-Strijbis Fonds; BirdLife-Netherlands; WWF-Netherlands; Nederlandse Organisatie voor Wetenschappelijk Onderzoek; Prins Bernhard Cultuurfonds; Rijksuniversiteit Groningen; Province of Fryslân; Ministry of Agriculture, Nature Management and Food Safety; Van der Hucht de Beukelaar Stichting; Paul and Louise Cook Endowment Ltd.; Anonymous Donor

Handling Editor: Francesca Cagnacci

Abstract

1. Longitudinal tracking studies have revealed consistent differences in the migration patterns of individuals from the same populations. The sources or processes causing this individual variation are largely unresolved. As a result, it is mostly unknown how much, how fast and when animals can adjust their migrations to changing environments.

2. We studied the ontogeny of migration in a long-distance migratory shorebird, the black-tailed godwit *Limosa limosa limosa*, a species known to exhibit marked individuality in the migratory routines of adults. By observing how and when these individual differences arise, we aimed to elucidate whether individual differences in migratory behaviour are inherited or emerge as a result of developmental plasticity.

3. We simultaneously tracked juvenile and adult godwits from the same breeding area on their south- and northward migrations. To determine how and when individual differences begin to arise, we related juvenile migration routes, timing and mortality rates to hatch date and hatch year. Then, we compared adult and juvenile migration patterns to identify potential age-dependent differences.

4. In juveniles, the timing of their first southward departure was related to hatch date. However, their subsequent migration routes, orientation, destination, migratory duration and likelihood of mortality were unrelated to the year or timing of migration, or their sex. Juveniles left the Netherlands after all tracked adults. They then flew non-stop to West Africa more often and incurred higher mortality rates than adults. Some juveniles also took routes and visited stopover sites far outside the well-documented adult migratory corridor. Such juveniles, however, were not more likely to die.

5. We found that juveniles exhibited different migratory patterns than adults, but no evidence that these behaviours are under natural selection. We thus eliminate the possibility that the individual differences observed among adult godwits are present at hatch or during their first migration. This adds to the

mounting evidence that animals possess the developmental plasticity to change their migration later in life in response to environmental conditions as those conditions are experienced.

KEYWORDS
evolution, godwit, migration, ontogeny, plasticity

1 | INTRODUCTION

It is becoming increasingly clear that migratory populations consist of individuals that each have their own routes, timing, use of stopover sites and levels of consistency between years (Delmore et al., 2020; Flack et al., 2016; Lok et al., 2011; Vardanis et al., 2011). The source of this individual variation in seasonal migration patterns, or the developmental phase during which such individual routines arise, remains unclear (Battley et al., 2020; Pedersen et al., 2018; Verhoeven et al., 2019). This hinders an understanding of the evolution of migration (Piersma, 2011) and is fundamental for assessing the extent to which migratory animals can cope with current rates of environmental change (Senner et al., 2020; Sutherland, 1998).

Three separate and interacting sources of variation in individual migratory behaviour have been identified: (epi-)genetic heritability, developmental plasticity and phenotypic flexibility (Piersma, 2011). Some individual differences in migratory behaviour have been attributed to genotypic differences, which can determine both how and when differences arise during an individual's life (Berthold et al., 1992; Pulido et al., 2001; Thorup et al., 2020). In such cases, aspects of migratory behaviour are both heritable and selected for by the environment. In a classic example, it has been argued that natural selection on genetic variation in blackcaps *Sylvia atricapilla* has enabled the use of a new migratory route connecting breeding populations in Germany with novel nonbreeding sites in Great Britain (Berthold et al., 1992). As a complex trait (Piersma et al., 2005), however, migration is unlikely to be encoded by a single gene. Instead, multiple or even many genes simultaneously contribute to an individual's migratory phenotype (Delmore et al., 2016; van Doren et al., 2017). Although epigenetic inheritance could lead to rapid phenotypic changes at the population level (Sheriff et al., 2010), adjustments through natural selection to polygenic traits are thought to be relatively slow, as they require genetic inheritance at presumably low-to-moderate heritabilities (Berthold & Pulido, 1994; Dochtermann et al., 2019).

Individual differences in migratory behaviour could also arise if individual seasonal routines are a consequence of developmental processes in response to environmental and social contexts—that is, developmental plasticity (sensu Piersma & Drent, 2003). For example, in Icelandic black-tailed godwits *Limosa limosa islandica* and pied flycatchers *Ficedula hypoleuca*, individual differences can arise because of different environmental conditions encountered during the first few months of life (Both, 2010; Gill et al., 2014). Year-to-year environmental variations at hatch, including atmospheric and magnetic properties, can also cause individual differences in migratory routines (Scott et al., 2014; Wynn et al., 2020). Populations that adjust migratory behaviour by means of developmental plasticity are expected to do so faster than those that must rely on genetic change (Eichhorn et al., 2009). However, most species exhibit only a limited window of time during which plastic adjustments can be made, potentially limiting the amount of among-individual variation that can be generated via this process (Lok et al., 2011; Piersma, 2011; Senner, Conklin, et al., 2015).

A second category of environmentally informed plasticity that can generate individual differences in migratory behaviour is phenotypic flexibility (sensu Piersma & Drent, 2003). In such cases, variations arise during adulthood; they are by definition impermanent, and are frequently caused by short-term environmental perturbations (Piersma & van Gils, 2011). The latter can include severe weather events (Boelman et al., 2017), interannual climatic fluctuations (Studds & Marra, 2005) and anthropogenic-driven variation in experienced habitat quality (Madsen, 2001). As a result, flexible differences in migratory behaviour are unlikely to explain consistent differences among individuals or across populations (Senner, Conklin, et al., 2015) but can interact with both genetic and developmentally plastic differences among individuals to help give rise to the dramatic variation in migratory behaviour that exists within some populations (Beaman et al., 2016).

Given the variety of processes by which phenotypic variation in migratory behaviours can arise, we need observations of individual animals followed from birth to adulthood, coupled with experiments, to determine whether, how and when in life individuals adjust their behaviours to the environment, in order to establish the precise nature of the environmental factors involved (Piersma, 2011). Recent studies incorporating individually unique colour markings and miniature tracking technologies have begun to approach these goals. For instance, Sergio et al. (2014) tracked black kites *Milvus migrans* throughout their lives and found that they exhibit extended developmental periods lasting up to 7 years during which they appear to improve their migratory performance and, thereafter, still have flexibility in their ability to respond to environmental conditions as they are encountered. Nonetheless, while the weather conditions occurring during an individual's first southward migration have been shown to play a role (Vansteelant et al., 2017), what remains unclear is exactly when during ontogeny differences among individuals begin to arise, and to what degree environmental conditions and genetics might be responsible for these differences.

To address this gap, we simultaneously tracked juvenile *and* adult continental black-tailed godwits *Limosa limosa limosa* (hereafter 'godwits') from the Netherlands on their south- and northward migrations. Godwits breeding in the Netherlands represent a potentially informative study species, because their migratory timing and destination vary considerably and consistently among adult individuals (Verhoeven et al., 2019; Verhoeven, Loonstra, McBride, Both, et al., 2021). For example, some adults spend the nonbreeding period north of the Sahara, whereas others cross the Sahara to West Africa (Hooijmeijer et al., 2013; Kentie et al., 2017; Verhoeven, Loonstra, McBride, Both, et al., 2021). Some adults leave West Africa to fly northward again as early as September while others leave more than 5 months later (Senner et al., 2019; Verhoeven et al., 2019). Finally, young godwits appear to have been the force behind recent shifts in the population's migration route over the course of only a few years (Verhoeven et al., 2018). In combination, these observations indicate that the variation in godwit migratory behaviours may have arisen from either inherited routines or developmental plasticity. Because adult godwits are consistent through time in their migratory behaviour (Verhoeven et al., 2019; Verhoeven, Loonstra, McBride, Both, et al., 2021), however, we can already rule out phenotypic flexibility as a mechanism for the emergence of individual differences. Therefore, in this study, we focused on disentangling two potential mechanisms for the emergence of individual differences in migratory behaviour: heritable (epi-)genetic factors and developmental plasticity.

We first explored whether the migratory behaviour of juveniles is related to environmental conditions during the first months of life, which would provide evidence for developmental plasticity. For this, we examined whether differences in the migration routes, timing and mortality rates of juveniles were related to their hatch date and hatch year—two among many potential variables influencing an individual's early-life environment. If individual differences among godwits arise as a result of hatch date, we predict that later hatch dates result in later departure on southward migration and a lower propensity to cross the Sahara (Both, 2010; Gill et al., 2014, 2019). Furthermore, if individual differences among godwits arise as a result of hatch year, we predict differences in migratory behaviour between annual cohorts (Scott et al., 2014; Wynn et al., 2020).

