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On the behaviour and ecology of the Black-tailed Godwit

Verhoeven, Mo; Loonstra, Jelle

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

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

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ABSTRACT

1. Seasonal migration is thought to be a behavioural adaptation of animals to changing environmental context. However, the mechanistic processes by which animals develop and potentially adjust their migratory behaviour are largely unresolved. As a result, it is mostly unknown how much, how fast, and when animals adjust their migration to their environments.

2. We studied the ontogeny of migration in a long-distance migratory shorebird, the Black-tailed Godwit (*Limosa limosa limosa*), known to exhibit marked individuality in their migratory routines. By observing how and when these individual differences arise, we aimed to elucidate how individuals adjust to and ultimately cope with their environment.

3. We tracked juvenile godwits born in 2016 and 2017 on their first southward and northward migrations. This allowed us to relate their migration routes, timing, and mortality rates to their hatch date and year of birth (both indicating environmental change over time). We simultaneously tracked adult godwits, which enabled us to compare the routes, timing, and mortality rates of adults and juveniles originating from the same breeding areas during the same years.

4. In juveniles, the timing of departure for their first southward migration was related to hatch date. However, their subsequent migration routes, orientation, destination, duration, and likelihood of mortality were not related to year of migration, sex, or the timing of migration. Juveniles left The Netherlands after all tracked adults had left. 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 that were far outside the well-documented adult migratory corridor, but such juveniles were not more likely to die.

5. We eliminate the possibility that the individual differences observed among adult godwits are already developed at birth or by their first migration. This adds to the mounting evidence that animals possess the developmental plasticity to change their migratory strategy later in life. We discuss how common this developmental plasticity may be among migratory animals, as well as the implications that this has for their ability to respond to environmental change.

INTRODUCTION

Seasonal migration is a fascinating phenomenon. Its causes and consequences have frequently been debated (Alerstam *et al.* 2003, Winger *et al.* 2019). In the current paradigm, there are two major hypotheses. One states that migration occurs because *breeding* at a location different from where an individual spends the non-breeding season confers an adaptive advantage. The other hypothesis states that migration occurs because spending the *nonbreeding* season in a location different

from where breeding takes place confers an adaptive advantage (reviewed in Winger *et al.* 2019). Under both hypotheses, migration is gained and lost over time depending on whether its occurrence is favoured by a population's environment (Chapman *et al.* 2011). However, the processes by which migratory behaviour adjusts to the environment are largely unresolved (Hegemann *et al.* 2019).

Three processes have been proposed to explain how migratory behaviour is adjusted to the environment. The first is microevolution, in which a genetic pathway

that influences migratory behaviour undergoes a heritable change that is selected for by the environment (Berthold *et al.* 1992, Pulido *et al.* 2001, Helm *et al.* 2019). The second is developmental plasticity, in which an inter-generational change results from individuals adjusting to environmental conditions during ontogeny alone (Lok *et al.* 2011, Gill *et al.* 2014, Verhoeven *et al.* 2018). The third is phenotypic flexibility, whereby adults and juveniles can repeatedly adjust their migratory routines to their environment (Mueller *et al.* 2013, Sergio *et al.* 2014, Teitelbaum *et al.* 2016, Tombre *et al.* 2019). How much, how fast, and when migratory animals can adjust to their environment depends on which of the three processes is occurring (Pulido *et al.* 2001, Tombre *et al.* 2019, Gill *et al.* 2019). The underlying mechanism is therefore not only important to understanding the evolution of migration (Piersma 2011), but also to conserving migratory species in a changing world (Sutherland 1998).

Exploring these mechanistic processes also has the potential to help explain the sources of the consistent and considerable individual differences in migratory behaviour that are now frequently observed among individuals of the same population (Lok *et al.* 2011, Flack *et al.* 2016, Verhoeven *et al.* 2019). Given the consistency of many individual migratory routines of adults, it is rare to observe adjustments (Battley *et al.* 2006, Vardanis *et al.* 2011, Pedersen *et al.* 2018, but see Senner *et al.* 2015a) and therefore difficult to make inferences about the underlying mechanistic processes involved. However, by observing individual animals from birth to adulthood, it is possible to determine whether, how, and – especially – when in life individuals adjust their behaviours to changing environmental conditions (Sergio *et al.* 2014).

For this reason, we tracked juvenile Continental Black-tailed godwits (*Limosa limosa limosa*, hereafter “godwits”) from The Netherlands throughout their first two annual cycles. The migratory routes and timing of adult godwits are known to vary considerably yet consistently among individuals (Verhoeven *et al.* 2019, Verhoeven *et al. in review*). Some adults spend the non-breeding period north of the Sahara, whereas others cross the Sahara to West Africa (Hooijmeijer *et al.* 2013, Kentie *et al.* 2017, Verhoeven *et al.* 2019). Furthermore, some adults leave West Africa in September, while others leave more than five months later, in March (Senner *et al.* 2019, Verhoeven *et al.* 2019). In this study, we examined whether a juvenile’s hatch date was related to its departure date and whether this departure date was associated with its route, destination, or likelihood of mortality during its first south-

and northward migrations. Additionally, we compared the migration of juveniles to adults breeding at the same sites and migrating at the same time in order to examine whether the differences among juveniles in migratory behaviour can explain the differences among adults. We found that juvenile godwits have strikingly different timing and routes compared to adults, but that individuals exhibiting alternative routes and timing are not selected against. This suggests that, like some other species, godwits possess the developmental plasticity to adjust their migration later in life and, at some point, adopt the consistently different routines we observe among adults (cf. Lok *et al.* 2011). We therefore discuss what this developmental plasticity means for the study of individual differences and the evolution of migration.

MATERIAL AND METHODS

Gathering tracking data

To track the timing of adult migration, we outfitted adult godwits with geolocators in each breeding season from 2015 to 2018 in our 12,000 ha study area in southwest Fryslân, The Netherlands (see Senner *et al.* 2015a for more details). We captured adults using walk-in-traps, automated drop cages, or mist nets placed over the nest. 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.

To track the spatial distribution and mortality of adult godwits, we deployed 32 solar-powered PTT-100s of 9.5 g from Microwave Technology Inc. in 2015 and 2016 (attachment ~10.5 g), and another four of 5 g in 2017. Thirty-four of these 36 transmitters were programmed to turn on for 8 hours and turn off for 24 hours. One of the remaining two transmitters was programmed to turn on for 8 hours and off for 25 hours, and the other was programmed to turn on for 10 hours and off for 48 hours. We captured all 36 adults on nests in the 220-ha Haanmeer polder, which lies in the centre of our larger study area. To attach the transmitters, we used a leg-loop harness of 2-mm Dyneema rope. Based on a combination of molecular sexing (using a ~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 birds consisted of 34 females and 2 males. In 2015 and 2016, the loading factor of the transmitters was $3.4\% \pm 0.2$ (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: Verhoeven *et al. in review*).

