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Non-inherited factors shape adaptive potential in migratory routes and destination in a long-distance migrant

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ABSTRACT

Despite great descriptive knowledge on migration in birds, hardly anything is known about the developmental sources of this behavior, and thus the potential adaptive value through individual learning or cultural transmission. In a translocation and delayed-release experiment with juvenile hand-raised Black-tailed Godwits *Limosa limosa limosa*, we demonstrate that displaced juveniles adopt the spatiotemporal organization of migration that is habitual for the population at release rather than at origin. This leads us to reject the hypothesis that unexperienced migrants only rely on an innate navigational program, but is consistent with the idea that unexperienced migrants gradually increase their navigational capabilities through individual learning or cultural transmission. The experimentally induced ontogenetic variation in wintering sites of juvenile godwits indicates that the process of developmental flexibility offers substrate for rapid adaptation of long-distance migration.

INTRODUCTION

In the course of history, all extant organisms have successfully adjusted to changing ecological circumstances imposed by alternating glacial and interglacial periods and the correlated geographic distribution of suitable habitats. The current challenges set by rapid global change may therefore not be new, but the speed and extent of changes probably exceeds the rates in the past, and it is unclear whether species are able to adjust (Parmesan 2006). It is thus important to understand by which mechanisms species adjust, how fast these mechanisms operate, and whether the speed of adaptation is sufficient to maintain a viable population (Parmesan 2006, Botero *et al.* 2015). These mechanisms include not-mutually exclusive processes like individual learning, adaptive phenotypic plasticity, cultural inheritance and genetic evolution (Botero *et al.* 2015). Generally, it is considered that genetic evolution is the mechanism with the slowest response, while other processes like individual learning and/or cultural inheritance are expected to make organisms more responsive to change (Keith & Bull 2016, Berdahl *et al.* 2018). To demonstrate the latter mechanisms, it is crucial to show how information is transmitted

between generations, but also how innovations arise (Mueller *et al.* 2013, Berdahl *et al.* 2018).

If different populations of migrant birds vary in breeding and wintering locations and in the timing and routes of migration, they are an ideal model for experimentally testing how populations adapt to the changing conditions they live in (Piersma 2007). Such intraspecific population variation in migratory itineraries may appear as a result of genetic evolution (mostly shown for passerines: Helbig 1991, Berthold 2001, Lundberg *et al.* 2017, Scordato *et al.* 2020), but in other species intraspecific variation in migratory strategies appears to have originated so recently that alternative inheritance pathways may be implicated (Piersma 2011). In fact, evidence on soaring migrants and migrants that travel in family groups confirms that migration routes can be culturally inherited (Chernetsov *et al.* 2004, Mueller *et al.* 2013, Meyburg *et al.* 2017, Flack *et al.* 2018, Oudman *et al.* 2019). Obviously, cultural inheritance and genetic variation could both be at play, and their relative importance likely depends on the social information available to young individuals (Keith & Bull 2016, Berdahl *et al.* 2018). In this experimental study we experimentally examine the relative importance of innate vs. environ-

mental cues like the use of social information in the spatiotemporal organization of migration, and test whether early life experiences can create new phenotypic variation which could serve as a source for new adaptive, culturally inherited, migratory itineraries.

We carried out a juvenile translocation experiment with naïve hand-raised birds over 1000 km, transferring birds from a Dutch to a Polish population of Black-tailed Godwits (*Limosa limosa limosa*; hereafter: Godwits; Figure 15.1). The large Dutch population and the smaller Polish population do not differ genetically (as tested using neutral markers, Trimbos *et al.* 2014), but differ in migration direction and wintering area (Figure 15.1; Loonstra *et al.* 2019). Whereas Dutch godwits migrate in SW-direction and spend the winter in (coastal) West-Africa and the Iberian Peninsula, the Polish godwits first take a S- to SE-direction, before changing to a more S to SW-route; they winter mostly in wetlands in the central Sahel (Lake Chad and Inner-Niger Delta, Figure 15.1; Loonstra *et al.* 2019). Godwits migrate in flocks of conspecifics or similar species, but not in family groups (Verhoeven *et al.* 2019, under review a).

We collected complete clutches of four eggs during the first week of incubation in our study area in South-west Fryslân, The Netherlands (see: Kentie *et al.* 2018). After hatch in an incubator, chicks were kept inside for seven days, and taken to meadow enclosures till an age of 25 days. For each nest of four eggs collected in the Dutch population, we randomly assigned chicks at an age of 35.7 ± 2.9 days to the treatments: (1) release NL (53.00°N 5.58°E), normal timing (19 June), (2) release Poland (52.92°N 23.45°E), normal timing (19 June), (3) release NL, delay 28 days, (4) release Poland, delay 28 days. We hypothesize that if genetic information is important, translocated juvenile godwits would match the migratory direction of the source population (Figure 15.1). If individual learning of the cultural transmission of information is the major cue, we expect the delayed treatments to adhere less with the migration direction of the population of release, and we expect them to (a) have a genetically predisposition to migrate to the SW, or (b) show in increased variation in direction as they need social cues (Figure 15.1). As we followed surviving individuals until their first northward migration back to the breeding grounds, we also hypothesize that if animals imprint on a goal during early independent life, translocated individuals will return to their release sites. In contrast, if individuals would imprint on their natal site, they would return to their original natal site for breeding.

Departing on their first southward migration, translocated juveniles initially orientated more eastwards than siblings released in The Netherlands. After crossing 44°N, translocated godwits orientated more westwards, resembling what experienced Polish adults do (Figure 15.1; Table 15.1, S2). Furthermore, the orientation of juveniles released in The Netherlands or Poland did not differ from the orientation of experienced birds of the population at release (Figure 15.1; Table S2-3). These results reject the hypothesis that naïve Godwits solely rely on a genetically inherited navigation program during their first southward migration and are consistent with the alternative hypothesis that unexperienced Godwits have the flexibility to migrate along different migratory routes which are modified through environmental differences like the presence of different information from conspecifics.

The experimental delay resulted in an average 30 day later departure (Table 15.1). However, departure date did not affect the directionality of orientation among juveniles, nor did 'family' explain a large portion of the variation (Figure S1; Table 15.1, S1). Consistently, there were no differences between the variation of migratory orientation in early and late departing juveniles within the first two latitudinal segments (Table S11). On average, during southward migration all juveniles departed later than adults, but early translocated juveniles caught up with the adults at 44°N. The average timing of southward migration of Dutch adult Godwits was earlier than juvenile Dutch Godwits (Figure 15.2; Table S4-5). These results are not consistent with the idea that later departures should be based on less social information, yet suggest that later individuals would either rely on inherited directional information or were less directional altogether. We propose that delayed birds likely have some information available, either from the rare adults that migrate late or from other shorebird species sharing habitats and migration routes but migrating later in the year (Cohen & Satterfield 2020). Nevertheless, we did find evidence for an timing effect on resulting wintering sites. Perhaps as a consequence of having relatively less information, later departing juveniles more often wintered north of the Sahara (Table S7; $\beta_{\text{departure day}} = -0.034$ with SD 0.01, $P = 0.03$). This was not without a cost, as later departing individuals had a higher chance to die during their first southward migration, irrespective of release site (Table S6; $\beta_{\text{departure day}} = -0.034$ with SD 0.01, $P = 0.01$).