Second, we compared the routes, timing and mortality rates of juveniles and adults from the same breeding areas during the same years, enabling us to assess whether individual differences among godwits may also have an inherited origin. Godwits breeding in the Netherlands have limited genetic variation (Trimbos et al., 2011) and limited dispersal distances (<20 km; Kentie et al., 2014), and are genetically distinct from the species' other European breeding populations (Trimbos et al., 2014). Thus, in combination with our extensive tracking work within the Dutch population (this study; Hooijmeijer et al., 2013; Senner et al., 2019; Senner, Verhoeven, et al., 2015; Verhoeven et al., 2019; Verhoeven, Loonstra, McBride, Both, et al., 2021), we predicted that if migratory routines are inherited, juveniles would exhibit largely similar migratory routines to those of adults and/or that those individuals exhibiting dissimilar

patterns would experience higher mortality rates and be selected out of the population before adulthood. Alternatively, if godwits exhibit a prolonged developmental window, we predicted that adults and juveniles would differ in their migratory routines, but that there would be no evidence of selection against these novel routines, and that the differences would be dissipated during ontogeny as juveniles arrive at individually consistent strategies that resemble those of adults.

In presenting the results, we start with a comparison of (a) the timing and (b) the geographic patterns of the southward migrations of juveniles and adults. This is followed by an analysis of whether the mortality patterns of the two age groups show evidence for natural selection on specific migratory behaviours. Taken together, our results have the potential to shed light on a persistent mystery not only in the study of migration, but in our understanding of the evolution of individual differences more generally.

2 | MATERIALS AND METHODS

2.1 | Satellite tracking data

In both 2016 and 2017, we deployed 40 solar-powered 5-g PTT-100s from Microwave Technology Inc. on juveniles, for a total deployment of 80 transmitters. All 80 transmitters were programmed to turn on for 8 hr and off for 24 hr. As a result of this duty cycle, we could only observe the timing of migration on a daily basis. We captured these juveniles by hand in the days just before they gained the ability to fly. Most juveniles were caught within our 12,000-ha study area in southwest Fryslân, the Netherlands (see Senner, Verhoeven, et al., 2015 for more details). However, in 2016, the number of fledged juveniles in our study area was considerably lower than average, so we also caught four juveniles on the island of Ameland (53.45°N, 5.83°E; see Loonstra, Verhoeven, Senner, et al., 2019). To attach the transmitters, we used a leg-loop harness of 2-mm Dyneema rope. We also took ~30 μl of blood from the brachial vein for molecular sexing.

We obtained migratory tracks from 28 of these juveniles (see Section 3): 24 from our study area and four from Ameland. Twenty-seven out of the 28 juveniles were molecularly sexed (12 males, 15 females); one analysis failed, so we sexed this bird based on its growth and morphological characteristics during five recaptures before fledging (Loonstra et al., 2018). Fifteen of the 28 juveniles were marked with a code flag in the nest and their exact hatch dates were therefore known. The other 13 tracked juveniles were not captured in the nest, so we estimated their hatch dates using a sex-specific growth curve (Loonstra et al., 2018). This method yields an estimated hatch date that is accurate to within ±3 days, which is acceptable for our purposes given the large variation in hatch dates included in the study (range 2 May–13 June). The weight of the transmitter and the harness (~6 g) represented 3.2% ± 0.4 (range: 2.5%–4.4%) of the total body mass at release, but this likely diminished to ~2% as the individuals continued to grow to adult size.

To track the spatial distribution and mortality of adult godwits, we deployed 32 solar-powered 9.5-g PTT-100s from Microwave Technology Inc. in 2015 and 2016 (attachment ~10.5 g), and another four transmitters of 5 g in 2017. Thirty-four of these 36 transmitters were programmed to turn on for 8 hr and turn off for 24 hr. One of the remaining two transmitters was programmed to turn on for 8 hr and off for 25 hr, and the other was programmed to turn on for 10 hr and off for 48 hr. We captured all 36 adults on nests in the 220-ha Haanmeer polder, which lies in the centre of our larger study area. We captured adults using walk-in traps, automated drop cages or mist nets placed over the nest. We attached the leg-loop harnesses as we did for the juveniles. Based on a combination of molecular sexing (using an ~30 μl blood sample taken from the brachial vein at capture, $n = 26$ individuals) and morphological characteristics (following Schroeder et al., 2008, $n = 10$ individuals), we determined that our sample of transmitter-carrying adults consisted of 34 females and two males. In 2015 and 2016, the loading factor of the transmitters was 3.4% ± 0.2 (range: 3.0%–4.0%) of a female's body mass at capture; in 2017, the loading factor was 1.9% for each of the two females and 2.2% for each of the two males (more details in Verhoeven, Loonstra, McBride, Both, et al., 2021).

We retrieved satellite-tracking locations via the CLS tracking system (www.argos-system.org) and passed them through the 'Best Hybrid-filter' algorithm (Douglas et al., 2012); this removed consecutive locations that exceeded a speed of 120 km/hr while retaining location classes with qualities of 3, 2, 1, 0, A and B. From these data, we knew where individual godwits crossed nine arbitrary spatial boundaries that were spaced 4° of latitude apart across the godwit migration corridor. These boundaries ranged from 52°N (the breeding grounds) to 20°N (just north of the southernmost African wintering grounds): 52˚N, 48˚N, 44˚N, 40˚N, 36˚N, 32˚N, 28˚N, 24˚N, 20˚N. This allowed us to estimate for both south- and northward migration (a) an individual's orientation, which we determined by calculating its longitudinal (i.e. east–west) movement, measured in kilometres, between the latitudinal boundaries; (b) the longitudinal distribution of tracks at each latitudinal boundary (see fig. 2 in Verhoeven, Loonstra, McBride, Both, et al., 2021); and (c) where and when mortality occurred (see paragraph below for details). We calculated distances between points with the function 'distHaversine' in the package GEOSPHERE (Hijmans, 2017).

2.2 | Geolocator data

To track the timing of adult migration, we used geolocators instead of satellite transmitters. We deployed 219 geolocators on 173 adult godwits from 2015 to 2018 in our study area. Geolocators were attached to a coloured flag that was placed on the adult's tibia. The total weight of the attachment was ~3.7 g, representing 1%–1.5% of an individual's body mass at capture. In subsequent years (2016–2019), we recaptured geolocator-carrying godwits to retrieve their geolocators and download the stored light-level data. We downloaded light-level data from 78 geolocators retrieved from 64 adult godwits (24 males,

40 females). Twenty geolocators contained data for more than one season, although the second season was often incompletely logged because the battery stopped working. Thus, we obtained light-level data for a total of 98 complete and incomplete migrations.

We used the package FLIGHTR (Rakhimberdiev et al., 2017) to reconstruct the annual schedules of godwits from these light-level data. Detailed examples of this analytical routine using our own godwit data can be found in Rakhimberdiev et al. (2016) and Rakhimberdiev et al. (2017). Briefly, using the FLIGHTR function 'find.times.distribution', we estimated when individual godwits crossed the same nine spatial boundaries mentioned above. In these analyses, we excluded the crossing of the spatial boundary at 36°N (the Strait of Gibraltar) because we could not distinguish between birds stopping in northern Morocco and those stopping in southern Spain (see Verhoeven et al., 2019 for more details).

The fieldwork for this study was conducted under license numbers 6350A, 6350G and AVD105002017823 granted by the national Dutch committee for animal experiments following the Dutch Animal Welfare Act Articles 9 and 11.

2.3 | Timing, routes and orientation of juveniles and adults

At each of the nine latitudinal boundaries, for both south- and northward migration, we used a general linear model with a Gaussian error distribution to examine the effects of hatching date, sex and year on the (a) timing of juvenile migration; (b) longitude of juvenile migration routes; and (c) longitudinal movement of migrating juveniles between consecutive latitudinal boundaries.

At each latitudinal boundary, for both south- and northward migration, we also compared the mean and variance of the (a) timing of crossing; (b) longitude of crossing; and (c) longitudinal movement between latitudinal boundaries of adults and juveniles tracked in the same years. Those years were 2016 and 2017 for southward migration and 2017–2019 for northward migration, because some individuals deferred northward migration (see Section 3). To test for the equality of variances between adults and juveniles, we used a Levene's test from the R-package CAR. If the variances were found to be equal, we used an ANOVA to test whether the mean was significantly different between adults and juveniles. If the variances were unequal, we compared the means with a Mann–Whitney U test. We did not account for an individual's sex in these analyses because we only tracked two adult males with satellite transmitters. However, we know from previous work that adult males and females do not differ in their migratory destinations (Hooijmeijer et al., 2013; Kentie et al., 2017; Senner et al., 2019; Verhoeven et al., 2019; Verhoeven, Loonstra, McBride, Both, et al., 2021), which is further supported by more recent satellite-tracking efforts (2019–2021) that include more males (T. Piersma, R. Howison, J. Hooijmeijer, A.H.J. Loonstra and M.A. Verhoeven unpubl. data). We have also previously shown that the only difference in the migratory timing of adult males and females is that males leave the Netherlands on average 5 days earlier.

The only likely consequence of a dataset with more males would therefore be an even bigger difference between adults and juveniles in their departure timing from the Netherlands than already observed (see Section 3). We therefore believe that our claims are robust and representative of godwit behaviour in general.

We used a generalized linear model with a binomial error structure and a logistic link function to test whether the likelihood that juveniles (a) crossed the Sahara on their first southward migration and (b) did so by flying non-stop from the Netherlands was related to their departure date, year or sex. We note that the dataset for the second analysis is a subset of the first dataset that includes only those individuals that crossed the Sahara. We also used a generalized linear model with a binomial error structure and a logistic link function to explore whether the adults and juveniles tracked in the same years on southward migration differed in the proportion of individuals that (a) crossed the Sahara and (b) did so with a non-stop flight from the Netherlands.