We also tracked the timing, spatial distribution, and mortality rates of juvenile godwits during their first south- and northward migrations. We deployed 40 solar-powered PTT-100s of 5 g from Microwave Technology Inc. on juveniles in both 2016 and 2017, for a total deployment of 80 transmitters. All 80 transmitters were programmed to turn on for 8 hours and off for 24 hours. 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. However, in 2016 the number of fledged juveniles in our study area was considerably lower than average, so we also caught 4 juveniles on the island of Ameland (53.45°N, 5.83°E; see Loonstra *et al.* 2019a). We attached the leg-loop harnesses as we did for the adults and took ~30 µl of blood from the brachial vein for molecular sexing. We obtained migratory tracks from 28 of these juveniles (see Results): 24 from our study area and 4 from Ameland. 27 out of 28 were molecularly sexed, but one analysis failed. We sexed this bird based on her 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; we therefore estimated their hatch dates using a sex-specific growth curve (see Loonstra *et al.* 2018). This method yields an estimated hatch date that is accurate to within ±3 days; this 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 is likely to have diminished to ~2% as the juvenile godwits continued to grow to adult size.

Processing tracking data

We downloaded light-level data from 78 geolocators retrieved from 64 adult godwits (24 males, 40 females). Twenty of these geolocators contained data for more than one season. 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 this light-level data. Detailed examples of this analytical routine using our own godwit data can be found in Rakhimberdiev *et al.* (2016, 2017). Using the

FLightR function “find.times.distribution,” we estimated when individual godwits crossed nine arbitrary spatial boundaries that were spaced 4° of latitude apart across the entire 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. In our analyses that use geolocator-derived timing, 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).

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 h⁻¹ while retaining location classes with qualities of 3, 2, 1, 0, A, and B. From this data, we estimated for both south- and northward migration: (1) when the nine latitudinal boundaries were crossed; (2) an individual's orientation, which we determined by calculating its longitudinal (i.e. east-west) movement, measured in kilometres, between the same latitudinal boundaries; (3) the longitudinal distribution of tracks at each latitudinal boundary; and, (4) where and when mortality occurred. We calculated distances between points with the function “distHaversine” in the package “geosphere” (Hijmans 2017).

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: (1) the effects of hatching date, sex, and year on the timing of juvenile migration; (2) the effects of date, sex, and year on the longitude of juvenile migration routes; and, (3) the effects of date, sex, and year on the 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: (1) the timing of crossing, (2) the longitude of crossing, and (3) the 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. 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 used a generalized linear model with a binomial error structure and a logistic link function to test whether the likelihood that juveniles (1) crossed the Sahara on their first southward migration and (2) did so by flying non-stop from The Netherlands was related to their departure date, year, or sex. We also used a generalized linear model to explore whether the adults and juveniles tracked in the same years on southward migration differed in (1) the proportion of individuals that crossed the Sahara and (2) in the proportion that did so with a non-stop flight from The Netherlands.

Mortality

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 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. That this is a reasonable assumption is 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 (Verhoeven *et al.* 2018, Loonstra *et al.* 2019a).

We used generalized linear models with a binomial error structure and a logistic link function to test whether (1) the likelihood that juveniles died on their first southward migration was related to their departure date, sex, or the year the juvenile hatched; and, (2) 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 14.3) and when (Figure 14.4) 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.

RESULTS

Timing of juveniles and adults

SOUTHWARD MIGRATION

We obtained migratory tracks from 28 individuals, because most of the tagged juveniles died between tagging and before migrating southward – a period known

to have high juvenile mortality (see Loonstra *et al.* 2019a). 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 14.2, Table S1). Furthermore, all juveniles departed The Netherlands later than did the tracked adults (Figure 14.2, Table S1). After crossing 40°N, juveniles first encountered tracked adults from our study population with whom they could potentially spend the nonbreeding season or migrate with towards 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 14.1). Of the juveniles, 4 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 (63%), while of the 28 adults that migrated to West Africa, only 2 flew non-stop (11%, statistics in Table 14.2). Furthermore, 5 of the 7 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 14.1). Because juveniles flew non-stop more and made shorter stops, the timing of southward Sahara crossing was less variable within juveniles than adults (Table S3). 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 14.1). Furthermore, of two juveniles born one day apart and that both departed the Netherlands on 6 August 2016, one stopped and one did not stop *en route* to West Africa (Figure 14.4).

NORTHWARD MIGRATION

By the time the northward migration period begins in godwits, juveniles are considered immatures. In total, we tracked 15 juveniles as immatures during 2017–2019. 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 14.2C). In the same vein, 25% of the immatures departed West Africa later than any of the adults tracked from 2016–2019.