During their first northern winter, juveniles wintering in sub-Saharan Africa concentrated in the Inner Niger Delta, Lake Chad and the coast of West-Africa

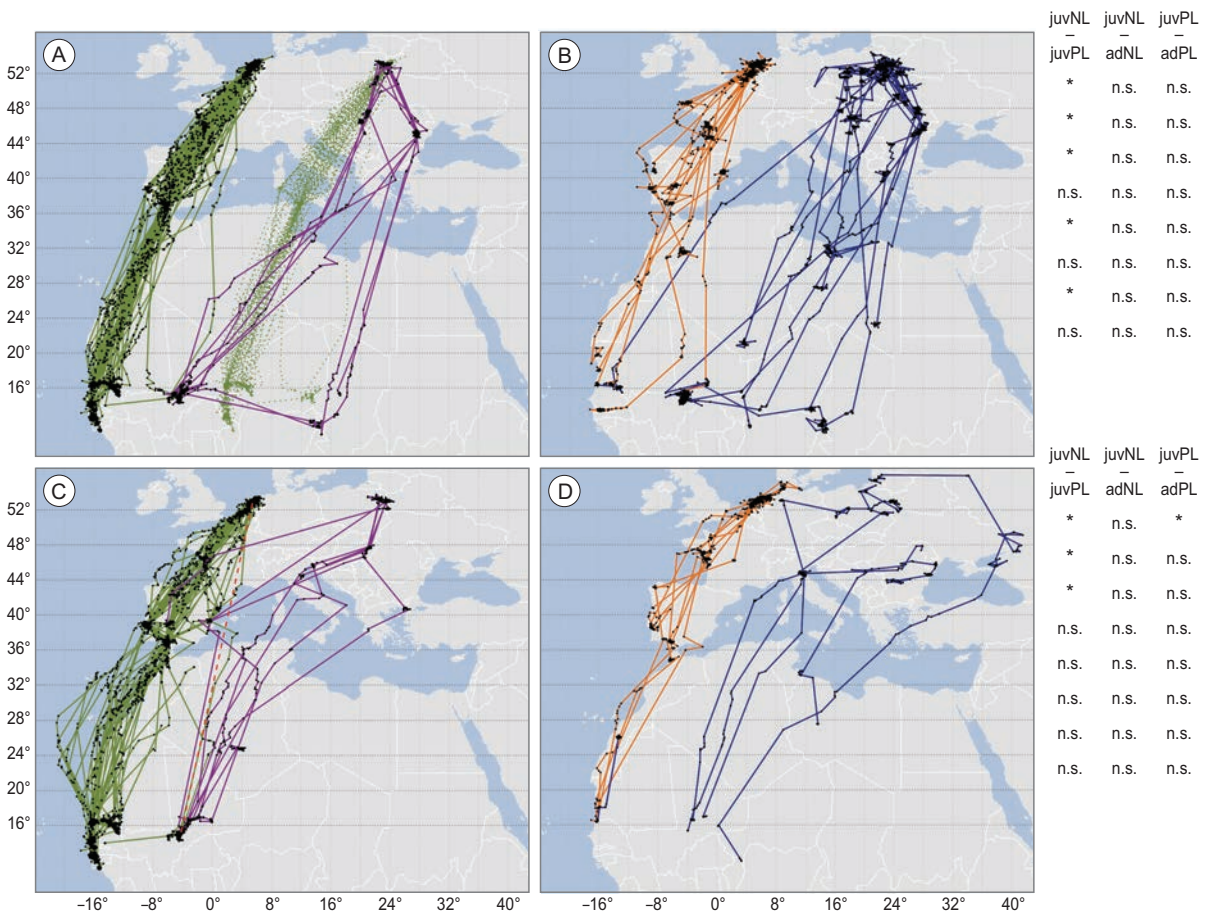


Figure 15.1. Observed migratory routes of adult godwits in Poland and The Netherlands and predicted and observed routes of hand-raised godwits during south- and northward migration. A) Observed migratory routes of Dutch (green) and Polish (purple) adult Godwits during southward migration (Loonstra *et al.* 2019, Verhoeven *et al.* under review *b*). Predicted range of routes of hand-raised godwits released in The Netherlands (green) during southward migration and predicted range of routes for translocated godwits when solely relying on an innate clock-compass mechanism (dotted-green) and predicted range of routes for translocated godwits when using social information (purple). B) Observed migratory routes of hand-raised godwits released in The Netherlands (orange) or released in Poland (blue) during southward migration. C) Observed migratory routes of Dutch (green) and Polish (purple) adult Godwits during northward migration. Predicted range of routes for hand-raised godwits released in The Netherlands (green) during northward migration and predicted range of routes for translocated godwits when individuals re-calibrated their compass and navigate back to The Netherlands (dotted-red) and predicted range of routes for translocated godwits when using social or learned information (purple). D) Observed migratory routes of hand-raised godwits released in The Netherlands (orange) or released in Poland (purple) during northward migration. Significant differences in orientation between juveniles released in The Netherlands or Poland, juveniles released in The Netherlands and Dutch adults and juveniles released in Poland and Polish adults are displayed per latitudinal boundary (see also: Table 15.1-2, S2-S3).

(ranging from Mauritania in the north to Guinée-Conakry in the south; Figure 15.1). While the within-winter movements of individual juvenile Godwits released in The Netherlands were within a range of 0 – 300 km, it is noticeable that all translocated juveniles except one clustered in the Inner Niger Delta (Mali) (Figure 15.1). Juveniles translocated to Poland wintering in sub-Saharan Africa reached the Inner Niger

Delta often after another (energetically demanding) westward migration of ~2500 km, similar to some adult Polish Godwits (Loonstra *et al.* 2019). Because the timing of these intra-Africa movements overlapped between experienced and unexperienced birds, we interpret this as additional evidence for juvenile Godwits actively using information from experienced individuals (Figure 15.1).

Table 15.1. Results of a linear mixed model examining the effect of release location (NL or PL), year (2016 or 2017) and initiation of migration (date of 52°N crossing) on orientation angle during the first southward migration between all nine latitudinal boundaries.

LatFromTo	n	Intercept		RLoc ¹ *DO52C		RLoc ¹		DO52C		Year ³		Family
		β ± SE	P	β ± SE	P	β ± SE	P	β ± SE	P	β ± SE	P	
52°N – 48°N	32	493.5 ± 104.5	<0.001	3.3 ± 4.2	0.43	-519.8 ± 146.6	<0.001	1.3 ± 2.0	0.51	-119.2 ± 156.7	0.46	0.11 (0.00 – 0.58)
48°N – 44°N	25	512.9 ± 96.0	<0.001	0.3 ± 3.9	0.93	-308.4 ± 133.1	0.02	0.1 ± 1.9	0.94	-125.8 ± 133.5	0.35	0.01 (0.00 – 0.65)
44°N – 40°N	25	229.2 ± 95.0	<0.001	2.4 ± 4.5	0.60	271.3 ± 126.0	0.03	-1.0 ± 2.2	0.66	-99.9 ± 132.5	0.46	0.11 (0.00 – 0.74)
40°N – 36°N	19	405.7 ± 73.8	<0.001	-3.7 ± 4.2	0.38	43.4 ± 138.8	0.76	4.5 ± 2.0	0.06	-46.1 ± 162.3	0.78	0.08 (0.00 – 0.89)
36°N – 32°N	19	-911.3 ± 489.5	<0.001	-2.6 ± 4.1	0.54	263.7 ± 143.3	0.03	4.6 ± 2.0	0.07	-20.4 ± 206.8	0.92	0.17 (0.00 – 0.91)
32°N – 28°N	17	370.5 ± 93.8	<0.001	2.4 ± 2.5	0.35	-7.6 ± 16.1	0.25	0.3 ± 2.5	0.84	223.2 ± 184.7	0.58	0.05 (0.00 – 0.81)
28°N – 24°N	16	371.5 ± 140.4	<0.001	-5.2 ± 2.7	0.08	140.4 ± 32.4	<0.01	3.9 ± 2.6	0.14	55.4 ± 225.8	0.84	0.04 (0.00 – 0.95)
24°N – 20°N	13	432.3 ± 82.3	<0.001	1.0 ± 4.5	0.91	116.7 ± 94.5	0.22	2.7 ± 2.1	0.22	-195.9 ± 157.1	0.86	–

¹ Reference level for release location is The Netherlands

² Date of 52°N crossing

³ Reference level for year is 2016

After spending 7–31 months at their wintering grounds, juveniles initiated their first northward migration. Juveniles released in The Netherlands returned to the breeding grounds using migratory routes that were similar to their first southward migration (Figure 15.1, S2; Table 15.2, S2-S3, S9). In contrast, the translocated juveniles made a return migration to their release site in Poland by routes that were rather dissimilar to their first southward migration (but see Figure S2: i157500) and strikingly different from those of the juveniles released in The Netherlands (Figure 15.1, S2; Table 15.2, S9). As the timing of departure and routes of translocated juveniles did not differ from the Polish adults (Figure 15.2; Table S4-5), translocated juveniles again could have made use of experienced Polish adults (Table S8). Although juveniles released in The Netherlands on average departed later than adults breeding in The Netherlands, there was still considerable overlap in departure dates and together with the observed high similarity with autumn routes, these first northward migrations may be steered by the previously social and asocial information or newly learned during this first northward migration.

