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Translocation of shorebird siblings shows intraspecific variation in migration routines to arise after fledging

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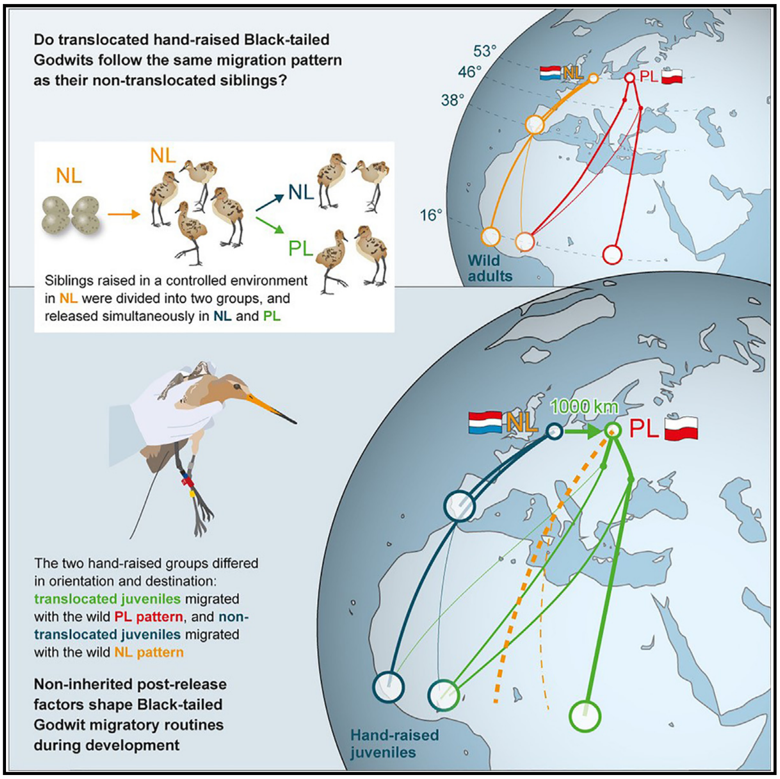
Report

Current Biology

Translocation of shorebird siblings shows intraspecific variation in migration routines to arise after fledging

Graphical abstract



Do translocated hand-raised Black-tailed Godwits follow the same migration pattern as their non-translocated siblings?

Siblings raised in a controlled environment in NL were divided into two groups, and released simultaneously in NL and PL

The two hand-raised groups differed in orientation and destination: translocated juveniles migrated with the wild PL pattern, and non-translocated juveniles migrated with the wild NL pattern

Non-inherited post-release factors shape Black-tailed Godwit migratory routines during development

Authors

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In brief

Loonstra et al. released hand-raised godwits (matched for parentage) either at home or 1,000 km eastward, in an area where godwits show a different timing and pattern of seasonal migration. The displaced juveniles adopt the pattern of migration of the population at release. This falsifies the idea that godwit migration routines are inherited.

Highlights

- Tracking reveals enormous variation in migratory routines, but what is the source?
- Young hand-raised godwits, matched for parentage, were moved 1,000 km east
- Translocated juveniles adopted the pattern of migration of the population at release
- Thus, migration of young godwits is not just shaped by genes and maternal material

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Report

Translocation of shorebird siblings shows intraspecific variation in migration routines to arise after fledging

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SUMMARY

Although many recent tracking studies have uncovered considerable variation in the migratory routines of birds,[1,2] the source of this variation is surprisingly poorly discussed.[3] We hypothesize that a wealth of possible factors, including factors other than genetics, translate into these variable outcomes. To demonstrate how factors that are not inherited can shape migratory routine during development, we performed a translocation and delayed-release experiment with juvenile, hand-raised black-tailed godwits *Limosa limosa limosa* that were carefully matched for ancestral background, releasing siblings 1,000 km apart. Translocated juveniles adopted the spatiotemporal pattern of migration that is habitual for the population at the release location rather than the origin. This leads to the rejection of the hypothesis that the migration of inexperienced birds is only shaped by pre-release factors, including genes, maternal material in the eggs, and a common environment from hatching to fledging. Instead, these findings are consistent with inexperienced migrants also developing their knowledge and capacities through contextual individual learning,[4] the precise nature of which now warrants study. The fact that hand-raised godwits, depending on the context in which they are released, can be induced to show different migratory routines, wintering sites, and breeding locations from their siblings indicates that processes during development offer the substrate for rapid adaptation of long-distance migration.