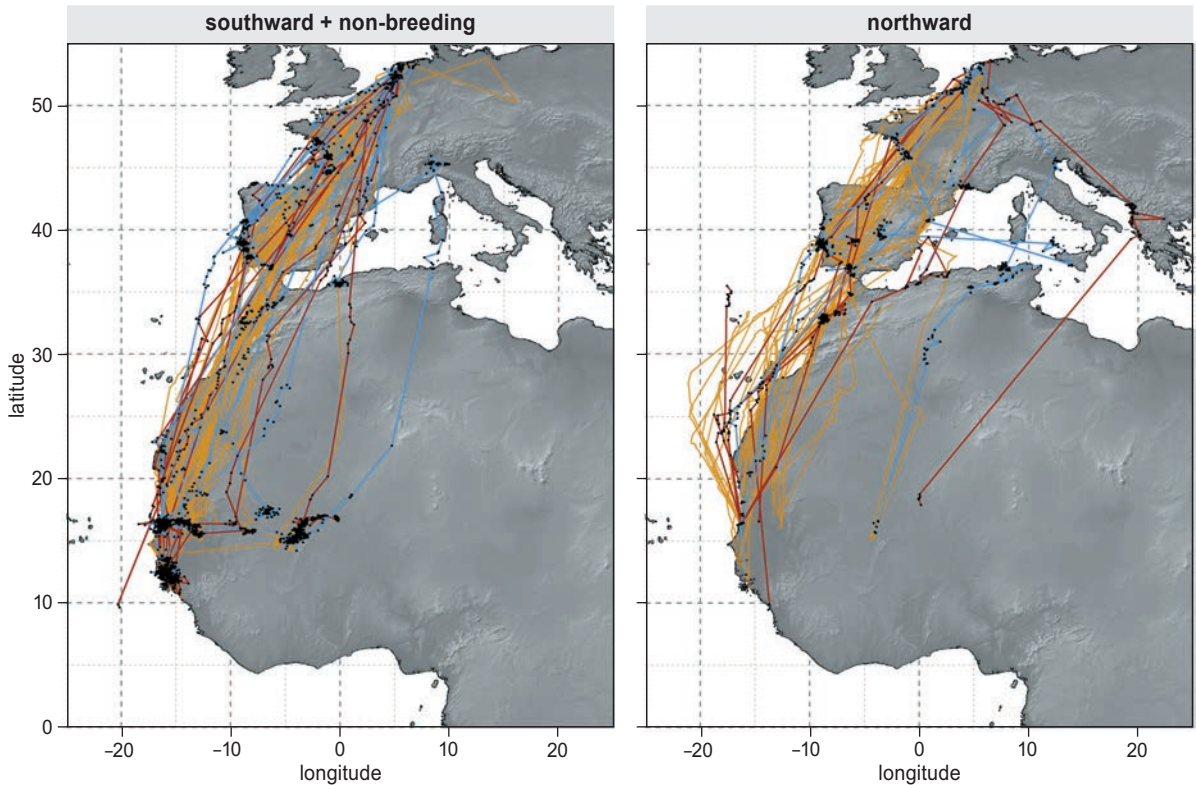


Figure 14.1. Migratory tracks of all adults from 2015 to 2019 (gold), juveniles born in 2016 (red), and juveniles born in 2017 (light blue).

Table 14.1. 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 were born. Similarly, we examined (4) whether a juvenile godwit dies between departure from and return to the Netherlands was related to its hatching date, sex or year born.

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

¹ Reference level for sex is female

² Reference level for year is 2016

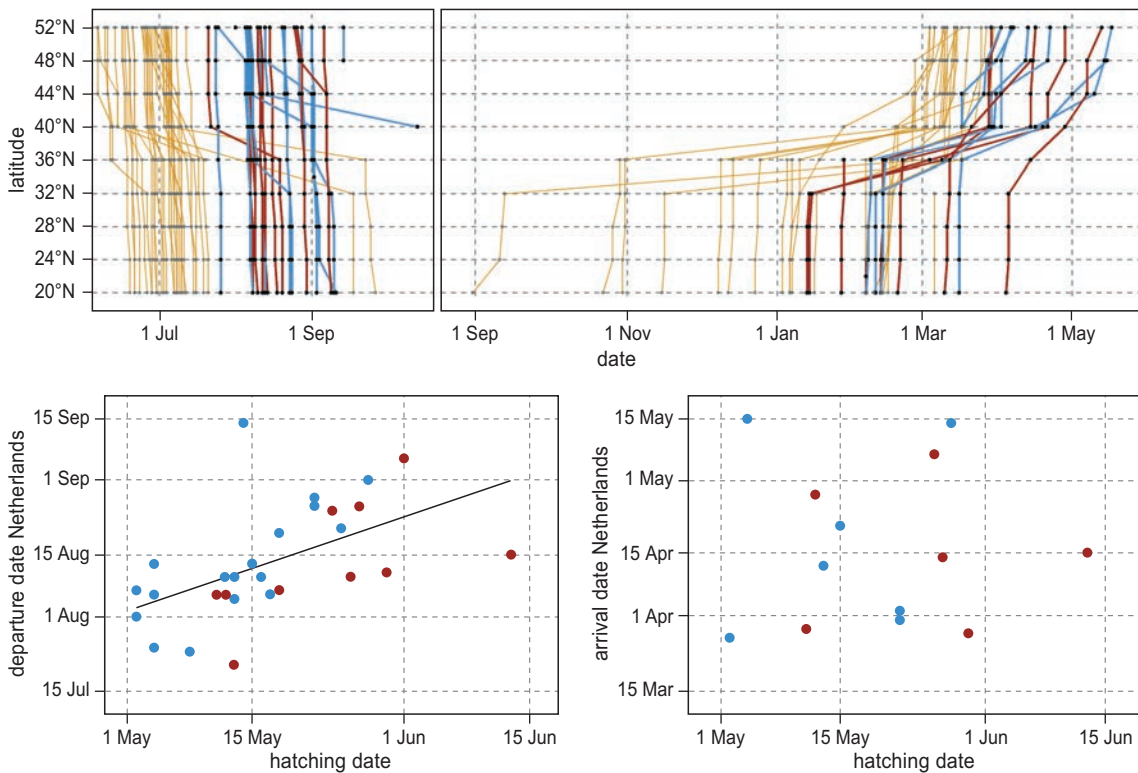


Figure 14.2. Top: Migratory timing of adults tracked with geolocators from 2015 to 2019 (gold), and of juveniles born in 2016 (red) and in 2017 (light blue). Bottom: Correlation between hatching date of juveniles and their departure and arrival to the Netherlands (colors same as above).

As a result, the northward migration of immatures was significantly later than that of adults (Figure 14.2, Table S3).

In contrast with southward migration, an immature's departure from West Africa was not related to its hatch date (Table S2). The immature birds that departed earliest for northward migration had the opportunity to continue on to The Netherlands with adults from the same breeding population. However, all but one of the immatures left the Mediterranean later than any of the adults (Figure 14.2). Consequently, the arrival of juveniles to The Netherlands was on average 36 days later than that of adults (Table S3), with some juveniles 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 by an adult: 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 was not associated with a juvenile's hatch date (Figure 14.2).

Routes and orientation of juveniles and adults

During southward migration, juveniles that migrated later tended to orient more toward the south and less toward the southwest after crossing the Mediterranean (from 36°N to 32°N, Table S7). This seasonal change in juvenile routes might also explain why their variance in longitudinal movement across this latitudinal segment was different from the variance observed in adult routes (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 (13.61°W), though not significantly so (Table S6). During northward migration, juveniles that migrated later tended to fly more toward the north and less toward 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 & S8).