Our experiment demonstrates that during their first southward migration godwits do not rely on an inherited navigational program. In fact, the migratory movements of translocated godwits suggest that routes of unexperienced migrants are modified through use of information from more experienced individuals (Figure 15.1). The prevalence of studies on orientation in unexperienced birds, i.e. carried out in experimental settings in laboratory conditions (Berthold 1992, Mouritsen *et al.* 2018), may have yielded a simplified view of orientation in unexperienced migrants (Wikelski *et al.* 2007, Piersma *et al.* 2020), or an underappreciation of the variation in orientational cues used during first migration in different species in the wild (Berthold & Terrill 1991). In fact, inspired by Hamilton (1962), Van Doren *et al.* (2018), Nussbaumer *et al.* (2019) and Winger *et al.* (2019), we suggest that the presence and the use of information from both conspecifics and non-conspecifics during migration is much more important and taxonomically widespread than has recently been granted (Berdahl *et al.* 2018, Piersma *et al.* 2020, Cohen & Satterfield 2020).

We provide evidence that induced ontogenetic variation results in different wintering destination. Our experimental demonstration of newly learned migratory routines shows that new routes could readily be established through unexperienced individuals. These results suggest that between-population variation in migratory itineraries may reflect considerable respon-

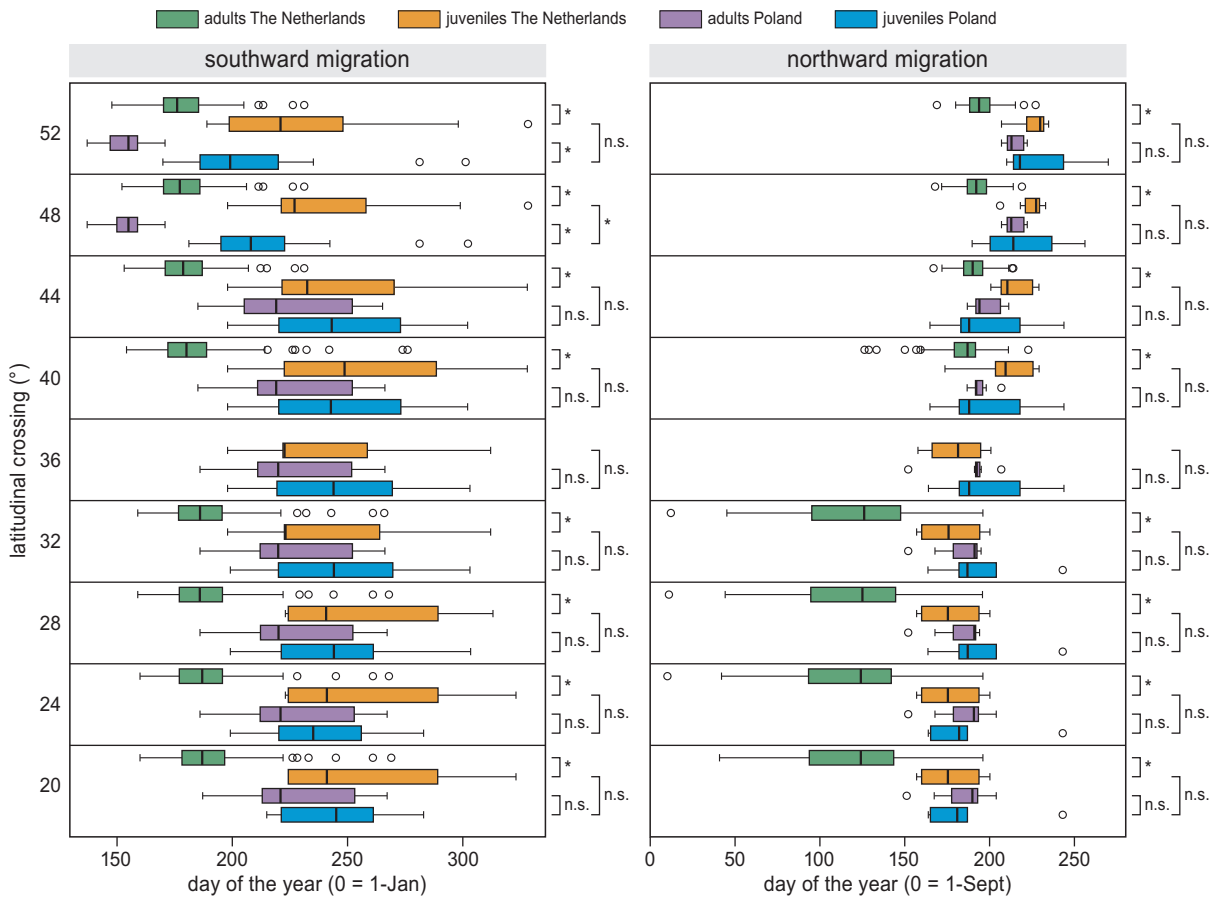


Figure 15.2. Timing of south- and northward migration of adult and hand raised godwits from Poland and The Netherlands. Observed variation in migratory timing during south- and northward migration of adult godwits from The Netherlands (green), adult godwits from Poland (purple), hand raised juveniles released in The Netherlands (orange) and hand-raised juveniles released in Poland (blue) per latitudinal crossing. Timing is expressed as the day of the year; 0 = 1st of January during southward migration and 1st of September during northward migration. Significant differences in timing between juveniles released in The Netherlands or Poland, juveniles released in The Netherlands and Dutch adults and juveniles released in Poland and Polish adults are displayed per latitudinal boundary (see also: Table S1, S4-S5).

Table 15.2. Results of a generalized linear model examining the effect of release location (Poland vs. The Netherlands) on the orientation of hand raised godwits during the first northward migration between all nine latitudinal boundaries.

LatFromTo	n	Intercept		Release location ¹	
		$\beta \pm SE$	P	$\beta \pm SE$	P
48°N – 52°N	11	-570.2 ± 109.6	<0.001	659.9 ± 209.9	0.01
44°N – 48°N	12	-532.2 ± 103.9	<0.001	638.4 ± 198.9	0.01
40°N – 44°N	13	-486.3 ± 44.5	<0.001	-147.0 ± 68.9	0.04
36°N – 40°N	13	-227.5 ± 157.9	0.19	-326.2 ± 211.9	0.17
32°N – 36°N	9	-536.8 ± 36.9	<0.001	-20.1 ± 49.5	0.97
28°N – 32°N	9	-511.1 ± 168.6	0.02	179.7 ± 226.2	0.45
24°N – 28°N	9	-500.4 ± 39.7	<0.001	-20.7 ± 56.1	0.72
20°N – 24°N	9	-479.2 ± 19.3	<0.001	-6.1 ± 25.9	0.82

¹ Reference level for release location is The Netherlands

siveness to environmental change. Furthermore, if cultural transmission during migration does not just rely on information of conspecifics (Cohen & Satterfield 2020), rapid population adjustments through developmental plasticity are even more likely (Verhoeven *et al.* 2018, Gill *et al.* 2019).