RESULTS AND DISCUSSION

Migratory birds must continually adapt to changes in their environment. At the heart of understanding how these birds respond to environmental change lies an identification of the factors that shape migratory routine. In past research, the role such factors play during development has often been neglected, mainly because (1) closely following migratory individuals throughout their development is very difficult logistically, but also, (2) examining development vastly increases the complexity of a study because it requires assessing how the environment itself shapes migratory phenotype. Although the simplified approach of past research has led to valuable insights, both theoretical[3,5,6] and empirical[2,7,8] results make it clear that this approach falls short of explaining the observed patterns of migratory birds. Including development in examining the many causal factors behind migratory routine is a necessary step in striving to reach a full understanding of migratory patterns.

To demonstrate the importance of development, we performed an experimental study of the ontogeny of long-distance migration in which some early-life factors (including genes, maternal material in the egg, and local environmental conditions during the first few weeks; Table 1) were held constant, whereas others were not. Displacing half of a group of hand-raised siblings 1,000 km to the east, a region where the local conspecifics migrate at different times, in different directions, and to different winter destinations, allowed us to examine whether these factors affected their migratory routines—namely, the timing and course of southward migration, winter destinations, and subsequent northward migration, and eventually the breeding grounds to which the young birds returned. More specifically, we transferred birds from a Dutch breeding population of black-tailed godwits (*Limosa limosa limosa*; hereafter, godwits) to a breeding area of Polish godwits.

The large Dutch population and the smaller Polish population are similar in terms of neutral genetic markers,[9] but they differ in

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Table 1. List of possible post-release factors that could affect the ontogeny of hand-raised godwits released after fledging either at home or after eastward displacement

Pre-release	Post-release
Maternal and paternal genes	ambient conditions at release area
Paternal egg proteins	social interactions with peers at release site
Maternal egg content	interactions with conspecifics in release area and along developing track
Ambient conditions at nest	interactions with conspecifics along developing track
Ambient conditions in incubator	interactions with other migrant species in release area
Social interactions with siblings and peers	interactions with other migrant species along developing track
Interactions with human keepers	ambient conditions along developing track
Ambient conditions during growth—indoors	–
Ambient conditions during growth—outdoors	–
Information on track between home and release site	–

A reliance on pre-release factors would lead to similarity between the displaced and non-displaced godwits, whereas the influence of post-release factors would lead to dissimilarity. Related to Figure 1.

migration direction and wintering area (Figure 1A).[10] Whereas Dutch godwits migrate in a southwest direction and spend the winter in (coastal) West Africa and on the Iberian Peninsula,[1,11] the Polish godwits first take a south or a southeast direction, then change to a more southerly or southwesterly route, respectively; they winter mostly in wetlands in the central Sahel (Lake Chad and Inner Niger Delta; Figure 1A).[10] Godwits migrate in flocks of conspecifics (or possibly also with locally co-occurring shorebird species, such as ruff *Calidris pugnax*; unpublished data), but not in family groups.[4]

We collected complete clutches of four eggs during the first week of incubation in our study area in southwest Fryslân, the Netherlands.[12] Chicks were hatched in an incubator and kept inside following a natural photoperiod for 7 days, taken to meadow enclosures from age 8 to 25 days, then kept inside again until release. For each four-egg clutch, at age 35.7 ± 2.9 days, we randomly assigned chicks to one of the four treatments: (1) release in the Netherlands (53.00°N 5.58°E), normal timing (19 June); (2) release in Poland (52.92°N 23.45°E), normal timing (19 June); (3) release in the Netherlands, delay 28 days (17 July); and (4) release in Poland, delay 28 days (17 July). A documentary on the work, featuring first author Loonstra and the changing daily chores of this work, is available online at https://youtu.be/eHNMnrrwyAM.