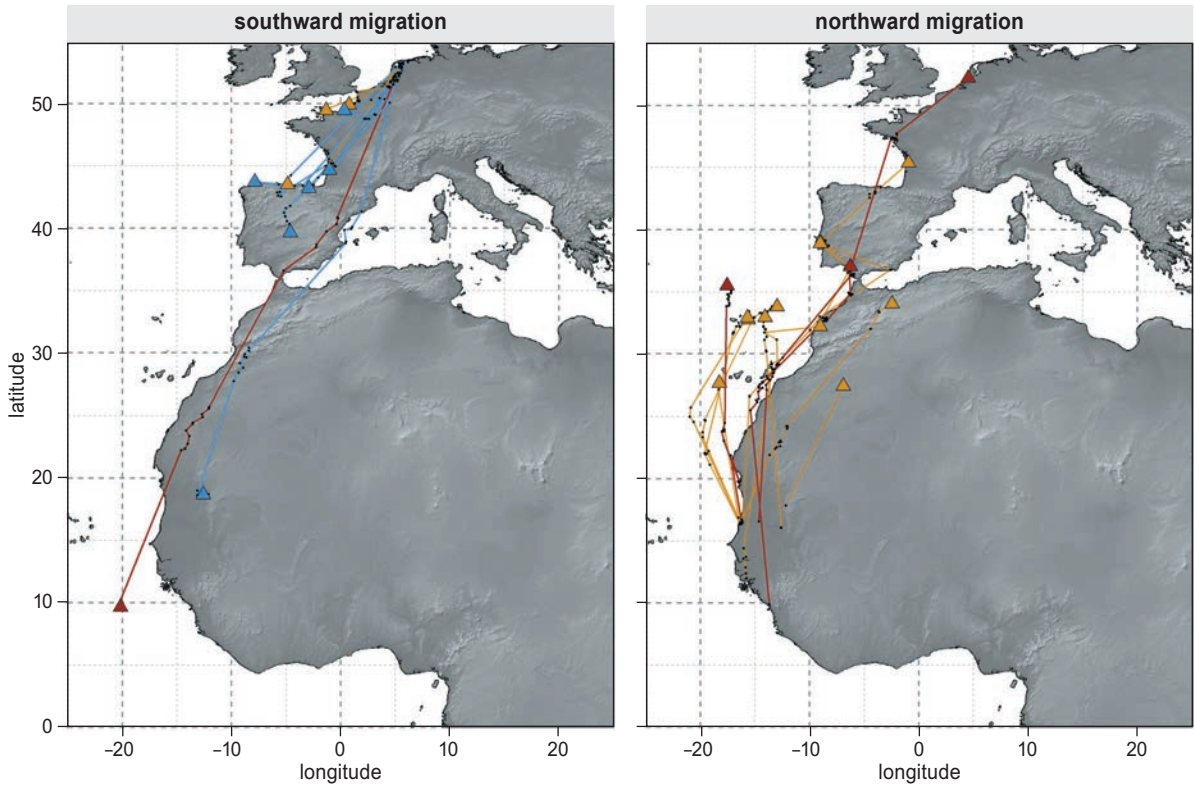


Figure 14.3. Mortality on migration for adults tracked with satellite transmitters from 2015 to 2019 (gold), and for juveniles born in 2016 (red) and 2017 (light blue).

On average, juveniles and adults took similar routes during southward migration (Figure 14.2, Table S6). However, one juvenile flew south via northern Italy, a stopping site well to the east of the migratory corridor of adults (Figure 14.1). The 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 toward West Africa (19/23, 83%) was the same as in adults (54/66, 82%, $P = 0.932$, Table 14.2). During northward 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

Table 14.2. Results from generalized linear models with binomial error structure and logistic link function that examines 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 ($n = 23$ juveniles, 66 adults)	Intercept	-1.50 ± 0.32		
	Age ¹	-0.05 ± 0.64	0.01	0.932
(2) Non-Stop to West Africa from The Netherlands ($n = 19$ juvenile tracks, 28 adult tracks)	Intercept	-2.64 ± 0.73		
	Age ¹	2.18 ± 0.82	9.64	0.002
(3) Mortality during southward migration ($n = 28$ juvenile tracks, 32 adults tracks)	Intercept	-2.77 ± 0.73		
	Age ¹	1.39 ± 0.84	4.27	0.039
(4) Mortality during northward migration ($n = 15$ juvenile tracks, 33 adults tracks)	Intercept	-0.98 ± 0.39		
	Age ¹	-0.41 ± 0.75	0.30	0.584

¹ Reference level for age is adult

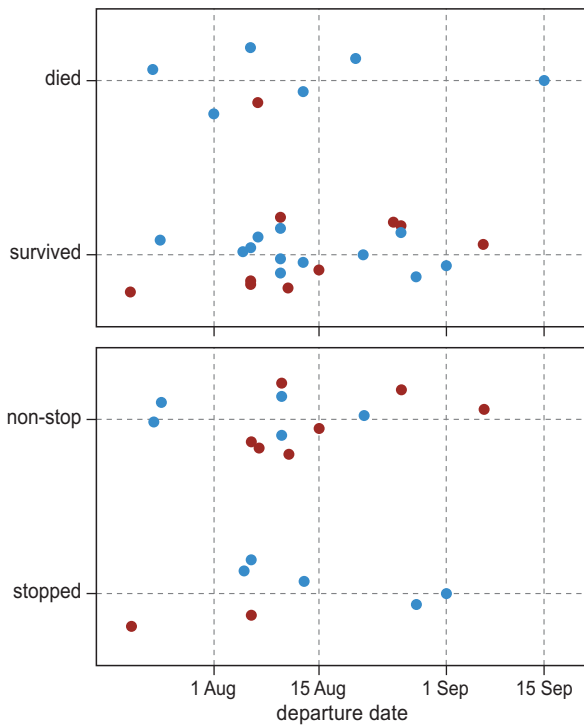


Figure 14.4. Survival (died or survived) and duration of the flight (non-stop or stopped) of juveniles born in 2016 (red) and in 2017 (light blue) on southward migration in relation to their timing of departure from The Netherlands (crossing 52°N). Top panel includes all tracked juveniles ($n = 28$). 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 14.3). Points are vertically offset in order to show multiple departures that took place on the same day and had the same survival or duration.

than a thousand kilometres outside of the adult corridor (Figure 14.1, Table S6). As a result, the northward routes of immatures, like their southward routes, were more variable than those of adults (Figure 14.1, Table S6). This is especially clear north of the Sahara (Figure 14.1, Table S6).

Mortality rates of juveniles and adults

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 sites in West Africa (Figure 14.3). During southward migration in 2017, six juveniles and one adult died (Figure 14.3). Mortality of juveniles on southward migration was not related to their date of departure, sex, or the year in which they hatched (Table 14.1). For example, we observed two juveniles of similar ages

departing on the same day, of which one died and the other survived (Figure 14.4). Most juveniles (5 of 7) that died during southward migration did so on 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 on southward migration was higher than that of adults (25% versus 6%, $P = 0.039$, Table 14.2).

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, France, whereas the other seven died at nonbreeding sites south of the Sahara. During northward migration, another three immatures died; all of them were born in 2016. One of these flew north from the coast of Senegal and perished in the Atlantic Ocean, 290 kilometres north of Madeira, Portugal (Figure 14.3). Another stopped for 26 days at a lagoon near Cadiz, Spain, then died immediately upon arrival at Doñana, Spain (Figure 14.3). The third died immediately upon arrival near Leiden, The Netherlands (Figure 14.3). The mortality of juveniles on northward migration was slightly lower than that of adults, but not significantly so (20% versus 27%, $P = 0.584$, Table 14.2). Furthermore, the mortality of juveniles outside The Netherlands – i.e. between departure from and subsequent arrival to The Netherlands one to three years later – was not related to their hatch date, sex, or year of hatch (Table 14.1).