Although we argue that developmental plasticity and thus the ability to learn new migratory routes enhances the adaptive potential of migratory behavior, multiple examples exist of supposedly sub-optimal routes (Sutherland 1998). These have been suggested to result from historical constraints (e.g. glacial refugia, Bairlein *et al.* 2012, Sokolovskis *et al.* 2018) and with our current knowledge it seems more likely that genetic constraints have prevented a more optimal route than the lack of phenotypic plasticity. However, we argue that species vary from being mostly controlled by innate factors to being mostly controlled by culturally transmitted information. The speed of adaptation of a species likely depends on these two axis. We argue that godwits are at the latter part of this continuum. Obviously, this does not mean that their adaptive possibilities are unlimited. Especially in wading birds, suitable habitats are few and far between and being lost continuously by human activity. Thus, while they may have adopted a strategy of rapid innovation, when suitable habitats are gone, they can no longer adapt.

MATERIAL AND METHODS

Experimental birds

Black-tailed Godwits *Limosa limosa limosa* used for this experiment were reared in captivity in The Netherlands (52.94°N; 5.48°E). During the breeding season of 2016 and 2017 we collected 72 eggs from 18 clutches; all eggs were collected in our 12.000 ha study area in southwest Fryslân, The Netherlands (see: Howison *et al.* 2018, Kentie *et al.* 2018). Eggs were incubated in an incubator (Heka STANDARD 9) at a temperature of 37.5°C and a relative humidity of 55–60%. To allow the assignment of hatchlings to their original nest, we marked each egg with a unique number; after hatching we individually marked chicks with a plastic engraved flag with a unique code of three characters. Chicks were kept indoors during the first week of their life. Single 100-W infrared lamps in each of the 6.25 m² indoor cages provided them with the necessary amount of warmth. Chicks were divided equally among the eight indoor cages and to prevent group effects, we randomly shuffled the chicks between the groups every day. Indoor day lengths were similar to the conditions

outside. With all nights spent indoors, before release the chicks were never exposed to night time skies. From ages greater than seven days, all chicks spent every other day outside in 2500 m² enclosure in a meadow from 08:00 to 17:00 h. Indoors, chicks were fed with waterfowl food (Micro Lundi, Lundi; Verl, Germany) and occasionally live buffalo worms (*Alphitobius diaperinus*). In the outside enclosures, chicks were able to forage on natural occurring prey-items. Both indoors and outdoors, water was made available *ad libitum* in shallow bowls. At age 25, chicks were kept inside and moved into in an aviary with a ground surface of 82 m² and a height of 3.5 m. In this aviary birds were able to fly and had *ad libitum* access to food and water.

Tracking and translocation

At an average age of 35.7 ± 2.3 days in 2016 and 35.6 ± 3.3 days in 2017, we divided the four family members over four different groups. The first two groups of naïve chicks were either released at their ‘natural’ fledging date (19 June) in The Netherlands (53.00°N 5.58°E) or translocated and released in Poland (52.92°N 23.45°E). The other two groups were delayed by 28 days and then released at the same locations. Prior to the transport and release of the birds, we checked the status and health of all birds. Birds were transported in individual cages of wood. During the 15 hr long car-transport to Poland, we stopped every ~2.5 hr to supply the birds with fresh food and water. All birds were outfitted with 5-g solar platform transmitting terminals (PTT; Model 100, Microwave Telemetry, Columbia, MD, USA). Transmitters were preprogrammed to turn on for 8 hours and to turn off for 24 hours year-round. We placed transmitters on the back of each bird using a leg-loop system consisting of Dynemaa-rope (Lankhorst Ropes, Sneek, The Netherlands), transmitters were slightly elevated by gluing a small piece of neoprene (24.6 mm × 15.2 mm × 1.9 mm; l × w × h) under the transmitter. The weight of the PTT and harness (~6.0 g) represented ~2.0% of the total body mass at release. All birds were monitored until the PTT stopped transmitting, or if the temperature sensor started to follow a day-night rhythm which indicated the death of a bird (see Loonstra *et al.* 2019). Locations were retrieved via the CLS tracking system (www.argos-system.org) and passed through the “Best Hybrid-filter” algorithm (Douglas *et al.* 2012) to remove unrealistic locations that exceeded 120 km h⁻¹, while retaining location-classes with quality 3, 2, 1, 0, A, B. On average this resulted in 2.56 ± 0.85 SD locations per duty cycle.

Data analysis

All statistical analyses were performed using R (v. 3.4.3; R Core Development Team 2018).

TIMING

To summarize the timing of migration during the first south- and northward migration of the hand-raised juveniles, for each individual we determined its crossing of the following nine latitudinal boundaries: 52°N, 48°N, 44°N, 40°N, 36°N, 32°N, 28°N, 24°N, 20°N. Timing of migration of adult godwits at these latitudinal boundaries was obtained from Verhoeven *et al.* (2019) for the Dutch population and Loonstra *et al.* (2019) for the Polish population. Unfortunately, we lack information on the timing of migration of Dutch adult godwits of the 36°N crossing, as a result we were not able to infer potential differences between Dutch adults and juveniles at this crossing during north- and southward migration (see: Verhoeven *et al.* 2019). Part of the adult data were collected in years prior to this experiment (southward migration data of Dutch adults collected in 2012–2018; northward migration data of Dutch adults collected in 2013–2019; southward migration data of Polish adults collected in 2015–2018; northward migration data of Polish adults collected in 2015–2019, Verhoeven *et al.* 2019, Loonstra *et al.* 2019).

To evaluate potential differences in timing during southward migration between juveniles released in The Netherlands and Poland, release moment (normal or delayed), and year (2016 or 2017), we constructed a linear mixed model per latitudinal boundary. Since we tracked multiple members of the same family at most crossings (Table S12), we included FamilyID as a random effect if the number of families exceeded three (i.e. in such cases we constructed a generalized linear model). In a second step, we compared the timing of hand-raised juvenile birds released in The Netherlands vs. Dutch adults and hand-raised juvenile birds released in Poland vs. adults in Poland during southward migration using a generalized linear model.

The statistical significance of potential differences in timing between juveniles released in Poland and The Netherlands during their first northward migration was compared using a generalized linear model (no siblings from the same family in this dataset). We also used a generalized linear model to compare the timing of juvenile birds released in The Netherlands vs. Dutch adults and juvenile birds released in Poland vs. adults in Poland during northward migration.

ORIENTATION

To tell and compare the migratory orientation during the first south- and northward migration between all hand-raised juveniles, for each individual we determined the east-west movement in km between all nine consecutive latitudinal boundaries. The east-west movement of adult godwits from Poland and The Netherlands within in the same segments was obtained and compared with data from Loonstra *et al.* 2019 (Polish-population) and Verhoeven *et al.* in prep. (Dutch-population).

Differences in orientation during southward migration between juveniles released in The Netherlands and Poland, release moment (normal or delayed), and year (2016 or 2017) per latitudinal boundary were evaluated using a linear mixed model. Since we tracked multiple members of the same family, we included FamilyID as a random effect if the total number of simultaneously tracked families was higher than three. We compared the orientation of juvenile birds released in The Netherlands vs. Dutch adults and juvenile birds released in Poland vs. adults in Poland during southward migration using a generalized linear model.

The statistical significance of differences in orientation between juveniles released in Poland and The Netherlands during their first northward migration was compared using a generalized linear model (no siblings in this dataset). Also, we used a generalized linear model to compare the orientation of juvenile birds released in The Netherlands vs. Dutch adults and juvenile birds released in Poland vs. adults in Poland during northward migration.

CROSSING OF SAHARA

Southward migration was considered ended after 24 November, the of the last southward migratory movement > 100 km of a juvenile (in this case of a bird that flew from The Netherlands to Portugal). The latest Sahara crossing occurred on 19 November. We determined the winter destination, and whether or not an individual crossed the Sahara (successful crossing of 20°N), of each individual alive at 24 November. Subsequently, we used a generalized linear mixed effect model with a binomial error distribution to examine the following fixed effects on Sahara crossing: departure date, year (2016 or 2017) and release location (The Netherlands or Poland). Departure date was defined as the day on which an individual crossed 52°N. To account for the non-independency of multiple individuals from the same family, we included “FamilyID” as a random intercept.