2.4 | Mortality

Where and when mortality occurred was assessed on the basis of data collected from our satellite transmitters. The adults outfitted with a 9.5-g transmitter were considered dead when their transmitter's built-in activity sensor remained constant. The 5-g transmitters that four adults and all juveniles carried did not have such an activity sensor but did have a temperature sensor; we considered these birds dead when the measured temperature started to follow a day–night rhythm. These assumptions are also supported by the fact that we have never subsequently observed any of these adults to be alive during our extensive resighting efforts of marked birds (Loonstra, Verhoeven, Senner, et al., 2019; Verhoeven et al., 2018).

For these known-fate data, we used generalized linear models with a binomial error structure and a logistic link function to test whether (a) the likelihood that juveniles died on their first southward migration was related to their departure date, sex or the year the juvenile hatched; and (b) the likelihood that juveniles died between departure from and return to the Netherlands was related to their hatch date, sex or the year they hatched. We also made two figures to illustrate where (Figure 3) and when (Figure 4) mortality occurred during juvenile migration. We used the same type of generalized linear models to explore whether the adults and juveniles tracked in the same years differed in the proportion of individuals that died during south- and northward migration.

3 | RESULTS

3.1 | Timing of juveniles and adults

3.1.1 | Southward migration

We obtained migratory tracks from only 28 juveniles, because most tagged juveniles died after being tagged and before migrating

southward—a period known to have high juvenile mortality (see Loonstra, Verhoeven, Senner, et al., 2019). All 28 juveniles started their initial southward migration at approximately the same age (88 ± 11 days). Thus, their departure date was positively correlated with their hatch date (Figure 2; Table S1). Furthermore, all juveniles departed the Netherlands later than did tracked adults (Figure 2; Table S2). After crossing 40°N, juveniles first encountered tracked adults from our study population with whom they could potentially spend the nonbreeding season or migrate alongside to West Africa; this is because some adults stopped for prolonged periods at sites around the Mediterranean, and either stayed there for the nonbreeding season or eventually continued on to cross the Sahara (Figure 1). Of the juveniles, four spent the nonbreeding season around the Mediterranean, and 19 migrated to the nonbreeding grounds in West Africa. However, of the 19 juveniles that migrated to the nonbreeding grounds in West Africa, 12 flew non-stop from the Netherlands (63%), while of the 28 adults that migrated to West Africa, only two flew non-stop (11%, statistics in Table 1). Furthermore, five of the seven juveniles that did stop on the Iberian Peninsula en route to West Africa stayed for only 1 or 2 days and departed before the tracked adults that stopped there for a prolonged time (Figure 1). Because juveniles flew non-stop more and made shorter stops, the timing of the southward Sahara crossing was less variable within juveniles than adults (Table S2). Whether juveniles flew non-stop to West Africa from the Netherlands did not depend on their departure date from the Netherlands ($\beta_{\text{departure date}} = 0.03 \pm 0.05$, $\chi^2 = 0.32$, $df = 1$, $p = 0.574$, Table 2). Anecdotal observations of two juveniles which hatched 1 day apart and which both departed the Netherlands on 6 August 2016 show that one stopped and one did not stop en route to West Africa (Figure 4).

3.1.2 | Northward migration

By the time the northward migration period begins in godwits, juveniles are considered immatures—morphologically adults but sexually immature. In total, we tracked 15 juveniles as immatures between 2017 and 2019. Twelve immatures spent their entire second calendar year in West Africa or the Mediterranean before migrating north for the first time in their third calendar year. Two immatures migrated north in their second calendar year, and a single immature waited until its fourth calendar year. The earliest departure of an immature from West Africa across years was on 13 January 2019; each year at least two-thirds of adults had already left by this date (Figure 2). In the same vein, 25% of the immatures departed West Africa later than any of the adults tracked during 2016–2019. As a result, the northward migration of immatures was significantly later than that of adults (Figure 2; Table S2).

In contrast with southward migration, an immature's departure from West Africa was not related to its hatch date (Table S3). The immature birds that departed earliest for northward migration had the opportunity to continue to the Netherlands with adults from the
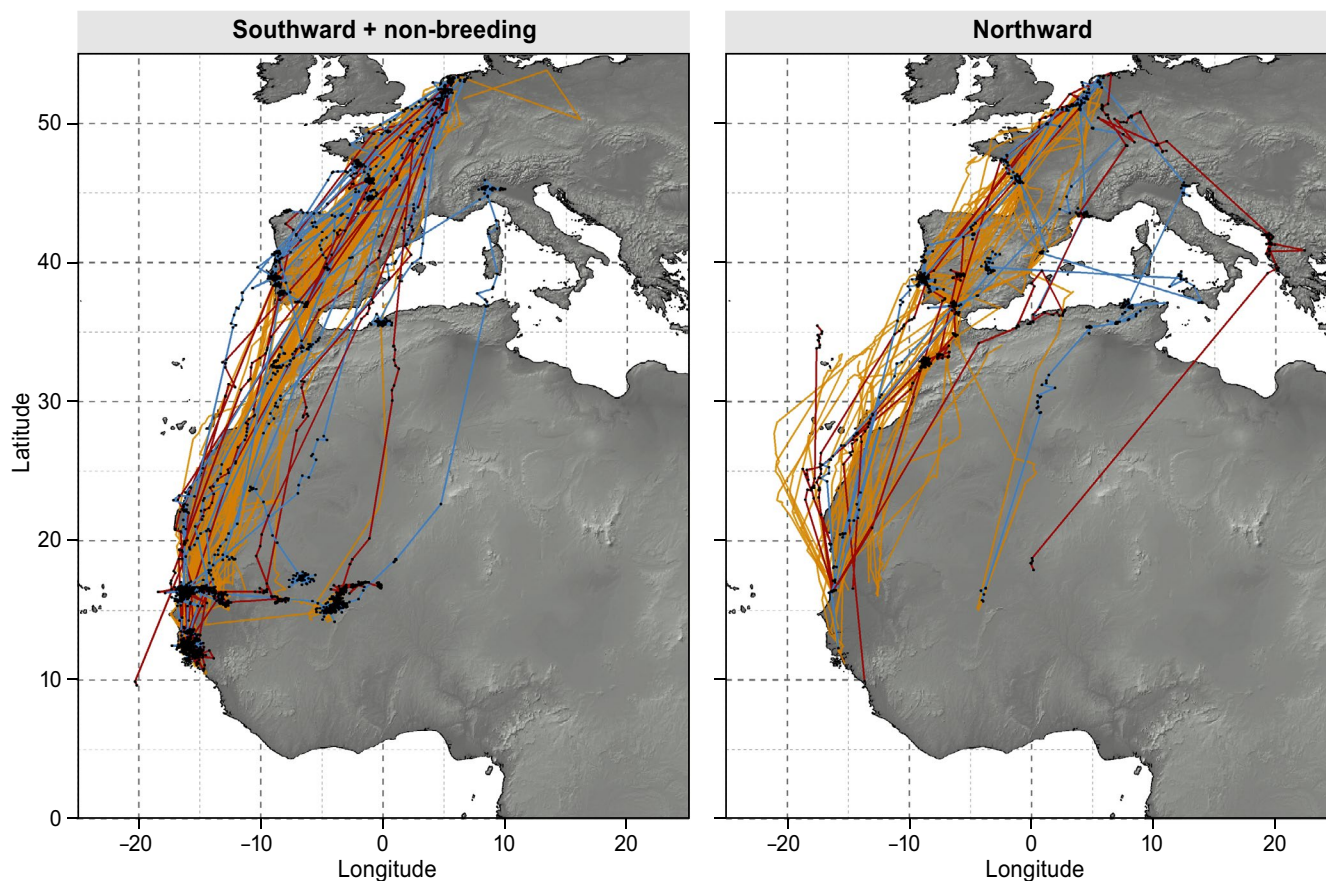
FIGURE 1 Migratory tracks of all adults from 2015 to 2019 (gold), juveniles hatched in 2016 (red) and juveniles hatched in 2017 (light blue)

TABLE 1 Results from generalized linear models with binomial error structure and logistic link function that examine whether juveniles and adults tracked in the same years differed in their proportion of individuals that (1) crossed the Sahara; (2) flew non-stop to West Africa from the Netherlands; (3) died on southward migration (2016 and 2017); and (4) died on northward migration (2017, 2018 and 2019)

Dependent variable	Fixed effects	$\beta \pm SE$	χ^2	p
(1) Crossing of the Sahara	Intercept	-1.50 ± 0.32		
(n = 23 juveniles, 66 adults)	Age[a]	-0.05 ± 0.64	0.01	0.932
(2) Non-stop to West Africa from the Netherlands	Intercept	-2.64 ± 0.73		
(n = 19 juvenile tracks, 28 adult tracks)	Age[a]	2.18 ± 0.82	9.64	**0.002**
(3) Mortality during southward migration	Intercept	-2.77 ± 0.73		
(n = 28 juvenile tracks, 32 adult tracks)	Age[a]	1.39 ± 0.84	4.27	**0.039**
(4) Mortality during northward migration	Intercept	-0.98 ± 0.39		
(n = 15 juvenile tracks, 33 adult tracks)	Age[a]	-0.41 ± 0.75	0.30	0.584

[a]Reference level for age is adult.