With this translocation, we experimentally tested the null hypothesis that hand-raised siblings released in Poland will migrate at the same times, in the same compass directions, and to the same destinations as their hand-raised siblings (and parent stock; Figure 1A) starting in the Netherlands. The presence of differences would cause us to reject the hypothesis that pre-release factors alone (Table 1) shape these migration routines. Instead, we would conclude that the development of these migrations also depends on factors at play after release (Table 1). By experimentally delaying the release for half of the young birds, we refined the precise nature of the post-release factors that the birds would experience (e.g., the presence of knowledgeable conspecific adults). Because we followed surviving individuals until their first northward migration back to the breeding grounds, we were able to also examine whether pre- and/or post-release factors shaped the locations of eventual breeding attempts.

Departing on their first southward migration, juveniles released in the Netherlands initially oriented more westward than translocated siblings released in Poland (Figure 1C; Tables 2 and S2). After crossing 44°N, translocated godwits also oriented more westward, resembling what experienced Polish adults do (Figure 1C). Furthermore, the orientation of juveniles released in the Netherlands or in Poland did not differ from the orientation of experienced birds of the population at release (Figures 1A and 1C; Tables 2 and S2).

Birds released with a 28-day delay departed for migration on average 30 days later than the juveniles released earlier (Table S3). However, departure date did not affect the directionality of orientation among juveniles, nor did "family" explain a large proportion of the variation (Figure S1; Table S3). There were no differences between early- and late-departing juveniles in the amount of variation in migratory orientation during the first two latitudinal segments (translocated juveniles 52°N [$F_{1,14} = 0.021$, $p = 0.88$] and 48°N [$F_{1,11} = 1.542$, $p = 0.24$]; Dutch control juveniles 52°N [$F_{1,12} = 2.037$, $p = 0.09$] and 48°N [$F_{1,11} = 1.830$, $p = 0.20$]). In the Netherlands, the average departure date of juvenile godwits was later than that of adult godwits (Figure 2A; Table S4). However, the early migrating juveniles showed considerable overlap with the late adults. Similarly, in Poland, the translocated juveniles departed on average later than the adults of the population at the release site (Figure 2B; Table S4), but early translocated juveniles caught up with them at 44°N.

Wintering sites and within-winter movements of the translocated individuals during their first winter were markedly different from their siblings released in the Netherlands. Whereas the juveniles released in the Netherlands migrated to the known wintering areas in sub-Saharan Africa, centered on wetlands along the west coast of Africa (ranging from Mauritania in the north to Guinea in the south; Figure 1A),[11] all but one translocated juvenile migrated to Sahelian wetlands, further east (Figure 1C). Two translocated juveniles ultimately wintered in the Inner Niger Delta, reaching this area after a second westward migration of ~2,500 km, similar to patterns shown by some adult godwits in the Poland population.[10] In contrast, the within-winter movements of individual juvenile godwits released in the Netherlands were much more limited, ranging 0–300 km.