MORTALITY DURING FIRST SOUTHWARD MIGRATION

We first determined the fate of all hand-raised juveniles at 24 November using the diagnostic rules explained above (Loonstra *et al.* 2019). Mortalities above 52°N were excluded, as these were considered to be unrelated to migration. We then used a generalized linear mixed effect model with a binomial error distribution to examine the following fixed effects on mortality during the first southward migration of hand-raised individuals: departure date, year (2016 or 2017) and release location (The Netherlands or Poland). Migratory departure date was defined as the day on which an individual crossed 52°N. To account for the non-independency of multiple individuals from the same family, we included “FamilyID” as a random intercept.

ROUTE SIMILARITY NORTH- AND SOUTHWARD MIGRATION JUVENILES.

We defined the similarity of the first south- and northward migration route of an individual by the distance between the north- and southward crossing of each arbitrary latitudinal boundary; 52°N, 48°N, 44°N, 40°N, 36°N, 32°N, 28°N, 24°N, 20°N. We then applied a generalized linear model to determine any significant differences in route similarity between juveniles translocated to Poland and juveniles released in The Netherlands.

VARIATION IN MIGRATORY ORIENTATION

To test for differences in the variation of migratory orientation within the first two latitudinal segments between juveniles that were released in The Netherlands or Poland and were either delayed or released at their natural fledging date we used a Levene’s test which is part of the package ‘car’ (Fox & Weisberg 2019).

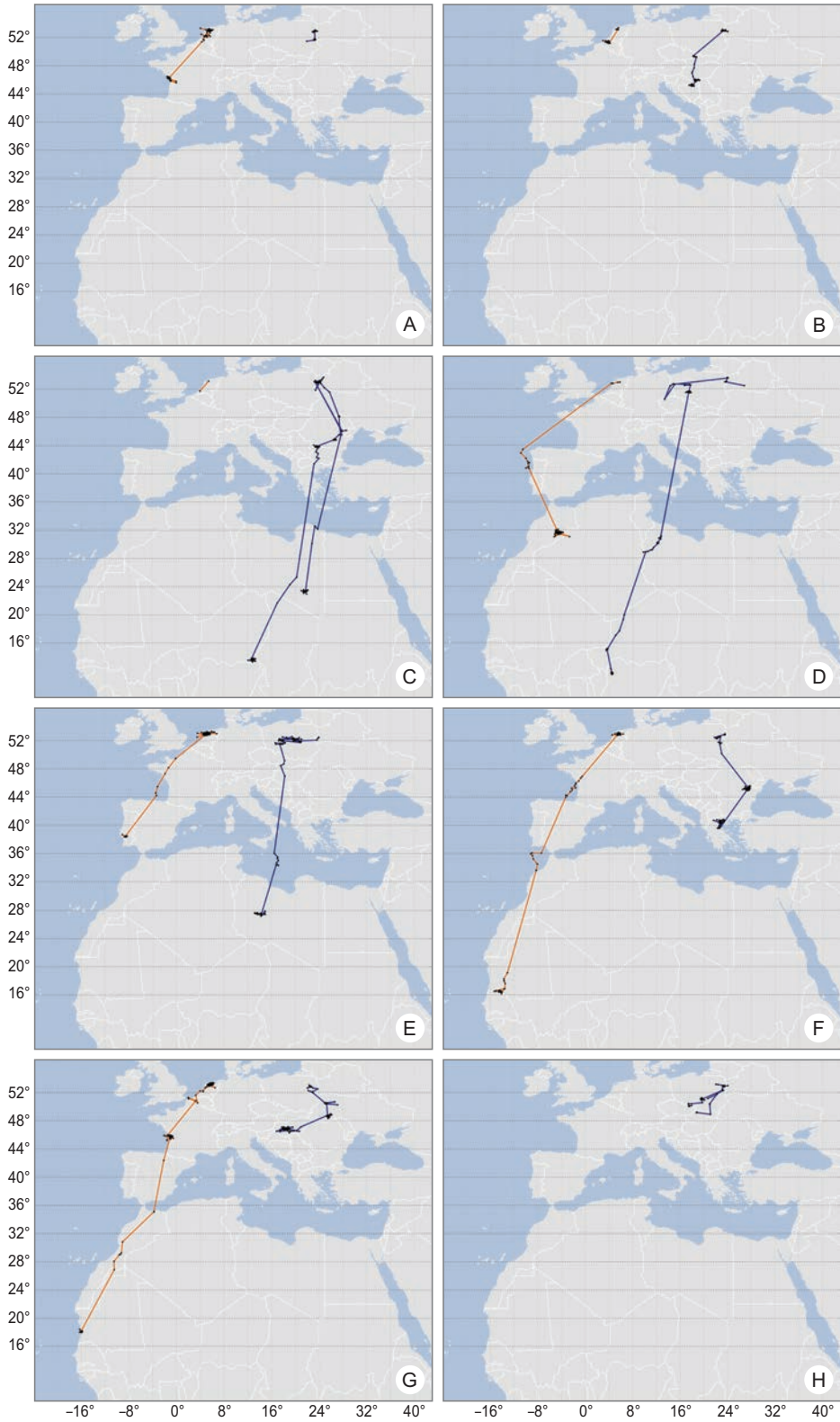
GENERAL

In all models the statistical significance of fixed effects was assessed using parametric bootstrapping tests using the ‘pbkrtest’ package (Halekoh & Højsgaard 2014). The adjusted repeatability of the random intercepts was computed using the package “rptR” (Stoffel *et al.* 2017). All calculated great circle distance were computed using the function “distHaversine” in the package “geosphere” (Hijmans 2017). Presented maps were constructed using background maps from Natural Earth (www.naturalearthdata.com).