Statistically significant effects ($p < 0.05$) shown in bold.

same breeding population. However, all but one of the immatures left the Mediterranean later than any adult (Figure 2). Consequently, the arrival of immatures to the Netherlands was on average 36 days later than that of adults (Table S2), with some immatures arriving as late as 7, 14 and 15 May. At that point in the breeding season, all adults have already laid their first clutch (latest first clutch initiation date: 1 May, Verhoeven et al., 2020). Similar to the departure from West Africa, the departure from stopping sites and the subsequent arrival at the breeding grounds were not associated with an immature's hatch date (Figure 2).

3.2 | Routes and orientation of juveniles and adults

During southward migration, juveniles that migrated later tended to orient more towards the south and less towards the southwest after crossing the Mediterranean (from 36°N to 32°N, Table S7). This gradual shift in juvenile routes might also explain why their variance in longitudinal movement across this latitudinal segment was different from the variance observed in adults (Table S9). The average longitude of juveniles upon arrival to the nonbreeding grounds (12.03°W at 20°N) was further to the east than that of adults

Dependent variable	Fixed effects	$\beta \pm SE$	χ^2	p
(1) Crossing of the Sahara	Intercept	9.22 ± 13.26		
(n = 23 juveniles)	Date of 52˚N crossing	-0.03 ± 0.05	0.38	0.537
	Sex[a]	0.97 ± 1.30	0.60	0.437
	Hatch year[a]	-1.04 ± 1.28	0.73	0.393
(2) Non-stop to West Africa from the	Intercept	-5.72 ± 11.28		
Netherlands	Date of 52˚N crossing	0.03 ± 0.05	0.32	0.574
(n = 19 juveniles)	Sex[a]	1.94 ± 1.23	2.95	0.086
	Hatch year[a]	-1.37 ± 1.13	1.64	0.200
(3) Mortality during southward migration	Intercept	2.65 ± 8.74		
(n = 28 juveniles)	Date of 52˚N crossing	-0.02 ± 0.04	0.16	0.690
	Sex[a]	-0.89 ± 1.02	0.10	0.753
	Hatch year[a]	1.45 ± 1.18	1.08	0.298
(4) Mortality between departure from	Intercept	5.99 ± 6.78		
and return to the Netherlands	Hatching date	-0.04 ± 0.05	0.91	0.340
(n = 28 juveniles)	Sex[a]	-0.21 ± 0.80	0.07	0.797
	Hatch year[a]	0.41 ± 0.93	0.20	0.657

[a]Reference level for sex is female.

[b]Reference level for year is 2016.

TABLE 2 Results from generalized linear models with binomial error structure and logistic link function that examined whether (1) crossing the Sahara or not; (2) flying non-stop to West Africa from the Netherlands or not; or (3) dying during southward migration or not were related to when juveniles departed (date of 52°N crossing), their sex or the year they hatched. Similarly, we examined (4) whether a juvenile godwit dying between departure from and return to the Netherlands was related to its hatching date, sex or hatch year
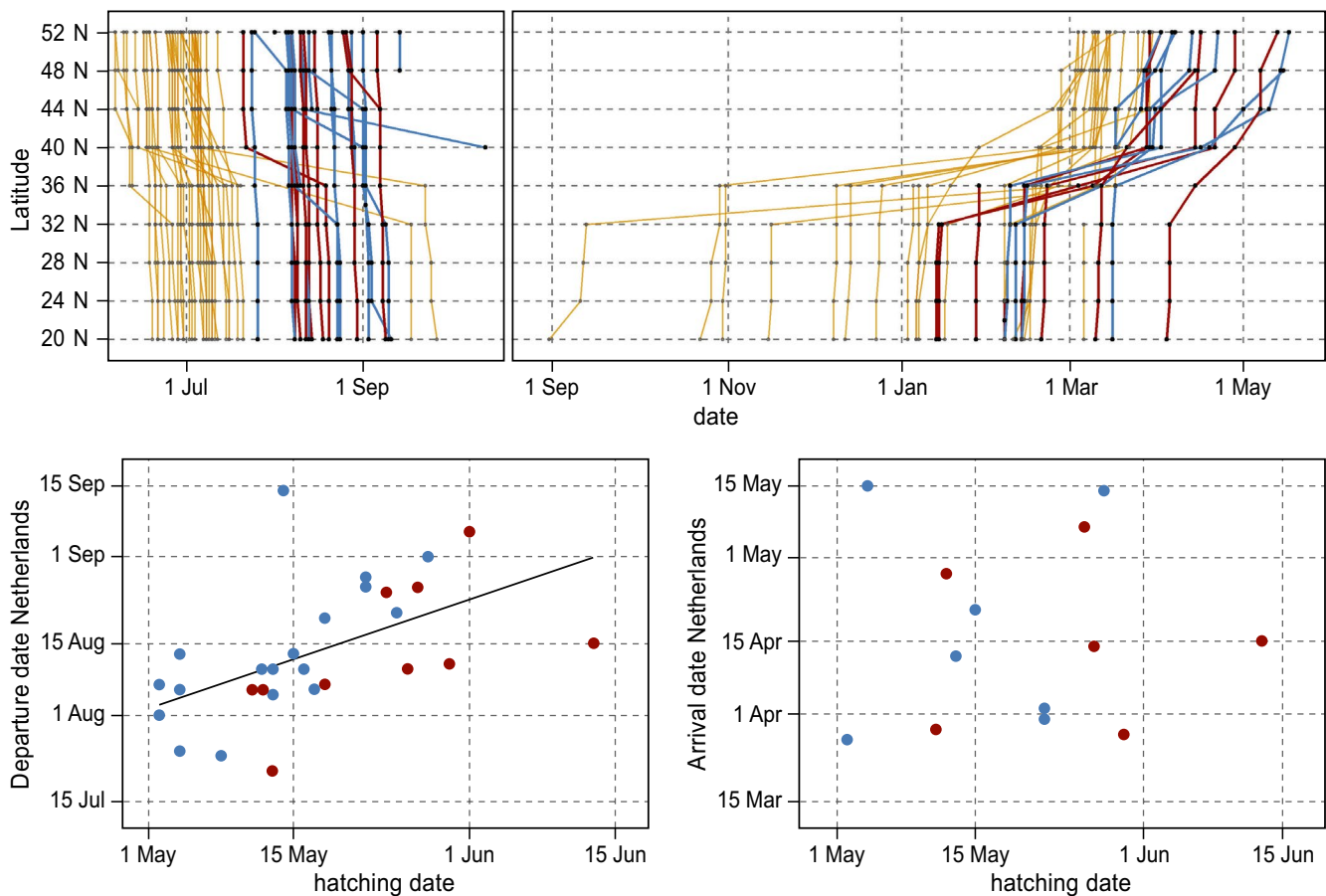

FIGURE 2 Top: Migratory timing of adults tracked with geolocators from 2015 to 2019 (gold), and of juveniles hatched in 2016 (red) and in 2017 (light blue). Bottom: Correlation between hatch date of juveniles and their departure and arrival to the Netherlands (colours same as above). Regression lines are shown for statistically significant correlations only
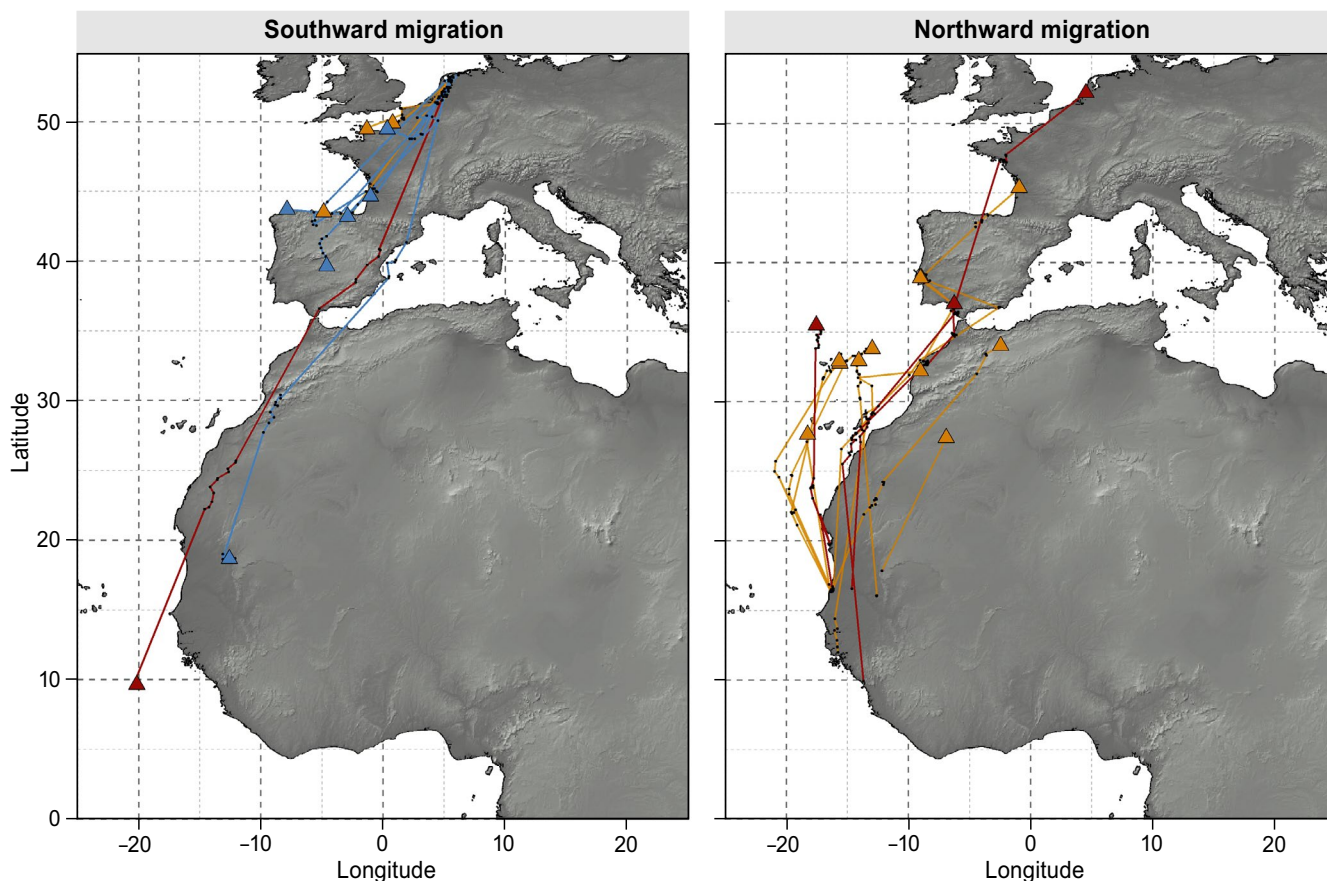
FIGURE 3 Mortality on migration for adults tracked with satellite transmitters from 2015 to 2019 (gold), and for juveniles hatched in 2016 (red) and 2017 (light blue)