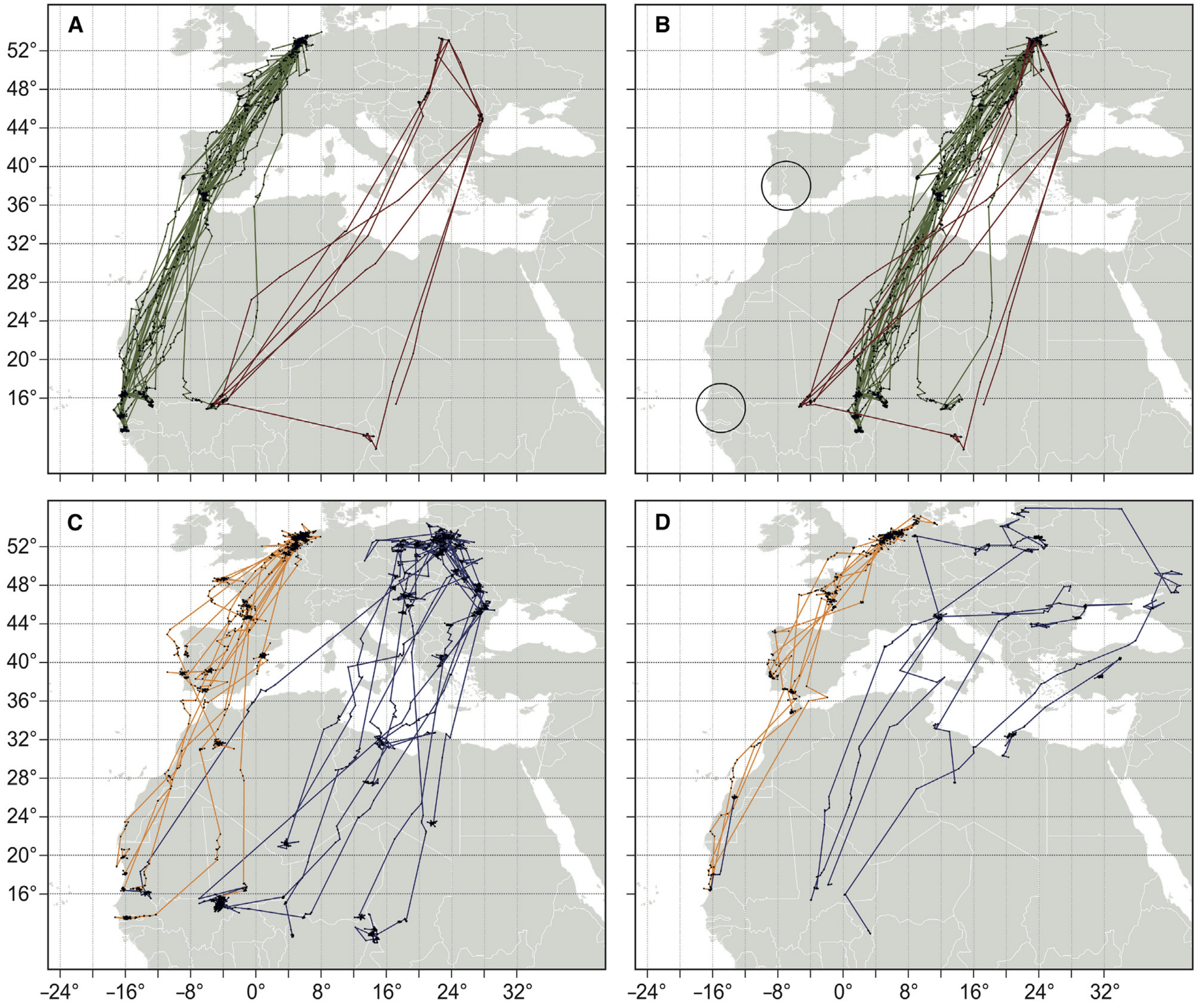

Figure 1. Baseline observations of adult migrations and results of testing various hypotheses on the ontogeny of migration routines in black-tailed godwits

(A) Baseline observations on southward migration by experienced adults (A; green, Dutch; red, Polish).

(B) Eastward displacement of naive juveniles would result in different migration routines and wintering areas depending on the kinds of information used. If birds were to follow an inherited clock-and-compass mechanism, they would copy the displaced tracks of the parent population (green lines). If birds showed goal orientation, they would migrate to areas indicated by the black circles. If birds were to learn routines from experienced local adults, they would show the red pattern of southward movement, although following local environments, winds, water, and food could also explain it.