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SUPPLEMENTARY MATERIAL



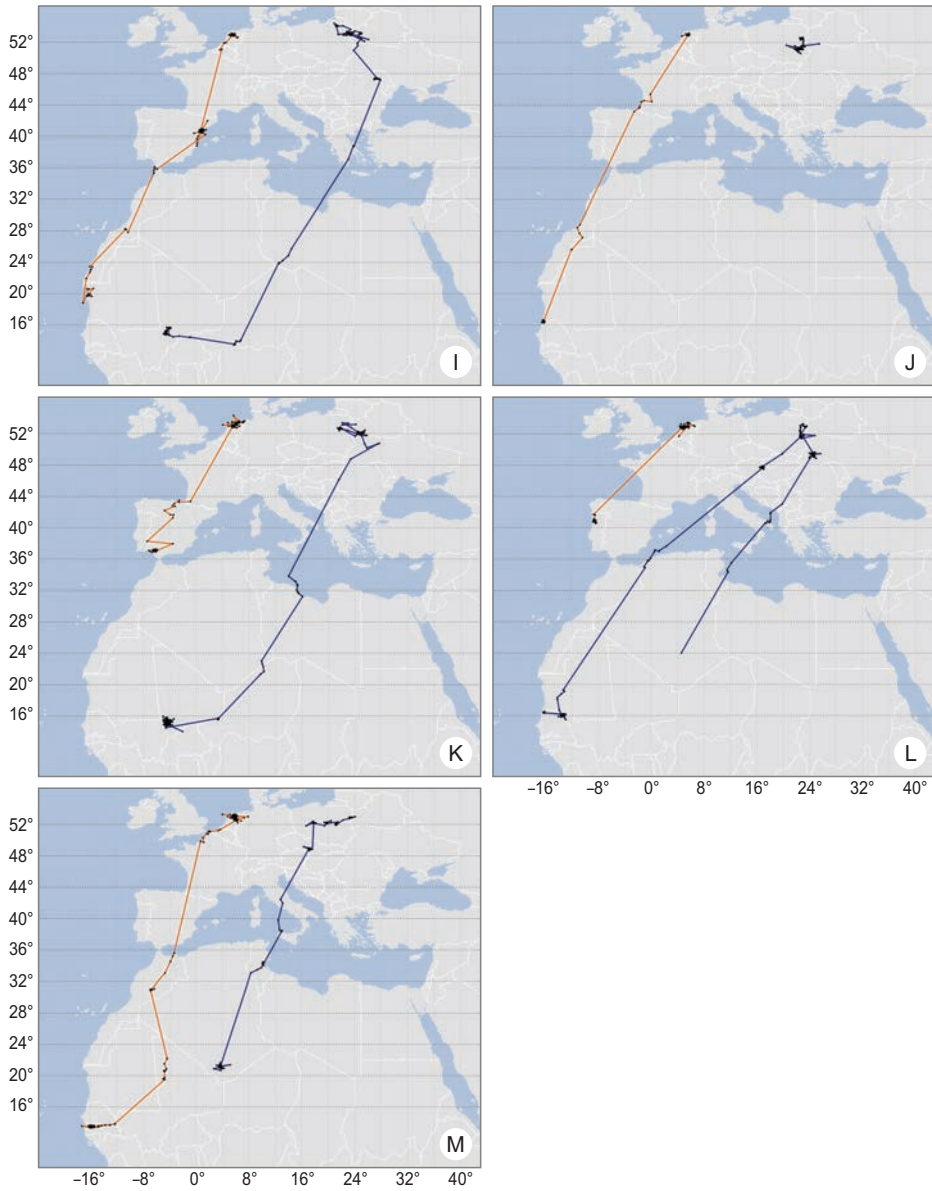
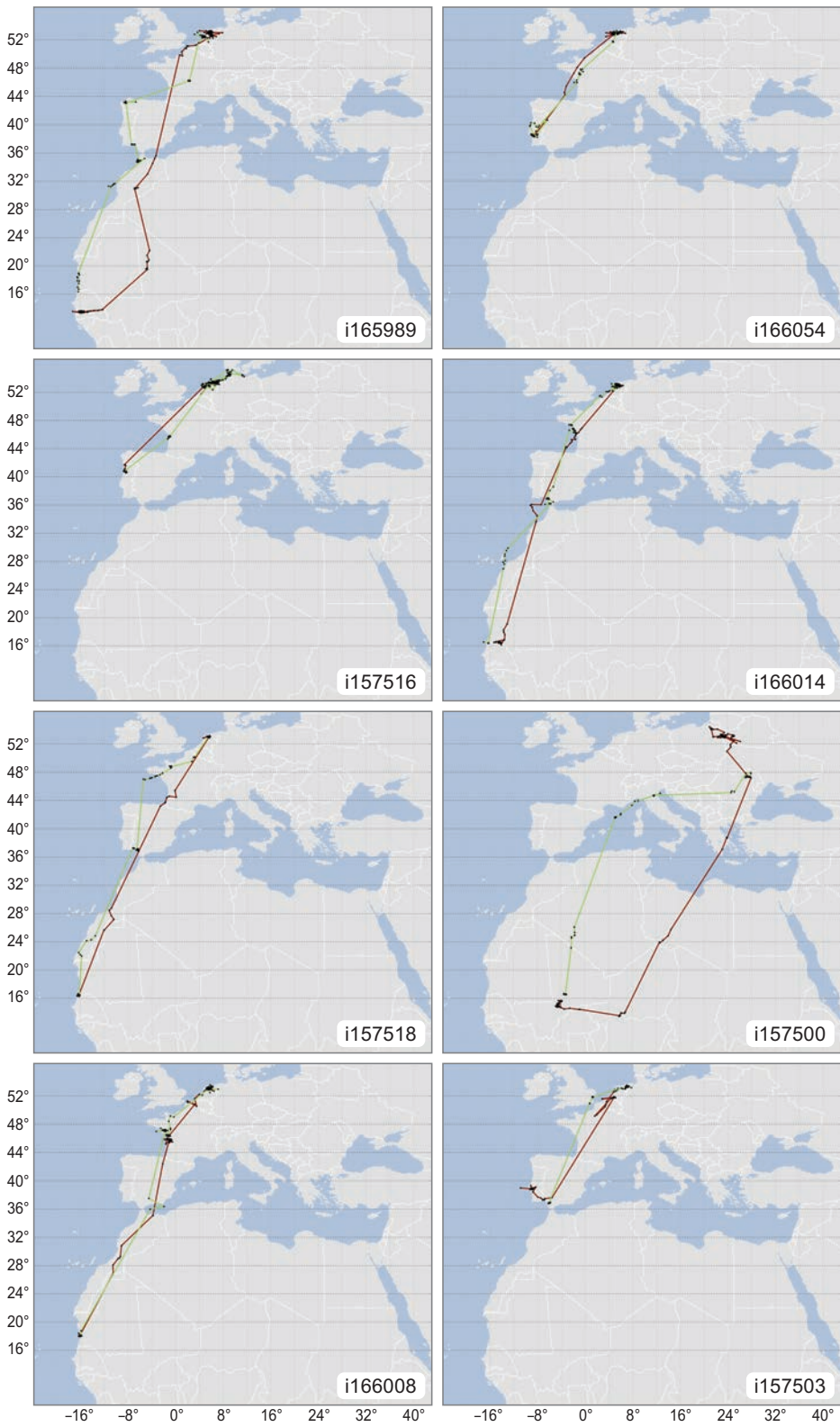


Figure S1. Migratory routes during southward migration of hand-raised juvenile Godwits per family. Each plot captures the migratory route of all siblings from one family. Blue lines correspond to siblings released in Poland, while yellow lines refer to family members released in The Netherlands.