(13.61°W), though not significantly so (Table S6). During north-ward migration, juveniles that migrated later tended to fly more towards the north and less towards the northeast after departing the nonbreeding grounds (from 20°N to 24°N, Table S8). However, we otherwise found no clear relationships between the route and orientation of juveniles and their date of migration, sex or the year of migration during either south- or northward migration (Tables S4, S5, S7 and S8).

On average, juveniles and adults took similar routes during southward migration (Figure 2; Table S6). However, one juvenile flew south via northern Italy, a stopping site well to the east of the migratory corridor of adults (Figure 1). The southward routes of juveniles were on the whole also more variable than those of adults (Table S6), although the proportion of juveniles that crossed the Sahara towards West Africa (19/23, 83%) was the same as in adults (54/66, 82%, $p = 0.932$, Table 1). During north-ward migration immatures again used similar routes to adults, but some made stops well outside of the adult migratory corridor, such as at sites in Libya, Sicily, northern Italy and even as far east as the coast of Albania, which is more than 1,000 km outside of the adult corridor (Figure 1; Table S6). As a result, the northward routes of immatures, like their southward routes, were more vari-able than those of adults, especially north of the Sahara (Figure 1; Table S6).

3.3 | Mortality rates of juveniles and adults

3.3.1 | Southward migration

During southward migration in 2016, one juvenile and one adult died. Notably, the juvenile perished in the Atlantic after overshooting the godwit nonbreeding area in West Africa (Figure 3). During south-ward migration in 2017, six juveniles and one adult died (Figure 3). Mortality of juveniles during southward migration was not related to their date of departure, sex or the year in which they hatched (Table 2). For example, we observed two juveniles of similar ages departing on the same day, of which one died and the other survived (Figure 4). Most juveniles (5/7) that died during southward migration did so during their very first flight from the Netherlands; one died at its first stopping site, and the other died during the second leg of its southward migration. The mortality of juveniles during southward migration was higher than that of adults (25% vs. 6%, $p = 0.039$, Table 1).

3.3.2 | Northward migration

Eight juveniles died while at their nonbreeding sites: one died north of the Sahara, on 15 November 2016 in the Bay of Biscay,
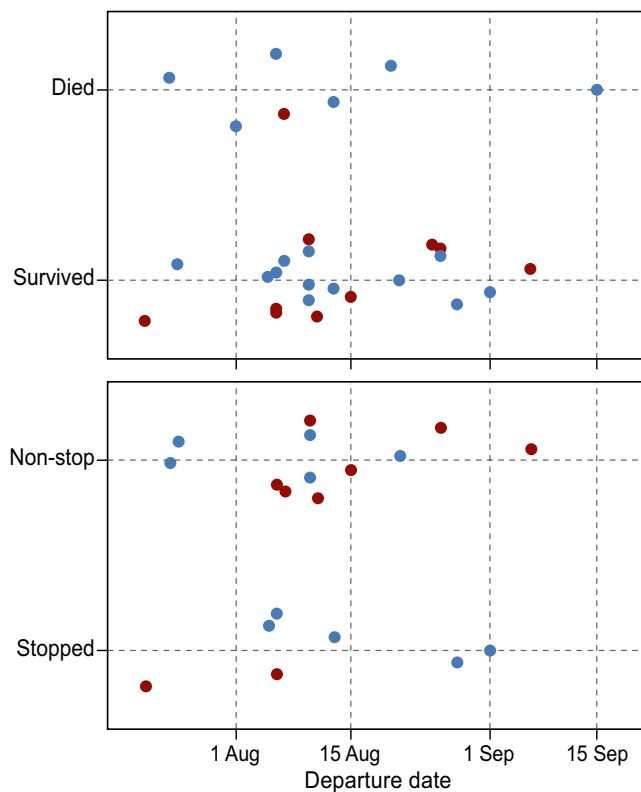
FIGURE 4 Survival (died or survived) and continuity of the flight (non-stop or stopped) of juveniles hatched in 2016 (red) and in 2017 (light blue) on southward migration in relation to their timing of departure from the Netherlands (crossing 52°N). Top panel includes all tracked juveniles (*n* = 28). Bottom panel includes all tracked juveniles that flew to West Africa (*n* = 19); two of these individuals died in or south of the Sahara (see Figure 3). Points are vertically offset in order to show multiple departures that took place on the same day and had the same survival or duration

France, whereas the other seven died at nonbreeding sites south of the Sahara. During northward migration, another three immatures died; all of them hatched in 2016. One of these flew north from the coast of Senegal and perished in the Atlantic Ocean, 290 km north of Madeira, Portugal (Figure 3). Another stopped for 26 days at a lagoon near Cádiz, Spain, then died immediately upon arrival at Doñana, Spain (Figure 3). The third died immediately upon arrival near Leiden, the Netherlands (Figure 3). The mortality of juveniles on northward migration was slightly lower than that of adults, but not significantly so (20% vs. 27%, *p* = 0.584, Table 1). Furthermore, the mortality of juveniles outside the Netherlands—that is, between departure from the Netherlands and subsequent return 1–3 years later—was not related to their hatch date, sex or hatch year (Table 2).

4 | DISCUSSION

We simultaneously tracked juvenile and adult godwits to elucidate how and when individual differences in migration patterns arise. Specifically, we aimed to disentangle whether individual differences

in the migratory patterns of adults are a result of inherited differences or experienced differences in environmental conditions, and thus result from developmental plasticity. Juveniles and adults appeared to be rather dissimilar, suggesting that differences among individuals in migratory patterns did not reflect (epi-)genetically inherited factors. One environmental factor did influence migratory behaviour: the departure timing of juveniles on southward migration correlated with their hatch date. However, we detected no other effects of hatch date, departure timing, year of migration or sex on their route, orientation, nonbreeding destination (north or south of the Sahara), migratory duration or mortality, during either their first southward or their first northward migration. Thus, the consistent individual differences among adult godwits are not the result of a plastic response to seasonally changing conditions during their first months of development. Indeed, the considerable differences between the migration patterns of adults and juveniles, especially in the case of timing, demonstrate that godwits have the plasticity to develop their migration patterns later in life. Continuing to track the migrations of these individuals in the future will hopefully indicate more fully when this development is completed.

4.1 | Individual differences and developmental plasticity

Our results demonstrate that juveniles differ from each other in whether they cross the Sahara and how they migrate south and north. One possibility is that these individual differences have a genetic or at least a heritable origin (e.g. Pulido et al., 2001). Confirming such a possibility requires simultaneously tracking juveniles and their parents. Unfortunately, we have succeeded in tracking only one mother–daughter pair thus far. On southward migration, both mother and daughter flew to West Africa, but their migratory timing was considerably different. After arriving in West Africa, and on northward migration, their migration again differed considerably (Figure S1). The tiny sample size makes these observations anecdotal. However, we have also performed a large-scale translocation and delay experiment with hand-raised siblings, which showed that siblings frequently migrate differently from each other, with some individuals crossing the Sahara on southward migration when their sibling did not (Loonstra et al., in review). In addition, we have previously shown that the use of stopover sites in Spain and Portugal is unlikely to be heritable (Verhoeven et al., 2018). We therefore currently have no reason to assume that the observed differences among juveniles are inherited.