DISCUSSION

We studied the ontogeny of migration in comparison with the migration of experienced adults in a long-distance migratory shorebird to elucidate how and when individual differences arise. The departure timing of juveniles on southward migration correlated with their hatch date. However, we detected no other effect of hatch date, departure timing, year of migration, or sex on their route, orientation, nonbreeding destination (north or south of the Sahara), duration, or mortality, during either their southward migration or their first northward migration. The sources of the observed individual differences among adults therefore remain mostly undetermined.

However, our results do demonstrate age-dependent differences and therefore developmental plasticity in a long-distance migratory bird. Juveniles left The Netherlands after all tracked adults had left, flew non-stop to West Africa more frequently, and had higher

mortality rates than did adults. However, these three factors – departing later, flying non-stop more and having higher mortality – appear to be unrelated. In contrast to these three factors, juveniles and adults were similar in their routes, orientation, and the proportion of individuals that crossed the Sahara. Despite their similarities, the migratory behaviours of juveniles were more variable than those of adults; some juveniles visited stopping sites and flew along routes never previously observed (Senner *et al.* 2019, Verhoeven *et al.* 2019), including one more than a thousand kilometers outside of the adult migratory corridor.

Environmental effects on juvenile migration

Because juveniles migrated significantly later than adults, that they also flew non-stop 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 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. Furthermore, among both the earliest and latest juveniles that crossed the Sahara, individuals both survived and died (Figure 14.4). We conclude from these observations that the destination, migration duration, and mortality rate of juveniles were not necessarily related 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.

There could be many other reasons why juveniles differed in their migratory behaviour. For example, the social context in which they migrated might have been different (Nemeth and Moore 2007, Loonstra *et al.* 2019b) – immature individuals during their first northward migration could have ended up in Italy and Albania instead of on the Iberian Peninsula by following adults from more easterly populations that also spend the winter in West Africa (e.g., Polish godwits, see Loonstra *et al.* 2019b). In addition, even those juveniles that were of similar age and exhibited differ-

ent migratory behaviours could have departed The Netherlands in different states (*sensu* McNamara and Houston 1996). Some might simply have been able to accumulate energy stores for a flight to West Africa, whereas in the same window between hatch and departure, others might only have been able to fuel for a shorter flight. Alternatively, they might have been raised in a higher-quality habitat and developed higher-quality wing feathers that ultimately enabled a longer flight with fewer risks (Hedenström 2008, de La Hera *et al.* 2010). Many more possibilities that lead to individual differences among juveniles must surely exist (Senner *et al.* 2015b).

Mortality

Two aspects about the observed juvenile mortality rate are noteworthy. First, during southward migration, the survival of juveniles was high in 2016, but lower in 2017. The opposite was true for northward migration: only individuals from 2016 died during northward migration. One possible interpretation of this pattern is that some of the individuals from both 2016 and 2017 were less adept at migrating. Those from 2017 were selected against during their southward migration, whereas those from 2016 were not selected against until their northward migration. Although we have no direct evidence about the environmental conditions encountered during these two years, such an explanation predicts that circumstances – such as wind conditions (Loonstra *et al.* 2019c) – for southward migration were harsher in 2017 than in 2016.

The second noteworthy aspect is that most juveniles that died 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 novel 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 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 spa-

tiotemporal distribution across the annual cycle (Vardanis *et al.* 2011, Conklin *et al.* 2013, Pedersen *et al.* 2018, Verhoeven *et al.* 2019). However, there are also migratory species that continue to make adaptive adjustments to their migratory routine throughout life (Mueller *et al.* 2013, Sergio *et al.* 2014, 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 and others do not.

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 are of a genetic 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, their migratory timing was considerably different, but both flew to West Africa. However, after arriving in West Africa, and on northward migration, their routines 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 stop-over 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 of genetic origin.

Our study also clearly demonstrates that juveniles and adults have different routines. 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 ten years (Hooijmeijer *et al.* 2013, Senner *et al.* 2015a, 2019, Verhoeven *et al.* 2019, *in review*, 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 the juveniles that have markedly different routines

from adults will either die or never breed. The third is that we observed normal juvenile godwit behaviour, but godwits change their routines later in life rather than continue 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, we believe that the most likely scenario in godwits is the third option.

We propose that juvenile godwits change their migratory routines later in life on the following grounds: (1) 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 born 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 born in The Netherlands return to The Netherlands and that their average lifespan is 4–5 years (Loonstra *et al.* 2019a). Yet, we have observed adults leaving The Netherlands as early as the end of May and beginning of June (Figure 14.2). It necessarily follows that in these cases, these adults left earlier than they did on their first southward migration as juveniles. Even if every tracked juvenile from 2016 and 2017 were to die before breeding, it would still not be possible to observe the current adult pattern without adult godwits migrating southward earlier than they did as juveniles.

Moreover, (2) ringing recoveries of juveniles banded in The Netherlands over the past 70 years indicate that the later migration and different routes of juveniles on northward migration are not a new phenomenon (Haverschmidt 1963, Beintema and Drost 1986). 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 strategies die, it is likely that these juvenile godwits change their routines later in life. We therefore expect godwits to make considerable changes to their migration later in life, but only the lifelong tracking of these same individuals will establish this for certain. Furthermore, because the timing of juvenile godwits is expected to change later in life, lifelong tracking might still give us more insight into why we observe large differences among adult individuals (Verhoeven *et al.* 2019).

Species-specific differences in developmental plasticity

If godwits do change their migratory routines during the first years of life, as we expect, they are similar to other migrant species that adjust their migratory routine later in life (Mueller *et al.* 2013, Sergio *et al.* 2014, Teitelbaum *et al.* 2016, Tombre *et al.* 2019). In contrast to these species, however, godwits do eventually adopt a consistent migratory routine that they maintain for the rest of their lives (see Verhoeven *et al.* 2018, 2019, *in review*). At first glance, this would suggest that there is a gradient in the amount of developmental plasticity that different species exhibit during their lives with respect to their migratory routines. The period in which developmental plasticity occurs would potentially range from a negligible window in species with a strong innate control of their migratory routine (Berthold *et al.* 1992, Gwinner 1996, Pulido *et al.* 2001), to a lifelong window in those species that continually make adjustments (Mueller *et al.* 2013, Sergio *et al.* 2014, Teitelbaum *et al.* 2016, Tombre *et al.* 2019). Godwits would lie somewhere in the middle. But what could cause such differences among species?

First, we find it intriguing that the species that continue to make adjustments throughout life – 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, on the other hand, 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 timescales, 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 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 plasticity in their

migrations (Flack *et al.* 2016, Loonstra *et al.* 2019b). 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). In fact, 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 encompass: (1) 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.); (2) experimentally revealing the organismal limits of these component traits, i.e. their full reaction norms; (3) employing transcriptomic and genomic approaches to understand the genetic basis that may underlie these component traits, which might help disentangle to what extent plasticity is organismal or conditional (Horton *et al.* 2019); and, (4) 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).