(C and D) Southward (C) and northward (D) migration of hand-raised individuals either released at home (orange) or translocated to eastern Poland (blue).

See also Figures S1–S3, Table S1, and Data S1.

Although the juveniles released later likely have less access to intraspecific social information that could influence their migration, the fact that their migratory directionality is similar to the local adults suggests that relevant post-release factors are still available; such factors could include information from adult godwits that migrate unusually late or from other shorebird species that share habitats and migration routes but migrate later in the year.[13] Interestingly, we do find evidence that timing affects the eventual wintering sites, with later-departing juveniles more often wintering north of the Sahara (Data S1C; mean departure date of juveniles wintering north of Sahara: 24 August, versus juveniles wintering south of the Sahara: 1 August). There is also an associated cost: later-departing individuals had a higher chance of dying during their first southward migration, irrespective of release site (Data S1D; mean departure date of surviving juveniles: 17 July, versus juveniles that died during migration: 11 August).

After spending 7–31 months at their wintering grounds, juveniles began their first northward migration. Juveniles released in the Netherlands returned to the breeding grounds using migratory routes that were quite similar to their first southward migration (Figures 1C, 1D, and S2; Tables S1 and S3; Data S1A). The

Table 2. Generalized linear mixed models for orientation

				Fixed effects								Random effect
		Intercept		RLoc[a]*DO52C[b]		RLoc[a]		DO52C[b]		Year[c]		Family
LatFromTo	N	β ± SE	p	β ± SE	p	β ± SE	p	β ± SE	p	β ± SE	p	*r* (95% CI)
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)
		$F_{1,\ 43.99}$ = 23.99		$F_{1,\ 23.86}$ = 2.61		$F_{1,\ 22.43}$ = 17.17		$F_{1,\ 22.73}$ = 0.42		$F_{1,\ 16.16}$ = 0.35		–
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)
		$F_{1,\ 15.98}$ = 26.81		$F_{1,\ 9.06}$ = 0.09		$F_{1,\ 13.68}$ = 11.61		$F_{1,\ 14.81}$ = 1.94		$F_{1,\ 12.77}$ = 0.89		–
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)
		$F_{1,\ 29.35}$ = 19.51		$F_{1,\ 13.08}$ = 0.17		$F_{1,\ 19.25}$ = 18.73		$F_{1,\ 19.09}$ = 0.02		$F_{1,\ 5.16}$ = 2.29		–
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)
		$F_{1,\ 37.16}$ = 39.12		$F_{1,\ 14.41}$ = 0.31		$F_{1,\ 18.06}$ = 0.59		$F_{1,\ 17.94}$ = 2.61		$F_{1,\ 8.17}$ = 0.17		–
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)
		$F_{1,\ 13.13}$ = 17.26		$F_{1,\ 19.35}$ = 0.78		$F_{1,\ 19.45}$ = 28.97		$F_{1,\ 2.68}$ = 3.31		$F_{1,\ 4.89}$ = 0.36		–
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)
		$F_{1,\ 26.31}$ = 15.26		$F_{1,\ 13.78}$ = 0.61		$F_{1,\ 12.11}$ = 2.21		$F_{1,\ 7.05}$ = 0.47		$F_{1,\ 9.48}$ = 0.46		–
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)
		$F_{1,\ 18.13}$ = 13.33		$F_{1,\ 26.35}$ = 3.18		$F_{1,\ 6.39}$ = 8.97		$F_{1,\ 5.89}$ = 0.53		$F_{1,\ 8.13}$ = 0.69		–
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	–
		χ^2 = 2.09, df = 1		χ^2 = 0.03, df = 2		χ^2 = 0.73, df = 1		χ^2 = 0.34, df =1		χ^2 = 0.11, df = 1		–

Results of a linear mixed model examining the effect of release location of hand-raised juvenile godwits (Poland versus the Netherlands), year (2016 or 2017), and initiation of migration (date of 52°N crossing) on the east-west displacement (orientation) during the first southward migration between all nine latitudinal boundaries. Related to Figure 1.