Our study also clearly demonstrates that juveniles and adults have different migration patterns. This is most obvious in terms of timing and route choice, as some juveniles visited sites we have never observed being used in the migrations of more than 200 adults tracked across more than 10 years (Hooijmeijer et al., 2013, Senner, Verhoeven, et al., 2015; Senner et al., 2019, Verhoeven et al., 2019; Verhoeven, Loonstra, McBride, Both, et al., 2021, this study). There are three possible explanations for this large

discrepancy between adults and juveniles. The first is that we have observed novel behaviour on the part of a cohort of individuals and these individuals will continue to follow their juvenile routine, thus yielding a new adult migration pattern if these individuals continue to survive. The second is that we observed normal juvenile godwit behaviour, and that those juveniles with markedly different migrations from adults will either die or never breed. The third is that we observed normal juvenile godwit behaviour, but godwits change their migration later in life rather than continuing the movement patterns exhibited in their first year of life. Under both of the latter two scenarios, the current adult pattern would persist. Although recent results from other species (e.g. Meyburg et al., 2017) are in line with the second option—selective death of dissimilar juveniles—we believe that the most likely scenario in godwits is the third option.

We propose that juvenile godwits change their migratory patterns later in life on the following grounds: (a) The timing of godwit breeding has not changed by more than a week in either direction in the past 15 years (Schroeder et al., 2012; Verhoeven et al., 2020). This means that in the past 15 years, the earliest juveniles—those hatched in the first week of May—could, at the earliest, have left the Netherlands by the end of June. In addition, we now know that juveniles hatched in the Netherlands return to the Netherlands and that their average life span is ~6 years (Loonstra, Verhoeven, Senner, et al., 2019). Yet, we have observed adults leaving the Netherlands as early as the end of May and beginning of June (Figure 2). It necessarily follows that in these cases, these adults left earlier than they did on their first southward migration as juveniles. Moreover, (b) ringing recoveries of juveniles banded in the Netherlands over the past 70 years indicate that the later migration and different routes of juveniles compared to adults during northward migration are not a new phenomenon (Beintema & Drost, 1986; Haverschmidt, 1963). More importantly, our results show that the juveniles that migrate later and use different routes than adults are not more likely to die. Thus, if these age-dependent routes and timing are consistent with 70 years of ringing data, and not all juveniles with these different migration patterns die, it is likely that these juvenile godwits change their migration following their first migrations. We therefore expect godwits to make considerable changes to their migration later in life, though only the lifelong tracking of these same individuals will establish this for certain. Because the timing of juvenile godwits is expected to change later in life, lifelong tracking might also give us still more insight into why we observe large differences among adults (Verhoeven et al., 2019; Verhoeven, Loonstra, McBride, Both, et al., 2021).

4.2 | Environmental effects on juvenile migration

If inherited routines do not explain differences among juveniles or between juveniles and adults, what factors do have an influence? Because juveniles migrated significantly later than adults, the fact that they also flew non-stop from the Netherlands to West Africa more frequently and had higher mortality rates during their first southward migration could be related to seasonal changes in the environment. For example, wind conditions might become more favourable later in the season or the availability of food and social information might decrease over time (e.g. Kölzsch et al., 2016). Within juveniles, however, we found no evidence for any seasonal patterns in their route, mortality rate or behaviour. Note that in two cases, we observed different migratory behaviours among pairs of juveniles that departed from the breeding areas on the same day. In one pair of juveniles, one individual migrated non-stop to West Africa while the other did not; in another pair, one survived southward migration while the other died before reaching its nonbreeding site. We realize that these anecdotal observations are not conclusive evidence that there are no seasonal patterns. However, we also observed that among both the earliest and latest juveniles that crossed the Sahara, individuals both survived and died (Figure 4). We conclude from these combined observations that the destination, migratory duration and mortality rate of juveniles are not simply a plastic response to seasonal changes in the physical environment. This further suggests that the differences in destination, duration and mortality rate between adults and juveniles are not a simple matter of timing-related changes in the environment.

4.3 | Mortality

Most juveniles that died during migration did so during their first migratory flight from the breeding grounds and at higher rates than adults. Similarly, on northward migration, most mortality occurred during the first northward flight or immediately after a juvenile arrived at a location which was new to that individual. Both the higher mortality of juveniles compared to adults and the specific moments at which juveniles died suggest that performing novel migratory actions is risky. Therefore, making use of experience by repeating what worked previously might be beneficial and lead to higher fitness through either higher survival, higher breeding success or both. The high degree of breeding and nonbreeding site fidelity of animals is thought to exist for this reason, and the benefits of fidelity might thus also explain why individuals adopt individually specific migratory routines (Cresswell, 2014, Winger et al., 2019, but see Lok et al., 2013). Support for this notion comes from tracking studies that have followed the same individuals for multiple years, with most showing that individuals are consistent in their spatiotemporal distribution across the annual cycle (Conklin et al., 2013; Pedersen et al., 2018; Vardanis et al., 2011; Verhoeven et al., 2019; Verhoeven, Loonstra, McBride, Both, et al., 2021). However, there are also migratory species with extended developmental periods during which they improve their migratory routines (Campioni et al., 2020; Mueller et al., 2013; Sergio et al., 2014) and even develop new routines (Teitelbaum et al., 2016; Tombre et al., 2019). This suggests either that it is not always beneficial to adhere to an individual's initial routine or that certain species have the capacity to change later in life while others do not.

4.4 | Species-specific differences in developmental plasticity

If godwits do change their migration pattern after their first year of life, as we expect, they are similar to other migratory species that have extended developmental periods (Mueller et al., 2013; Sergio et al., 2014; Teitelbaum et al., 2016; Tombre et al., 2019). In contrast to these species, the developmental period in species with a strong 'innate' control of their migratory routine is thought to be negligible (Berthold et al., 1992; Gwinner, 1996; Pulido et al., 2001). Thus, there appears to be a gradient in the amount of developmental plasticity that different species exhibit during their lives with respect to their migratory routines. But what could cause such differences among species?

First, we find it intriguing that the species with extended developmental periods—black kites *Milvus migrans*, whooping cranes *Grus americana* and barnacle geese *Branta leucopsis*—are all long-lived (Sergio et al., 2014; Teitelbaum et al., 2016; Tombre et al., 2019). Short-lived passerines are often hypothesized to be less plastic in developing routines throughout life (Cresswell, 2014, Pedersen et al., 2018; and see Karagicheva et al., 2018). This suggests that the general life history of a species, like a species' longevity, might play an important role in whether or not different levels of developmental plasticity are adaptive. Over evolutionary time-scales, different species might therefore have evolved different levels of developmental plasticity depending on what is most adaptive in their particular circumstance (Botero et al., 2015; Karagicheva et al., 2018). These differences might then have become genetically assimilated, leading to species-specific responses to environmental contexts (i.e. reaction norms) and setting *organismal* limits on the amount of plasticity they can exhibit (Pigliucci et al., 2006). Experiments with hand-raised siblings of different species, for instance, have clearly shown that such species-specific reaction norms exist under laboratory conditions (Berthold, 1996; Gwinner, 1996).

However, the observed levels of species-specific developmental plasticity must also be *conditional* on the environment. For example, populations of the same species exhibit different degrees of variability in their migrations (Flack et al., 2016; Loonstra, Verhoeven, Zbyryt, et al., 2019). Similarly, individuals from the same population can vary considerably (Gill et al., 2019; Verhoeven et al., 2019), especially in populations that are partially migratory (Chapman et al., 2011). For example, hand-raised godwit siblings can be induced to show different migratory strategies depending on the context in which they are released (Loonstra et al., in review). Even a single individual can be resident or migratory at different stages of its life (Hegemann et al., 2015). Thus, the apparent gradient in developmental plasticity between species, populations and individuals could be the result of both *organismal* and *conditional* differences.

In order to understand how much, how fast and when animals can adjust their migrations, we need to identify to what extent the differences between species, populations or individuals are currently *organismal* or *conditional*. Since seasonal migration is a 'syndrome'

(i.e. an amalgamation of many different traits, Piersma et al., 2005), such an analysis will be daunting and need to encompass: (a) determining more comprehensively which component traits contribute to an individual's observed migratory routine (e.g. photoperiodic control of pre-migratory fattening, physiological control of fattening rates, absolute potential fuel loads, etc.); (b) experimentally revealing the organismal limits of these component traits, that is, their full reaction norms; (c) employing transcriptomic and genomic approaches to understand the genetic basis that may underlie these component traits, to try to disentangle the extent to which plasticity is organismal or conditional (Horton et al., 2019); and (d) developing an ecological understanding of how trade-offs among these component traits may limit the potential for plastic responses to changes within the environmental range covered by individual reaction norms. Studies of bird migration thus have the potential to illuminate the most fundamental questions about the generation of phenotypic variation and also help us understand the organismal limits to contemporary global change (Gienapp et al., 2014).

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS
M.A.V., A.H.J.L. and T.P. conceived the idea; M.A.V., A.H.J.L., A.D.M., W.K., N.R.S., J.C.E.W. and T.P. collected the data; M.A.V. and A.H.J.L. analysed the data; M.A.V. and A.D.M. wrote an initial version of the manuscript, which was then critically edited and revised by all authors.