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SUPPLEMENTARY MATERIAL

Table S1. Results of a linear model examining the effects of hatching date, sex and year on the timing of southward migration of juvenile godwits.

Southward Migration											
Latitude	Intercept	Hatching date			Sex ¹			Year ²			N_Juv
	$\beta \pm SE$	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	
52°N	97.77 ± 33.0	0.91 ± 0.23	15.93	0.001	-6.02 ± 3.98	2.28	0.144	8.83 ± 4.76	3.45	0.076	28
48°N	109.95 ± 34.62	0.83 ± 0.24	12.05	0.002	-5.80 ± 4.08	2.02	0.169	8.72 ± 4.81	3.29	0.083	27
44°N	105.38 ± 34.58	0.86 ± 0.24	13.08	0.002	-3.10 ± 4.13	0.56	0.461	7.46 ± 4.83	2.39	0.137	26
40°N	102.34 ± 60.29	0.87 ± 0.41	4.43	0.048	0.75 ± 6.98	0.01	0.915	13.79 ± 7.76	3.16	0.091	24
36°N	127.82 ± 38.76	0.71 ± 0.29	7.09	0.016	-0.80 ± 4.84	0.03	0.870	6.74 ± 5.38	1.57	0.228	20
32°N	132.60 ± 43.65	0.71 ± 0.30	5.72	0.030	-2.79 ± 5.25	0.28	0.603	9.09 ± 5.58	2.65	0.124	19
28°N	128.71 ± 44.46	0.71 ± 0.30	5.55	0.033	-2.92 ± 5.35	0.30	0.593	9.16 ± 5.68	2.60	0.128	19
24°N	128.73 ± 44.46	0.71 ± 0.30	5.57	0.032	-3.24 ± 5.35	0.37	0.553	9.24 ± 5.68	2.65	0.125	19
20°N	130.35 ± 46.33	0.71 ± 0.31	5.07	0.040	-4.06 ± 5.57	0.53	0.478	9.41 ± 5.57	2.53	0.133	19

¹ Reference level for sex is female
² Reference level for year is 2016

Table S2. Results of a linear model examining the effects of hatching date, sex and year on the timing of northward migration of juvenile godwits.

Northward Migration											
Latitude	Intercept	Hatching date			Sex ¹			Year ²			N_Juv
	$\beta \pm SE$	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	
20°N	-2.13 ± 147.45	0.30 ± 0.98	0.10	0.767	10.86 ± 19.69	0.30	0.598	-27.71 ± 34.12 ³ 0.95 ± 18.99 ⁴	0.34	0.724	12
24°N	-5.40 ± 149.12	0.33 ± 0.99	0.11	0.749	10.49 ± 19.91	0.28	0.615	-28.21 ± 34.51 ³ 1.12 ± 19.20 ⁴	0.34	0.720	12
28°N	-3.69 ± 148.99	0.30 ± 0.99	0.10	0.767	13.26 ± 21.74	0.37	0.564	-28.35 ± 34.48 ³ 4.19 ± 21.38 ⁴	0.36	0.710	12
32°N	-1.25 ± 147.57	0.31 ± 0.98	0.09	0.774	10.20 ± 19.71	0.35	0.576	-27.58 ± 34.15 ³ 0.68 ± 19.00 ⁴	0.34	0.721	12
36°N	43.96 ± 100.96	0.09 ± 0.67	0.02	0.896	19.46 ± 13.91	1.96	0.211	-49.37 ± 23.42 ³ -8.54 ± 13.68 ⁴	2.33	0.178	11
40°N	58.27 ± 65.78	0.25 ± 0.44	0.31	0.591	5.18 ± 9.58	0.29	0.602	-1.95 ± 9.85	0.04	0.848	13
44°N	58.51 ± 84.43	0.29 ± 0.57	0.26	0.621	1.73 ± 12.29	0.20	0.891	0.67 ± 12.64	0.00	0.959	13
48°N	71.05 ± 85.23	0.20 ± 0.57	0.13	0.728	7.03 ± 12.41	0.32	0.584	6.84 ± 12.76	0.29	0.605	13
52°N	45.30 ± 82.44	0.43 ± 0.56	0.60	0.465	0.15 ± 13.5	0.00	0.991	2.29 ± 13.74	0.03	0.872	11

¹ Reference level for sex is female
² Reference level for year is 2018
³ Estimate for 2017 (1 individual)
⁴ Estimate for 2019

Table S3. Results of a generalized linear model examining the difference in timing of southward and northward migration between adult and juvenile godwits tracked in the same years.

Latitude	Southward Migration							Northward Migration						
	Mean date of crossing			SD (in days)			N_Ad	Mean date of crossing			SD (in days)			N_Ad
	Ad	Juv	P	Ad	Juv	P		Ad	Juv	P	Ad	Juv	P	
52°N	25 Jun	13 Aug	0.000	11	13	0.441	50	12 Mar	17 Apr	0.000	8	17	0.005	38
48°N	26 Jun	15 Aug	0.000	11	13	0.594	50	10 Mar	16 Apr	0.000	8	18	0.001	38
44°N	27 Jun	15 Aug	0.000	11	13	0.547	50	8 Mar	10 Apr	0.000	9	17	0.009	38
40°N	28 Jun	19 Aug	0.000	11	18	0.048	50	3 Mar	4 Apr	0.000	14	14	0.536	38
36°N	-	17 Aug	-		12	-	42	-	1 Mar	-	-	21	-	-
32°N	8 Jul	19 Aug	0.000	20	12	0.739	41	1 Jan	15 Feb	0.001	41	24	0.141	35
28°N	8 Jul	19 Aug	0.000	20	13	0.743	41	31 Dec	15 Feb	0.001	41	24	0.157	35
24°N	9 Jul	20 Aug	0.000	20	13	0.771	41	31 Dec	15 Feb	0.001	41	24	0.151	35
20°N	9 Jul	20 Aug	0.000	20	13	0.815	41	30 Dec	14 Feb	0.001	42	24	0.155	35

Table S4. Results of a linear model examining the effects of crossing date, sex and year on the longitude of southward migration of juvenile godwits.