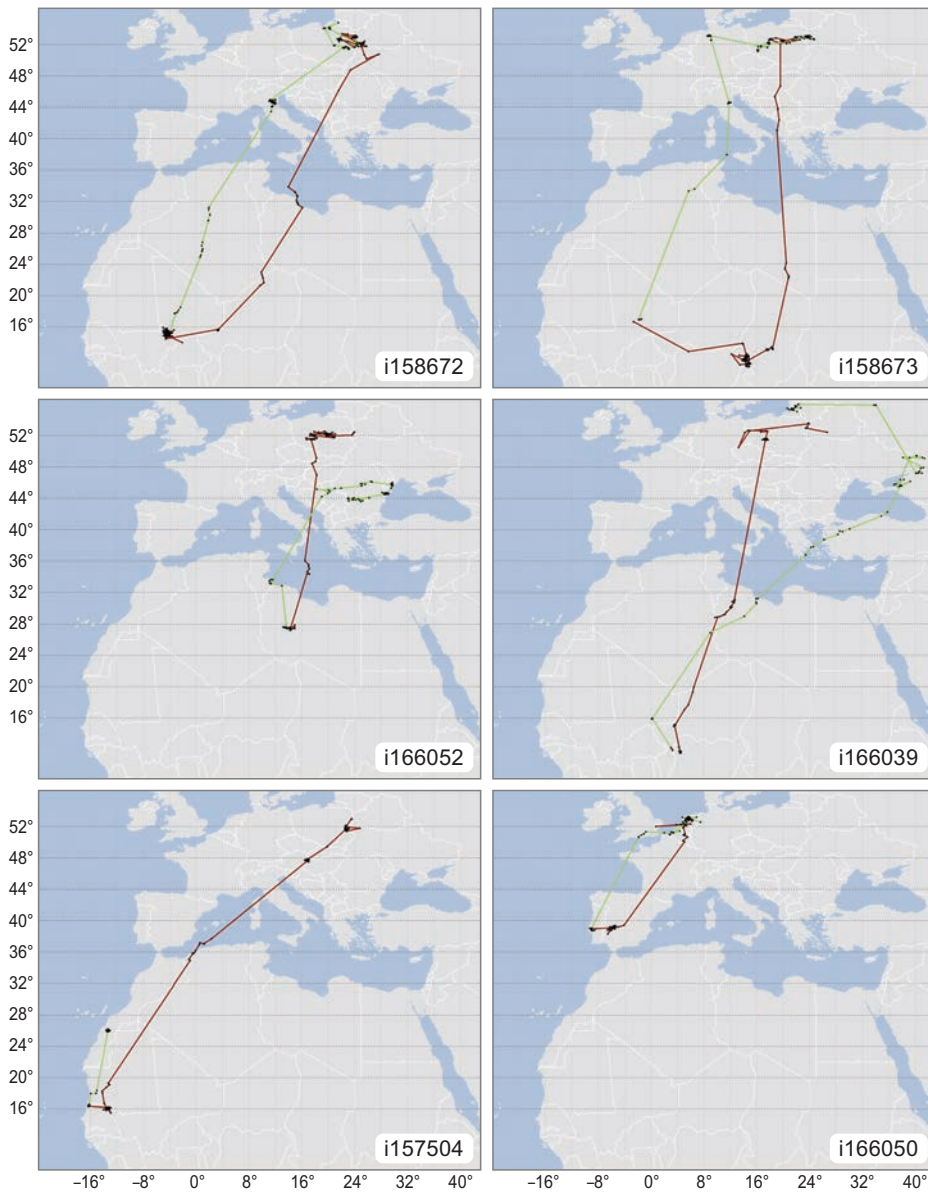


Figure S2. Migratory routes of juvenile hand-raised godwits during their first south- and northward migration. Each plot corresponds to one of the fourteen juvenile godwits that could be tracked during the first south- and northward migration. Red lines correspond to route of an individual during southward migration, while dark-green lines display the first northward migration of an individual.

Table S1. Results of a linear mixed model examining the effect of release location (NL or PL), year (2016 or 2017) and release moment (normal or delayed) on timing of migration during the first southward migration at all nine latitudinal boundaries.

LatCross	Fixed Effects								Random Effect
	Intercept		Loc ¹		Release Moment ²		Year ³		Family
	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>	<i>r</i> (95%CI)
52°N	204.6 ± 7.6	<0.001	-17.7 ± 9.7	0.08	30.0 ± 10.6	<0.01	-1.1 ± 11.1	0.93	0.12 (0.00 – 0.53)
48°N	223.4 ± 9.5	<0.001	-23.4 ± 10.8	0.04	34.2 ± 11.0	<0.01	-8.3 ± 11.5	0.48	0.04 (0.00 – 0.52)
44°N	232.9 ± 8.4	<0.001	-8.7 ± 13.0	0.92	31.4 ± 12.7	0.02	-1.3 ± 13.0	0.51	0.08 (0.00 – 0.56)
40°N	251.1 ± 7.2	<0.001	-9.7 ± 13.9	0.49	23.6 ± 13.9	0.10	1.3 ± 14.5	0.93	0.03 (0.00 – 0.64)
36°N	244.0 ± 7.7	<0.001	-0.8 ± 18.7	0.97	12.7 ± 16.2	0.44	3.8 ± 16.8	0.83	0.00 (0.00 – 0.81)
32°N	244.9 ± 7.8	<0.001	-1.3 ± 19.0	0.94	11.4 ± 16.4	0.50	5.8 ± 17.1	0.74	0.00 (0.00 – 0.76)
28°N	247.6 ± 8.5	<0.001	-24.7 ± 13.6	0.21	15.5 ± 17.5	0.39	8.8 ± 16.6	0.61	0.29 (0.00 – 0.90)
24°N	244.6 ± 8.5	<0.001	-20.1 ± 15.8	0.23	17.5 ± 20.7	0.42	5.9 ± 18.0	0.77	0.24 (0.00 – 0.92)
20°N	248.3 ± 9.1	<0.001	29.0 ± 24.6	0.26	42.9 ± 25.8	0.13	11.8 ± 19.0	0.55	–

¹ Reference level for release location is The Netherlands² Reference level for release moment is 'normal'³ Reference level for year is 2016**Table S2.** Results of a generalized linear model examining the difference in orientation between adult Godwits breeding in Poland and juveniles released in Poland during south- and northward migration.

Southward migration					Northward migration				
LatFromTo	Intercept		Age ¹		LatFromTo	Intercept		Age ¹	
	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>		$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>
52°N – 48°N	6.1 ± 38.7	0.88	52.8 ± 81.7	0.52	48°N – 52°N	-265.2 ± 129.9	0.07	207.0 ± 291.7	0.50
48°N – 44°N	62.8 ± 31.6	0.06	39.7 ± 57.2	0.24	44°N – 48°N	-453.1 ± 106.2	<0.01	345.0 ± 213.4	0.07
44°N – 40°N	167.3 ± 30.3	<0.001	-6.1 ± 62.9	0.92	40°N – 44°N	-324.3 ± 112.3	<0.05	-160.9 ± 233.4	0.51
40°N – 36°N	208.2 ± 36.6	<0.001	-82.2 ± 73.5	0.28	36°N – 40°N	-301.5 ± 76.4	<0.01	-15.43 ± 161.5	0.93
36°N – 32°N	242.4 ± 40.5	<0.001	-157.6 ± 75.7	0.21	32°N – 36°N	-231.2 ± 70.1	<0.01	-74.4 ± 147.3	0.62
32°N – 28°N	248.9 ± 37.2	<0.001	-113.9 ± 71.9	0.13	28°N – 32°N	-229.3 ± 55.5	<0.01	65.3 ± 116.2	0.59
28°N – 24°N	255.0 ± 34.1	<0.001	89.6 ± 159.7	0.58	24°N – 28°N	-195.9 ± 38.1	<0.001	-70.3 ± 80.2	0.40
24°N – 20°N	244.3 ± 35.5	<0.001	95.4 ± 89.4	0.29	20°N – 24°N	-178.3 ± 24.5	<0.001	8.4 ± 52.4	0.88

¹ Reference level for age is adult¹ Reference level for age is adult

Table S3. Results of a generalized linear model examining the difference in orientation between adult Godwits breeding in The Netherlands and juveniles released in The Netherlands during south- and northward migration.

Southward migration					Northward migration				
LatFromTo	Intercept		Age ¹		LatFromTo	Intercept		Age ¹	
	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>		$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>
52°N – 48°N	234.3 ± 10.1	<0.001	49.6 ± 36.0	0.60	48°N – 52°N	-307.8 ± 15.8	<0.001	-60.2 ± 42.4	0.16
48°N – 44°N	220.5 ± 16.4	<0.001	-60.3 ± 42.4	0.51	44°N – 48°N	-244.5 ± 20.0	<0.001	-36.3 ± 53.5	0.50
44°N – 40°N	210.5 ± 12.1	<0.001	52.3 ± 104.3	0.62	40°N – 44°N	-231.2 ± 21.3	<0.001	-61.84 ± 58.5	0.35
40°N – 36°N	199.0 ± 20.2	<0.001	-48.1 ± 62.6	0.45	36°N – 40°N	-194.7 ± 37.2	<0.001	173.3 ± 117.9	0.15
36°N – 32°N	171.5 ± 13.4	<0.001	-61.0 ± 40.8	0.14	32°N – 36°N	-268.6 ± 24.8	<0.001	-33.6 ± 79.8	0.68
32°N – 28°N	177.2 ± 10.5	<0.001	-49.2 ± 33.8	0.15	28°N – 32°N	223.9 ± 25.7	<0.001	-33.0 ± 89.3	0.71
28°N – 24°N	163.7 ± 12.7	<0.001	-13.9 ± 44.9	0.76	24°N – 28°N	-144.8 ± 18.8	<0.001	-79.4 ± 64.5	0.23
24°N – 20°N	171.2 ± 13.1	<0.001	-37.3 ± 69.3	0.59	20°N – 24°N	-84.9 ± 20.3	<0.001	-87.2 ± 70.8	0.23

¹ Reference level for age is adult

Table S4. Results of a generalized linear model examining the difference in timing between adult Godwits breeding in Poland and translocated juveniles released in Poland during south- and northward migration at all nine latitudinal boundaries.