ORCID

Mo A. Verhoeven https://orcid.org/0000-0002-2541-9786

A. H. Jelle Loonstra https://orcid.org/0000-0002-5694-7581

Christiaan Both https://orcid.org/0000-0001-7099-9831

Nathan R. Senner https://orcid.org/0000-0003-2236-2697

Theunis Piersma https://orcid.org/0000-0001-9668-466X

REFERENCES

Battley, P. F., Conklin, J. R., Parody-Merino, A. M., Langlands, P. A., Southey, I., Burns, T., Melville, D. S., Schuckard, R., Riegen, A. C., & Potter, M. A. (2020). Interacting roles of breeding geography and early-life settlement in godwit migration timing. *Frontiers in Ecology and Evolution*, 8, 52.

Beaman, J. E., White, C. R., & Seebacher, F. (2016). Evolution of plasticity: Mechanistic link between development and reversible acclimation. *Trends in Ecology & Evolution*, 31, 237–249.

Beintema, A. J., & Drost, N. (1986). The migration of the black-tailed godwit. *Gerfaut*, 76, 37–62.

Berthold, P. (1996). *Control of bird migration*. Chapman and Hall.

Berthold, P., Helbig, A. J., Mohr, G., & Querner, U. (1992). Rapid micro-evolution of migratory behaviour in a wild bird species. *Nature*, 360, 668–670.

Berthold, P., & Pulido, F. (1994). Heritability of migratory in a natural bird population. *Proceedings of the Royal Society B: Biological Sciences*, 257, 311–315.

Boelman, N. T., Krause, J. S., Sweet, S. K., Chmura, H. E., Perez, J. H., Gough, L., & Wingfield, J. C. (2017). Extreme spring conditions in the Arctic delay spring phenology of long-distance migratory songbirds. *Oecologia*, 185, 1–12.

Botero, C. A., Weissing, F. J., Wright, J., & Rubenstein, D. R. (2015). Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 184–189.

Both, C. (2010). Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Current Biology*, 20, 243–248.

Campioni, L., Dias, M. P., Granadeiro, J. P., & Catry, P. (2020). An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: Timings and destinations change progressively during maturation. *Journal of Animal Ecology*, 89, 29–43.

Chapman, B. B., Bronmark, C., Nilsson, J., & Hansson, L. (2011). The ecology and evolution of partial migration. *Oikos*, 120, 1764–1775.

Conklin, J. R., Battley, P. F., & Potter, M. A. (2013). Absolute consistency: Individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS One*, 8, e54535.

Cresswell, W. (2014). Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: The serial residency hypothesis. *Ibis*, 156, 493–510.

Delmore, K. E., Toews, D. P. L., Germain, R. R., Owens, G. L., & Irwin, D. E. (2016). The genetics of seasonal migration and plumage color. *Current Biology*, 26, 2167–2173.

Delmore, K. E., Van Doren, B. M., Conway, G. J., Curk, T., Garrido-Garduño, T., Germain, R. R., Hasselmann, T., Dieter, H. D., van der Jeugd, H. P., Justen, H., Ramos, J. S. L., Maggini, I., Meyer, B. S., Phillips, R. J., Remisiewicz, M., Roberts, G. C. M., Sheldon, B. C., Vogl, W., & Liedvogel, M. (2020). Individual variability and versatility

in an eco-evolutionary model of avian migration. *Proceedings of the Royal Society B: Biological Sciences*, 287(1938), 20201339.

Dochtermann, N. A., Schwab, T., Anderson, B. M., Dalos, J., & Royauté, R. (2019). The heritability of behavior: A meta-analysis. *Journal of Heredity*, 110, 403–410.

Douglas, D. C., Weinzierl, R., Davidson, S. C., Kays, R., Wikelski, M., & Bohrer, G. (2012). Moderating Argos location errors in animal tracking data. *Methods in Ecology and Evolution*, 3, 999–1007.

Eichhorn, G., Drent, R. H., Stahl, J., Leito, A., & Alerstam, T. (2009). Skipping the Baltic: The emergence of a dichotomy of alternative spring migration strategies in Russian Barnacle Geese. *Journal of Animal Ecology*, 78, 63–72.

Flack, A., Fiedler, W., Blas, J., Pokrovsky, I., Kaatz, M., Mitropolsky, M., Aghababyan, K., Fakriadis, I., Makrigianni, E., Jerzak, L., Azafzaf, H., Feltrup-Azafzaf, C., Rotics, S., Mokotjomela, T. M., Nathan, R., & Wikelski, M. (2016). Costs of migratory decisions: A comparison across eight white stork populations. *Science Advances*, 2, 1.

Gienapp, P., Reed, T. E., & Visser, M. E. (2014). Why climate change will invariably alter selection pressures on phenology. *Proceedings of the Royal Society B: Biological Sciences*, 281, 1793.

Gill, J. A., Alves, J. A., & Gunnarsson, T. G. (2019). Mechanisms driving phenological and range change in migratory species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374, 20180047.

Gill, J. A., Alves, J. A., Sutherland, W. J., Appleton, G. F., Potts, P. M., & Gunnarsson, T. G. (2014). Why is timing of bird migration advancing when individuals are not? *Proceedings of the Royal Society B: Biological Sciences*, 281, 20132161.

Gwinner, E. (1996). Circadian and circannual programmes in avian migration. *Journal of Experimental Biology*, 199, 39–48.

Haverschmidt, F. (1963). *The Black-tailed Godwit*. E. J. Brill.

Hegemann, A., Marra, P. M., & Tieleman, B. I. (2015). Causes and consequences of partial migration in a passerine bird. *The American Naturalist*, 186, 531–546.

Hijmans, R. J. (2017). *geosphere: Spherical Trigonometry*. R package version 1.5-7. https://CRAN.R-project.org/package=geosphere

Hooijmeijer, J. C. E. W., Senner, N. R., Tibbitts, T. L., Gill Jr., R. E., Douglas, D. C., Wymenga, L. W., Bruinzeel, E., & Piersma, T. (2013). Post-breeding migration of Dutch-breeding black-tailed godwits: Timing, routes, use of stopovers, and nonbreeding distributions. *Ardea*, 101, 141–152.

Horton, W. J., Jensen, M., Sebastion, A., Prail, C. A., Albert, I., & Bartell, P. A. (2019). Transcriptome analyses of heart and liver reveal novel pathways for regulating songbird migration. *Scientific Reports*, 9, 6058.

Karagicheva, J., Rakhimberdiev, E., Saveliev, A., & Piersma, T. (2018). Annual chronotypes functionally link life histories and life cycles in birds. *Functional Ecology*, 32, 2369–2379.

Kentie, R., Both, C., Hooijmeijer, J. C. E. W., & Piersma, T. (2014). Age-dependent dispersal and habitat choice in black-tailed godwits *Limosa limosa limosa* across a mosaic of traditional and modern grassland habitats. *Journal of Avian Biology*, 45, 396–405.

Kentie, R., Marquez-Ferrando, R., Figuerola, J., Gangoso, L., Hooijmeijer, J. C. E. W., Loonstra, A. H. J., Robin, F., Sarasa, M., Senner, N., Valkema, H., Verhoeven, M. A., & Piersma, T. (2017). Does wintering north or south of the Sahara correlate with timing and breeding performance in black-tailed godwits? *Ecology and Evolution*, 7, 2812–2820.

Kölzsch, A., Müskens, G. J. D. M., Kruckenberg, H., Glazov, P., Weinzierl, R., Nolet, B. A., & Wikelski, M. (2016). Towards a new understanding of migration timing: Slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. *Oikos*, 125, 1496–1507.

Lok, T., Overdijk, O., & Piersma, T. (2013). Migration tendency delays distributional response to differential survival prospects along a flyway. *The American Naturalist*, 181, 520–531.

Lok, T., Overdijk, O., Tinbergen, J. M., & Piersma, T. (2011). The paradox of spoonbill migration: Most birds travel to where survival rates are lowest. *Animal Behavior*, *82*, 837–844.

Loonstra, A. H. J., Verhoeven, M. A., Both, C., & Piersma, T. (in review). Experiment shows non-inherited factors to shape variation in migratory routes of a long-distance migrant.

Loonstra, A. H. J., Verhoeven, M. A., & Piersma, T. (2018). Sex-specific growth in chicks of the sexually dimorphic black-tailed godwit. *Ibis*, *160*, 89–100.

Loonstra, A. H. J., Verhoeven, M. A., Senner, N. R., Hooijmeijer, J. C. E. W., Piersma, T., & Kentie, R. (2019). Natal habitat and sex-specific survival rates result in a male-biased adult sex ratio. *Behavioral Ecology*, *30*, 843–851.

Loonstra, A. H. J., Verhoeven, M. A., Zbyryt, A., Schaaf, E., Both, C., & Piersma, T. (2019). Individual long-distance migratory shorebirds do not necessarily stick to single routes: A hypothesis on how low population densities decrease social conformity. *Ardea*, *107*, 251–261.

Madsen, J. (2001). Spring migration strategies in pink-footed geese *Anser brachyrhynchus* and consequences for spring fattening and fecundity. *Ardea*, *89*, 43–55.