Latitude	Southward Migration											N_Juv
	Intercept	Date of crossing			Sex ¹			Year ²				
	$\beta \pm SE$	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P		
52°N	4.92 ± 0.22	0.10 ± 0.12	0.62	0.439	0.18 ± 0.24	0.56	0.460	-0.21 ± 0.24	0.761	0.392	28	
48°N	1.28 ± 0.43	0.35 ± 0.43	0.64	0.432	0.83 ± 0.81	1.05	0.315	0.14 ± 0.80	0.03	0.862	27	
44°N	-1.10 ± 0.99	0.54 ± 0.58	0.87	0.361	0.88 ± 1.06	0.686	0.417	-0.07 ± 1.07	0.00	0.951	26	
40°N	-3.63 ± 1.75	-0.31 ± 0.75	0.17	0.683	0.73 ± 1.90	0.15	0.706	0.15 ± 1.96	0.01	0.940	24	
36°N	-6.63 ± 1.89	1.26 ± 1.20	1.11	0.308	1.60 ± 2.06	0.60	0.449	1.85 ± 2.05	0.81	0.381	20	
32°N	-9.26 ± 1.96	2.14 ± 1.24	2.98	0.105	2.29 ± 2.20	1.09	0.313	1.32 ± 2.15	0.38	0.549	19	
28°N	-11.16 ± 2.07	2.43 ± 1.29	3.55	0.079	2.54 ± 2.32	1.20	0.291	1.00 ± 2.27	0.20	0.665	19	
24°N	-13.32 ± 2.20	2.65 ± 1.35	2.66	0.121	2.96 ± 2.47	2.04	0.171	0.97 ± 2.40	0.03	0.855	19	
20°N	-14.41 ± 2.17	2.43 ± 1.30	3.51	0.080	2.70 ± 2.43	1.23	0.285	0.85 ± 2.35	0.13	0.724	19	

¹ Reference level for sex is female² Reference level for year is 2016

Table S5. Results of a linear model examining the effects of crossing date, sex and year on the longitude of northward migration of juvenile godwits.

Northward Migration											
Latitude	Intercept	Date of crossing			Sex ¹			Year ²			N_Juv
	$\beta \pm SE$	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	
20°N	-9.15 ± 4.43	2.65 ± 3.05	0.75	0.41	-2.89 ± 4.27	0.046	0.521	1.23 ± 8.07 ³ -0.35 ± 4.21 ⁴	0.02	0.980	12
24°N	-6.27 ± 4.93	4.10 ± 3.40	1.45	0.268	-4.39 ± 4.81	0.83	0.392	2.10 ± 9.10 ³ -0.85 ± 4.75 ⁴	0.06	0.944	12
28°N	-3.82 ± 5.23	4.35 ± 3.62	1.44	0.269	-3.97 ± 5.11	0.60	0.462	0.15 ± 9.67 ³ -2.07 ± 5.05 ⁴	0.09	0.913	12
32°N	-0.73 ± 5.34	4.27 ± 3.75	1.30	0.292	-3.82 ± 5.24	0.53	0.490	-0.10 ± 9.91 ³ -3.71 ± 5.18 ⁴	0.28	0.767	12
36°N	1.94 ± 5.42	9.89 ± 6.23	2.48	0.166	-5.24 ± 6.65	0.62	0.461	9.90 ± 13.53 ³ 0.91 ± 6.04 ⁴	0.27	0.769	11
40°N	1.93 ± 6.55	-4.87 ± 6.86	0.50	0.496	-0.82 ± 5.55	0.02	0.886	-0.70 ± 5.58	0.02	0.903	13
44°N	-0.003 ± 5.32	0.50 ± 4.31	0.01	0.910	0.25 ± 4.43	0.00	0.956	1.78 ± 4.44	0.16	0.695	13
48°N	3.16 ± 3.73	-1.04 ± 3.02	0.12	0.739	0.61 ± 3.15	0.04	0.851	0.73 ± 3.14	0.05	0.823	13
52°N	2.29 ± 0.70	1.12 ± 0.49	5.27	0.055	1.23 ± 0.52	5.57	0.050	1.24 ± 0.52	5.65	0.049	11

¹ Reference level for sex is female
² Reference level for year is 2018
³ Estimate for 2017 (1 individual)
⁴ Estimate for 2019

Table S6. Results of a generalized linear model examining the difference in the longitudinal distribution of southward and northward migration between adult and juvenile godwits tracked in the same years.

Latitude	Southward Migration							Northward Migration						
	Mean longitude of crossing			SD (° longitude)			N_Ad	Mean longitude of crossing			SD (° longitude)			N_Ad
	Ad	Juv	P	Ad	Juv	P		Ad	Juv	P	Ad	Juv	P	
52°N	4.69	4.83	0.023	0.24	0.58	0.007	32	4.39	4.54	0.901	0.40	1.06	0.023	24
48°N	1.43	1.67	0.390	1.20	1.93	0.008	32	0.25	2.75	0.399	1.58	4.74	0.003	24
44°N	-1.72	-0.27	0.104	1.52	3.33	0.001	31	-2.37	1.11	0.436	2.11	6.77	0.015	24
40°N	-4.42	-3.23	0.346	1.78	4.47	0.002	31	-4.89	-1.86	0.735	2.62	8.59	0.011	25
36°N	-6.55	-4.85	0.689	1.62	4.45	0.002	25	-7.06	-3.13	0.361	2.78	8.05	0.053	19
32°N	-8.34	-7.11	0.653	2.09	4.75	0.022	25	-10.51	-7.89	0.190	3.98	7.85	0.277	24
28°N	-10.30	-8.94	0.248	2.54	5.06	0.057	25	-12.64	-10.48	0.286	4.42	7.59	0.434	24
24°N	-12.02	-11.02	0.420	3.05	5.18	0.149	25	-14.02	-12.32	0.356	4.11	7.11	0.314	26
20°N	-13.61	-12.03	0.214	2.97	5.22	0.076	25	-14.74	-13.04	0.251	3.11	5.94	0.281	26

Table S7. Results of a linear model examining the effects of crossing date, sex and year on the longitudinal displacement per latitudinal segment on southward migration of juvenile godwits.

Southward Migration											
Segment	Intercept	Date of crossing			Sex ¹			Year ²			N_Juv
	$\beta \pm SE$	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	
52°N – 48°N	270.43 ± 45.86	-21.84 ± 24.23	0.81	0.377	-50.46 ± 50.18	1.01	0.325	-28.41 ± 49.39	0.33	0.571	27
48°N – 44°N	188.90 ± 37.94	-6.26 ± 23.06	0.07	0.789	-4.96 ± 41.22	0.01	0.905	18.58 ± 41.17	0.20	0.656	26
44°N – 40°N	235.44 ± -79.02	0.86 ± 0.24	2.26	0.149	-54.09 ± 87.37	0.38	0.543	8.28 ± 86.64	0.01	0.925	24
40°N – 36°N	230.32 ± 56.69	-44.51 ± 30.57	2.12	0.165	6.28 ± 62.48	0.01	0.921	-98.93 ± 61.98	2.55	0.130	20
36°N – 32°N	202.92 ± 51.25	-75.78 ± 30.17	6.31	0.024	19.55 ± 56.56	0.12	0.734	-33.04 ± 55.79	0.35	0.562	19
32°N – 28°N	182.31 ± 31.34	-29.75 ± 18.28	2.65	0.124	-23.38 ± 34.88	0.45	0.513	30.96 ± 34.08	0.83	0.378	19
28°N – 24°N	209.89 ± 32.17	-18.99 ± 18.43	1.06	0.319	-34.03 ± 35.70	0.91	0.356	0.76 ± 34.87	0.00	0.983	19
24°N – 20°N	99.65 ± 70.94	18.41 ± 40.52	0.21	0.656	40.16 ± 78.80	0.26	0.618	10.33 ± 78.71	0.02	0.895	19

¹ Reference level for sex is female
² Reference level for year is 2016

Table S8. Results of a linear model examining the effects of crossing date, sex and year on the longitudinal displacement per latitudinal segment on northward migration of juvenile godwits.