Southward migration					Northward migration				
LatCross	Intercept		Age ¹		LatCross	Intercept		Age ¹	
	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>		$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>
52°N	153.3 ± 9.3	<0.001	55.7 ± 11.2	<0.001	52°N	220.2 ± 5.8	<0.001	17.8 ± 11.8	0.17
48°N	154.3 ± 9.4	<0.001	61.8 ± 11.6	<0.001	48°N	216.2 ± 4.8	<0.001	3.6 ± 10.5	0.74
44°N	227.4 ± 6.8	<0.001	23.3 ± 13.2	0.09	44°N	198.9 ± 5.8	<0.001	1.2 ± 12.3	0.93
40°N	237.8 ± 6.7	<0.001	22.4 ± 13.1	0.10	40°N	196.6 ± 5.7	<0.001	4.8 ± 12.0	0.70
36°N	236.5 ± 6.9	<0.001	20.3 ± 13.4	0.15	36°N	193.3 ± 6.8	<0.001	10.2 ± 14.1	0.49
32°N	236.9 ± 6.8	<0.001	20.6 ± 13.4	0.14	32°N	188.3 ± 6.6	<0.001	13.1 ± 13.3	0.35
28°N	235.2 ± 6.9	<0.001	17.9 ± 13.6	0.21	28°N	188.2 ± 6.6	<0.001	13.4 ± 13.3	0.34
24°N	232.1 ± 6.3	<0.001	11.6 ± 12.6	0.37	24°N	186.4 ± 6.3	<0.001	3.0 ± 13.5	0.83
20°N	233.9 ± 7.1	<0.001	17.6 ± 14.0	0.23	20°N	185.8 ± 6.3	<0.001	3.5 ± 13.5	0.80

¹ Reference level for age is adult

Table S5. Results of a generalized linear model examining the difference in timing between adult Godwits breeding in The Netherlands and juveniles released in The Netherlands during south- and northward migration at all nine latitudinal boundaries.

Southward migration					Northward migration				
LatCross	Intercept		Age ¹		LatCross	Intercept		Age ¹	
	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>		$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>
52°N	177.8 ± 1.2	<0.001	51.8 ± 3.9	<0.001	52°N	195.3 ± 0.8	<0.001	31.0 ± 3.4	<0.001
48°N	178.5 ± 4.2	<0.001	61.2 ± 4.2	<0.001	48°N	193.1 ± 0.7	<0.001	31.3 ± 3.2	<0.001
44°N	179.8 ± 1.2	<0.001	66.8 ± 4.8	<0.001	44°N	190.6 ± 0.8	<0.001	23.9 ± 3.4	<0.001
40°N	182.9 ± 1.4	<0.001	72.8 ± 6.1	<0.001	40°N	184.5 ± 1.2	<0.001	25.5 ± 5.1	<0.001
36°N	--	--	--	--	36°N	--	--	--	--
32°N	187.4 ± 1.5	<0.001	53.4 ± 7.1	<0.001	32°N	119.7 ± 3.3	<0.001	57.5 ± 18.2	<0.01
28°N	187.8 ± 1.5	<0.001	67.2 ± 7.4	<0.001	28°N	118.6 ± 3.2	<0.001	58.4 ± 17.9	<0.01
24°N	186.0 ± 2.5	<0.001	70.9 ± 12.9	<0.001	24°N	117.5 ± 3.2	<0.001	59.5 ± 17.9	<0.01
20°N	188.8 ± 1.5	<0.001	68.2 ± 7.6	<0.001	20°N	117.4 ± 3.3	<0.001	59.6 ± 18.2	<0.01

¹ Reference level for age is adult

Table S6. Generalized linear mixed model predicting mortality chance during the first southward migration in relation to release location (NL vs. PL), year (2016 vs. 2017) and initiation of migration (date of 52°N crossing). In total 22 birds completed their first southward migration, whereas 18 birds died during migration.

Dependent variable	Fixed effects	$\beta \pm SE$	<i>P</i>
Mortality during migration	Intercept	7.08 ± 3.25	0.03
	Release location ¹	-0.45 ± 0.87	0.61
	Date of 52°N crossing	-0.04 ± 0.02	0.01
	Year ²	-0.42 ± 0.77	0.59
	Random effect	<i>r</i> (95%CI)	
	Family	0.01 (0.00 – 0.42)	

¹ Reference level for release location is The Netherlands
² Reference level for year is 2016

Table S7. Generalized linear mixed model predicting the chance to cross the Sahara during the first southward migration in relation to release location (NL vs. PL), year (2016 vs. 2017) and initiation of migration (date of 52°N crossing).

Dependent variable	Fixed effects	$\beta \pm SE$	<i>P</i>
Crossing of the Sahara	Intercept	8.27 ± 3.81	0.03
	Release location ¹	-1.00 ± 1.56	0.52
	Date of 52°N crossing	-0.03 ± 0.02	0.03
	Year ²	-2.40 ± 1.32	0.09
	Random effect	<i>r</i> (95%CI)	
	Family	0.02 (0.00 – 0.62)	

¹ Reference level for release location is The Netherlands
² Reference level for year is 2016

Table S8. Results of a generalized linear model examining the effect of release location (Poland vs. The Netherlands) on the timing of migration hand raised godwits during the first northward migration at all nine latitudinal boundaries.

Northward migration				
LatCross	Intercept		Release location ¹	
	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>
52°N	228.0 ± 5.1	<0.001	6.4 ± 11.8	0.60
48°N	222.4 ± 4.7	<0.001	-5.9 ± 10.3	0.58
44°N	208.8 ± 5.9	<0.001	-14.9 ± 11.8	0.23
40°N	205.9 ± 6.5	<0.001	-10.6 ± 13.5	0.45
36°N	190.9 ± 9.0	<0.001	18.7 ± 18.0	0.33
32°N	187.7 ± 8.8	<0.001	18.8 ± 17.6	0.32
28°N	187.6 ± 8.8	<0.001	19.0 ± 17.6	0.32
24°N	183.2 ± 8.9	<0.001	11.2 ± 18.7	0.57
20°N	183.1 ± 8.9	<0.001	11.0 ± 18.7	0.57

¹ Reference level for release location is The Netherlands

Table S9. Results of a generalized linear model examining the effect of release location (Poland or The Netherlands) on the route similarity between the first south- and northward migration at all nine latitudinal crossings.

South- and Northward migration				
LatCross	Intercept		Release location ¹	
	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>
52°N	49.9 ± 110.3	0.04	643.9 ± 211.2	0.01
48°N	379.3 ± 127.2	0.01	491.8 ± 236.5	0.04
44°N	195.4 ± 135.3	0.17	801.1 ± 218.2	< 0.01
40°N	190.1 ± 158.3	0.26	709.3 ± 245.3	0.02
36°N	180.6 ± 206.5	0.41	741.5 ± 277.1	0.03
32°N	176.7 ± 243.8	0.49	823.3 ± 327.1	0.04
28°N	668.4 ± 223.2	0.02	670.6 ± 407.8	0.14
24°N	735.2 ± 223.3	0.01	645.6 ± 413.9	0.06
20°N	743.2 ± 241.7	0.02	613.4 ± 465.5	0.23

¹ Reference level for release location is The Netherlands

Table S10. Total number of tracked hand-raised godwits per latitudinal crossing and the number of families with more than one siblings tracked per crossing. Both numbers are displayed for south and northward migration separately.

LatCross	Southward migration		Northward migration	
	Individuals	Families with >1 sibling	Individuals	Families with >1 sibling
52°N	40	14	11	0
48°N	32	10	12	0
44°N	25	8	13	1
40°N	25	8	13	1
36°N	19	5	9	0
32°N	19	5	9	0
28°N	17	4	9	0
24°N	16	4	9	0
20°N	13	1	9	0

Table S11. Results of a Levene’s test examining the effect of release moment on a difference in variation of orientation within the first two latitudinal boundaries per release location.

Southward migration				
LatCross	Juveniles released in Poland		Juveniles released in The Netherlands	
	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>
52°N	0.88		0.09	
48°N	0.24		0.20	