[a] Reference level for release location is the Netherlands

[b] Date of 52°N crossing

[c] Reference level for year is 2016

translocated juveniles made a return migration to their release site in Poland by routes that were more dissimilar to their first southward migration (but see Figure S2, i157500, and below) and strikingly different from those of their siblings released in the Netherlands (Figures 1D and S2; Table 2; Data S1A), although there were no timing differences between the two release groups (Data S1B).

That migration patterns by the hand-raised juveniles conform to those of conspecifics in the area of release (as opposed to the area of origin, for the translocated birds) leads us to reject the null hypotheses that the first southward migration of naive juvenile godwits is shaped solely by pre-release factors, including genes, maternal material in the eggs, and a common pre-release environment. In fact, the migratory movements of translocated godwits suggest that routes of inexperienced migrants were informed by post-release factors, which could realistically include information learned from more experienced individuals, either conspecifics or of a different species. Especially interesting are en route observations made about what at first appeared to be an exception to the general pattern of juveniles exhibiting movements similar to adults from the area of release—namely, the bird that was released in Poland but ended up in West Africa among its Dutch brethren (Figure 1C). On the morning of 19 July 2016, L. Kihl found translocated juvenile B2BRLY (carrying transmitter number i157504; Figure S2) in a small lake east of Neusiedler See in Austria (Figure S3). The bird was in the company of 62 adult conspecifics and more than 200 ruff. Two days later all godwits had left the lake, including the translocated juvenile, which began traveling toward the western Mediterranean and Sahara, and eventually ended up at the Senegal river. We suspect that this bird happened to encounter a flock of experienced godwits aiming for West Africa as a wintering site and joined them on their route (Figures 1C and S2). This individual went on to survive two winters, but was lost over the Sahara during its first northward migration while traveling on a route typical of adult godwits from the Netherlands (Figure 1D).[14]

Studies of bird migration continue to struggle with what Oyama[3] identified as the "privilege of genes over other causes of development." This mindset is essentially a form of preformationism, one in which "the organism is not preformed in the egg, but the information that programs its development is preformed in the genes." Experimental studies on which claims of "genetic control" are based[15] were carried out in laboratory settings that created precisely the simplified environmental contexts that would increase the statistical effect of the single remaining variable, i.e., parental background.[16] We assert that the present experimental study on the development of migration in godwits—a shorebird species that feeds, roosts, and migrates in flocks but does not travel in family groups[17]—disproves the common but overly simplified view that the migration of many inexperienced birds results only from inherited factors, as embodied in what is often called an "innate" migration program. In fact, inspired by observations on the intense in-flight vocalizations of many species,[18–21] we suggest that the availability of usable information from conspecifics and other species during actual migration is both much more important and more taxonomically widespread than has been previously considered.[22] Consistent with the idea that juvenile godwits actively use information from experienced individuals is the overlap in timing of