Northward Migration											
Segment	Intercept	Hatching date			Sex ¹			Year ²			N_Juv
	$\beta \pm SE$	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	$\beta \pm SE$	F	P	
20°N – 24°N	-296.74 ± 70.59	-151.41 ± 49.11	9.51	0.018	166.26 ± 71.58	5.40	0.053	-93.05 ± 135.14 ³ 52.80 ± 70.56 ⁴	0.71	0.525	12
24°N – 28°N	-249.06 ± 76.73	-26.30 ± 53.42	0.24	0.638	-43.98 ± 78.63	0.31	0.593	199.68 ± 148.78 ³ 126.46 ± 77.71 ⁴	1.76	0.240	12
28°N – 32°N	-305.15 ± 86.12	15.02 ± 60.07	0.06	0.810	-14.17 ± 88.35	0.03	0.877	23.45 ± 167.20 ³ 162.98 ± 87.27 ⁴	1.82	0.231	12
32°N – 36°N	-279.64 ± 95.46	-59.82 ± 66.76	0.80	0.405	-152.49 ± 100.04	2.32	0.178	0.43 ± 181.97 ³ -43.46 ± 100.04 ⁴	0.10	0.907	11
36°N – 40°N	-190.95 ± 80.59	-24.01 ± 95.99	0.06	0.811	68.21 ± 105.85	0.42	0.543	-117.18 ± 23.42	1.48	0.269	10
40°N – 44°N	-67.41 ± 151.82	-91.75 ± 139.94	0.43	0.529	-77.47 ± 117.77	0.43	0.527	-168.90 ± 118.47	2.03	0.188	13
44°N – 48°N	-254.76 ± 177.24	104.88 ± 128.73	0.66	0.436	-54.11 ± 137.76	0.15	0.704	102.15 ± 138.00	0.55	0.478	13
48°N – 52°N	-418.20 ± 203.31	-20.46 ± 131.86	0.02	0.881	294.95 ± 149.72	3.88	0.090	300.44 ± 149.88	4.02	0.085	11

¹ Reference level for sex is female
² Reference level for year is 2018
³ Estimate for 2017 (1 individual)
⁴ Estimate for 2019

Table S9. Results of a generalized linear model examining the difference in orientation between adult juveniles from The Netherlands during south- and northward migrations.

Segment	Southward Migration							Northward Migration						
	Longitudinal movement (km)			SD (km)			<i>N_Ad</i>	Longitudinal movement (km)			SD (km)			<i>N_Ad</i>
	Ad	Juv	<i>P</i>	Ad	Juv	<i>P</i>		Ad	Juv	<i>P</i>	Ad	Juv	<i>P</i>	
52°N – 48°N	242.73	234.57	0.665	79.90	120.30	0.026	32	-311.33	-169.70	0.114	106.76	243.97	0.015	24
48°N – 44°N	249.97	199.49	0.066	105.26	96.16	0.961	31	-215.42	-130.70	0.183	130.85	224.81	0.144	24
44°N – 40°N	242.16	217.90	0.566	96.69	206.36	0.067	31	-216.75	-253.24	0.466	130.42	199.11	0.246	24
40°N – 36°N	216.30	183.23	0.410	121.25	145.40	0.295	25	-232.81	-199.74	0.667	218.93	133.42	0.363	19
36°N – 32°N	169.11	189.79	0.448	78.76	135.35	0.020	25	-249.33	-338.52	0.106	132.24	155.40	0.641	19
32°N – 28°N	192.85	179.92	0.599	84.63	73.63	0.805	25	-211.67	-254.19	0.415	147.68	141.51	0.956	24
28°N – 24°N	174.71	187.75	0.591	84.19	71.89	0.498	25	-145.94	-186.69	0.381	130.19	129.11	0.854	24
24°N – 20°N	166.04	130.94	0.361	99.21	152.40	0.299	25	-76.14	-75.91	0.997	165.72	160.39	0.919	26

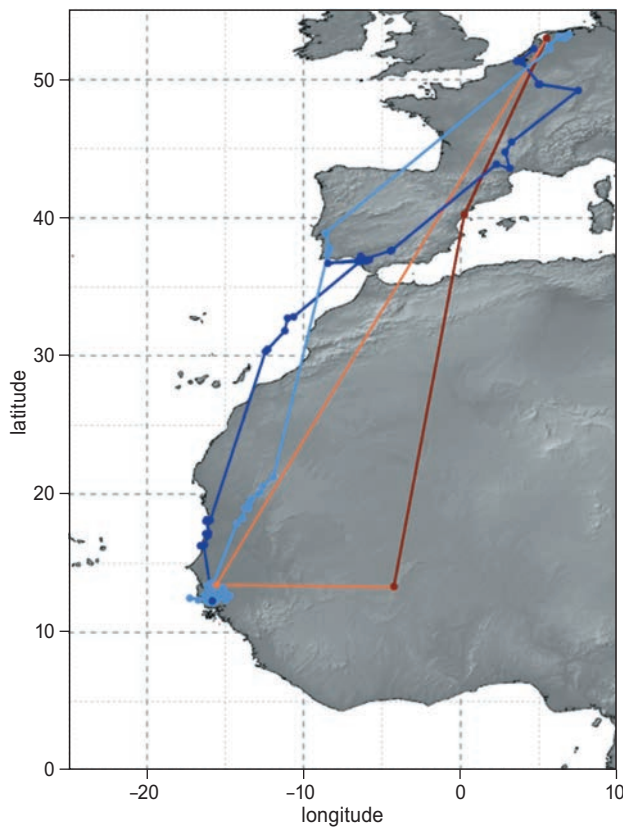


Figure S1. Tracks from a mother-daughter pair: mother tracked with a geolocator (red), daughter with satellite transmitter (blue). Light colours show southward migration and time spent on the non-breeding grounds, whereas dark colours show northward migration. On southward migration, the migratory timing of the pair was considerably different, but both mother and daughter flew to West Africa. However, after arriving in West Africa, and on northward migration, their routines again differed considerably. For the mother, the mean estimated locations of stationary periods are given.