Meyburg, B.-U., Bergmanis, U., Langgemach, T., Graszynski, K., Hinz, A., Börner, I., Meyburg, C., & Vansteelant, W. M. G. (2017). Orientation of native versus translocated juvenile lesser spotted eagles (*Clanga pomarina*) on the first autumn migration. *Journal of Experimental Biology*, *220*, 2765–2776.

Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P., & Fagan, W. F. (2013). Social learning of migratory performance. *Science*, *341*, 999–1002.

Pedersen, L., Jackson, K., Thorup, K., & Tøttrup, A. P. (2018). Full-year tracking suggests endogenous control of migration timing in a long-distance migratory songbird. *Behavioral Ecology and Sociobiology*, *72*, 139.

Piersma, T. (2011). Flyway evolution is too fast to be explained by the modern synthesis: Proposals for an 'extended' evolutionary research agenda. *Journal of Ornithology*, *152*, S151–S159.

Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, *18*, 228–233.

Piersma, T., Pérez-Tris, J., Mouritsen, H., Bauchinger, U., & Bairlein, F. (2005). Is there a 'migratory syndrome' common to all migrant birds? *Annals of the New York Academy of Sciences*, *1046*, 282–293.

Piersma, T., & van Gils, J. A. (2011). *The flexible phenotype: A body-centred integration of ecology, physiology, and behaviour*. Oxford University Press.

Pigliucci, M., Murren, C. J., & Schlichting, C. D. (2006). Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, *209*, 2362–2367.

Pulido, F., Berthold, P., Mohr, G., & Querner, U. (2001). Heritability of the timing of autumn migration in a natural bird population. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *268*, 953–959.

Rakhimberdiev, E., Saveliev, A., Piersma, T., & Karagicheva, J. (2017). FLightR: An R package for reconstructing animal paths from solar geolocation loggers. *Methods in Ecology and Evolution*, *8*, 1482–1487.

Rakhimberdiev, E., Senner, N. R., Verhoeven, M. A., Winkler, D. W., Bouten, W., & Piersma, T. (2016). Comparing inferences of solar geolocation data against high-precision GPS data: Annual movements of a double-tagged black-tailed godwit. *Journal of Avian Biology*, *47*, 589–596.

Schroeder, J., Lourenço, P. M., van der Velde, M., Hooijmeijer, J. C. E. W., Both, C., & Piersma, T. (2008). Sexual dimorphism in plumage and size in black-tailed godwits *Limosa limosa limosa*. *Ardea*, *96*, 25–37.

Schroeder, J., Piersma, T., Groen, N. M., Hooijmeijer, J. C. E. W., Kentie, R., Lourenço, P. M., Schekkerman, H., & Both, C. (2012). Reproductive timing and investment in relation to spring warming and advancing agricultural schedules. *Journal of Ornithology*, *153*, 327–336.

Scott, R., Marsh, R., & Hays, G. C. (2014). Ontogeny of long-distance migration. *Ecology*, *95*, 2840–2850.

Senner, N. R., Conklin, J. R., & Piersma, T. (2015). An ontogenetic perspective on individual differences. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151050.

Senner, N. R., Morbey, Y. E., & Sandercock, B. K. (2020). Editorial: Flexibility in the migration strategies of animals. *Frontiers in Ecology and Evolution*, *8*, 111.

Senner, N. R., Verhoeven, M. A., Abad-Gómez, J. M., Alves, J. A., Hooijmeijer, J. C. E. W., Howison, R. A., Kentie, R., Loonstra, A. H. J., Masero, J. A., Rocha, A., Stager, M., & Piersma, T. (2019). High migratory survival and highly variable migratory behaviour in black-tailed godwits. *Frontiers in Ecology and Evolution*, *7*, 96.

Senner, N. R., Verhoeven, M. A., Abad-Gómez, J. M., Gutiérrez, J. S., Hooijmeijer, J. C. E. W., Kentie, R., Masero, J. A., Tibbitts, T. L., & Piersma, T. (2015). When Siberia came to The Netherlands: The response of Black-tailed Godwits to a rare spring weather event. *Journal of Animal Ecology*, *84*, 1164–1176.

Sergio, F., Tanferna, A., De Stephanis, R., Jiménez, L. J., Blas, J., Tavecchia, G., Preatoni, D., & Hiraldo, F. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature*, *515*, 410–413.

Sheriff, M. J., Krebs, C. J., & Boonstra, R. (2010). The ghosts of predators past: Population cycles and the role of maternal programming under fluctuating predation risk. *Ecology*, *91*, 2983–2994.

Studds, C. E., & Marra, P. P. (2005). Nonbreeding habitat occupancy and population processes: An upgrade experiment with a migratory bird. *Ecology*, *86*, 2380–2385.

Sutherland, W. J. (1998). Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*, *29*, 441–446.

Teitelbaum, C. S., Converse, S. J., Fagan, W. F., Bohning-Gaese, K., O'Hara, R. B., Lacy, A. E., & Mueller, T. (2016). Experience drives innovation of new migration patterns of whooping cranes in response to global change. *Nature Communications*, *7*, 12793.

Thorup, K., Vega, M. L., Snell, K. R. S., Lubkovskaia, R., Willemoes, M., Sjöberg, S., Sokolov, L. V., & Bulyuk, V. (2020). Flying on their own wings: Young and adult cuckoos respond similarly to long-distance displacement during migration. *Scientific Reports*, *10*, 7698.

Tombre, I. M., Oudman, T., Shimmings, P., Griffin, L., & Prop, J. (2019). Northward range expansion in spring-staging barnacle geese is a response to climate change and population growth, mediated by individual experience. *Global Change Biology*, *25*, 3680–3693.

Trimbos, K. B., Doorenweerd, C., Kraaijeveld, K., Musters, C. J. M., Groen, N. M., de Knijff, P., Piersma, T., & de Snoo, G. R. (2014). Patterns in nuclear and mitochondrial DNA reveal historical and recent isolation in the black-tailed godwit (*Limosa limosa*). *PLoS One*, *9*, e83949.

Trimbos, K. B., Musters, C. J. M., Verkuil, I. V., Kentie, R., Piersma, T., & de Snoo, G. R. (2011). No evident spatial genetic structuring in the rapidly declining black-tailed godwit *Limosa limosa limosa* in The Netherlands. *Conservation Genetics*, *12*, 629–636.

Van Doren, B. M., Campagna, L., Helm, B., Illera, J. C., Lovette, I. J., & Liedvogel, M. (2017). Correlated patterns of genetic diversity and differentiation across an avian family. *Molecular Ecology*, *26*, 3982–3997.

Vansteelant, W. M. G., Kekkonen, J., & Byholm, P. (2017). Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 1–9.

Vardanis, Y., Klaassen, R. H. G., Strandberg, R., & Alerstam, T. (2011). Individuality in bird migration: Routes and timing. *Biology Letters*, *7*, 502–505.

Verhoeven, M. A., Loonstra, A. H. J., Hooijmeijer, J. C. E. W., Masero, J. A., Piersma, T., & Senner, N. R. (2018). Generational shift in spring staging site use by a long-distance migratory bird. *Biology Letters*, *14*, 20170663.

Verhoeven, M. A., Loonstra, A. H. J., McBride, A. D., Both, C., Senner, N. R., & Piersma, T. (2021). Migration routes, stopover sites and non-breeding destinations of adults Black-tailed godwits breeding in southwest Fryslân in 2015–2015. *Journal of Ornithology*, *162*, 61–76.

Verhoeven, M. A., Loonstra, A. H. J., McBride, A. D., Kaspersma, W., Hooijmeijer, J. C. E. W., Both, C., Senner, N. R., & Piersma, T. (2021). Data from: Age-dependent timing and routes demonstrate developmental plasticity in a long-distance migratory bird. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.02v6wwq4j

Verhoeven, M. A., Loonstra, A. H. J., McBride, A. D., Torres, P. M., Kaspersma, W., Hooijmeijer, J. C. E. W., van der Velde, E., Both, C., Senner, N. R., & Piersma, T. (2020). Geolocators lead to better measures of timing and renesting in Black-tailed Godwits and reveal the bias of traditional observation methods. *Journal of Avian Biology*, *51*, e02259.

Verhoeven, M. A., Loonstra, A. H. J., Senner, N. R., McBride, A. D., Both, C., & Piersma, T. (2019). Variation from an unknown source: Large inter-individual differences in migrating black-tailed godwits. *Frontiers in Ecology and Evolution*, *7*, 31.

Winger, B. M., Auteri, G. G., Pegan, T. M., & Weeks, B. C. (2019). A long winter for the Red Queen: Rethinking the evolution of seasonal migration. *Biological Reviews*, *94*, 737–752.

Wynn, J., Padget, O., Mouritsen, H., Perrins, C., & Guilford, T. (2020). Natal imprinting to the Earth's magnetic field in a pelagic seabird. *Current Biology*, *30*, 2869–2873.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Verhoeven, M. A., Loonstra, A. H. J., McBride, A. D., Kaspersma, W., Hooijmeijer, J. C. E. W., Both, C., Senner, N. R., & Piersma, T. (2022). Age-dependent timing and routes demonstrate developmental plasticity in a long-distance migratory bird. *Journal of Animal Ecology*, 91, 566–579. https://doi.org/10.1111/1365-2656.13641