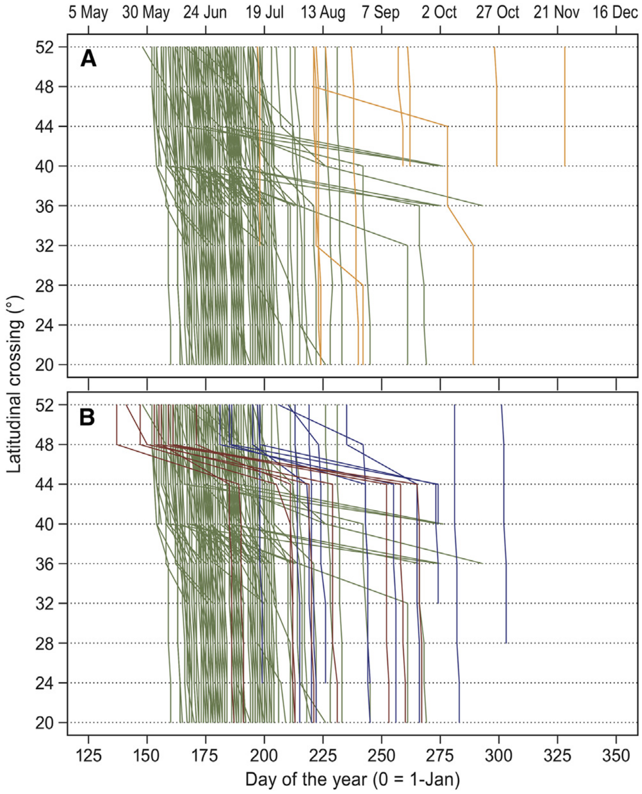

Figure 2. Timing and progress during southward migration black-tailed godwits

The Dutch parent population of black-tailed godwits (green in A) is compared with hand-raised juveniles released at home in the Netherlands (orange in A) and with the adults from eastern Poland (red in B), as well as the translocated juveniles released in Poland (blue in B). Timing is expressed as the day of the year; 0 = 1 January. The significance of differences in the timing of the different groups is noted in Table S2.
See also Tables S3 and S4 and Data S1.

long-distance intra-Africa movements south of the Sahara (Figure 1C).

These are important considerations in a conservation context, given that the use of post-fledging factors will influence the rate of adaptation in a presently fast-changing world.[23,24] Of course, this does not mean that adaptive possibilities are unlimited. Especially for specialized shorebirds such as godwits, suitable wetland habitats are few and far between,[11,25] and these are lost continuously as a result of human activity.[26] Thus, although migratory birds may well be able to rapidly innovate, if suitable habitats continue to disappear, despite great capacity to adjust and adapt, they will no longer be able to keep pace.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2023.05.014.

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AUTHOR CONTRIBUTIONS

A.H.J.L., M.A.V., and T.P. conceived the experiment; A.H.J.L., M.A.V., and T.P. collected the data; A.H.J.L. and M.A.V. analyzed the data; and A.H.J.L. wrote initial versions of the manuscript, M.A.V. and T.P. took care of the final versions, and all authors contributed during the process.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

1. Verhoeven, M.A., Loonstra, A.H.J., Senner, N.R., McBride, A.D., Both, C., and Piersma, T. (2019). Variation from an unknown source: large inter-individual differences in migrating black-tailed godwits. Front. Ecol. Evol. *7*, 31.
2. Flack, A., Aikens, E.O., Kölzsch, A., Nourani, E., Snell, K.R.S., Fiedler, W., Linek, N., Bauer, H.G., Thorup, K., Partecke, J., et al. (2022). New frontiers in bird migration research. Curr. Biol. *32*, R1187–R1199.

3. Oyama, S. (1985). The Ontogeny of Information: Developmental Systems and Evolution, Second Revised Edition 2000 (Cambridge University Press, Duke University Press).
4. Verhoeven, M.A., Loonstra, A.H.J., McBride, A.D., Kaspersma, W., Hooijmeijer, J.C.E.W., Both, C., Senner, N.R., and Piersma, T. (2022). Age-dependent timing and routes demonstrate developmental plasticity in a long-distance migratory bird. J. Anim. Ecol. *91*, 566–579.
5. Oyama, S. (2000). Evolution's Eye. A Systems View of the Biology-Culture Divide (Duke University Press).
6. Oyama, S., Griffiths, P.E., and Gray, R.D. (2000). Introduction: what is developmental systems theory? In Cycles of Contingency. Developmental Systems and Evolution, S. Oyama, P.E. Griffiths, and R.D. Gray, eds. (MIT Press), pp. 1–11.
7. Wynn, J., Padget, O., Mouritsen, H., Perrins, C., and Guilford, T. (2020). Natal imprinting to the Earth's magnetic field in a pelagic seabird. Curr. Biol. *30*, 2869–2873.e2.
8. Thorup, K., Vega, M.L., Snell, K.R.S., Lubkovskaia, R., Willemoes, M., Sjöberg, S., Sokolov, L.V., and Bulyuk, V. (2020). Flying on their own wings: young and adult cuckoos respond similarly to long-distance displacement during migration. Sci. Rep. *10*, 1.
9. Trimbos, K.B., Doorenweerd, C., Kraaijeveld, K., Musters, C.J.M., Groen, N.M., de Knijff, P., Piersma, T., and de Snoo, G.R. (2014). Patterns in nuclear and mitochondrial DNA reveal historical land recent isolation in the black-tailed godwit (*Limosa limosa*). PLoS One *9*, e83949.
10. Loonstra, A.H.J., Verhoeven, M.A., Zbyryt, A., Schaaf, E., Both, C., and Piersma, T. (2019). Individual black-tailed godwits do not stick to single routes: a hypothesis on how low population densities might decrease social conformity. Ardea *107*, 251–261.
11. Verhoeven, M.A., Loonstra, A.H.J., McBride, A.D., Both, C., Senner, N.R., and Piersma, T. (2021). Migration route, stopping sites, and non-breeding destinations of adult black-tailed godwits breeding in southwest Fryslân, the Netherlands. J. Ornithol. *162*, 61–76. https://doi.org/10.1007/s10336-020-01807-3.
12. Kentie, R., Coulson, T., Hooijmeijer, J.C.E.W., Howison, R.A., Loonstra, A.H.J., Verhoeven, M.A., Both, C., and Piersma, T. (2018). Warming springs and habitat alteration interact to timing of breeding and population dynamics in a migratory bird. Glob. Change Biol. *24*, 5292–5303.
13. Cohen, E.B., and Satterfield, D.A. (2020). 'Changing on a spectacle:' co-occurring animal migrations and interspecific interactions. Ecography *43*, 1657–1671.
14. Loonstra, A.H.J., Verhoeven, M.A., Senner, N.R., Both, C., and Piersma, T. (2019). Adverse wind conditions during northward Sahara crossings increase the in-flight mortality of black-tailed godwits. Ecol. Lett. *22*, 2060–2066.
15. Helbig, A.J. (1991). Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). Behav. Ecol. Sociobiol. *28*, 9–12.
16. Lewontin, R.C. (1974). The analysis of variance and the analysis of cause. Am. J. Hum. Genet. *26*, 400–411.
17. Piersma, T., Zwarts, L., and Bruggemann, J.H. (1990). Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. Ardea *78*, 157–184.
18. Hamilton, W.J. (1962). Evidence concerning the function of nocturnal call notes of migratory birds. Condor *64*, 390–401.
19. Van Doren, B.M., and Horton, K.G. (2018). A continental system for forecasting bird migration. Science *361*, 1115–1118.
20. Nussbaumer, R., Benoit, L., Mariethoz, G., Liechti, F., Bauer, S., and Schmid, B. (2019). A geostatistical approach to estimate high resolution nocturnal bird migration densities from a weather radar network. Remote Sens. *11*, 2233.
21. Winger, B.M., Weeks, B.C., Farnsworth, A., Jones, A.W., Hennen, M., and Willard, D.E. (2019). Nocturnal flight-calling behaviour predicts vulnerability to artificial light in migratory birds. Proc. R. Soc. Lond. B *286*, 20190147.
22. Aikens, E.O., Bontekoe, I.D., Blumenstiel, L., Schlicksupp, A., and Flack, A. (2022). Viewing animal migration through a social lens. Trends Ecol. Evol. *37*, 985–996. https://doi.org/10.1016/j.tree.2022.06.008.
23. Laland, K.N., Toyokawa, W., and Oudman, T. (2019). Animal learning as a source of developmental bias. Evol. Dev. *22*, e12311.
24. Botero, C.A., Weissing, F.J., Wright, J., and Rubenstein, D.R. (2015). Evolutionary tipping points in the capacity to adapt to environmental change. Proc. Natl. Acad. Sci. USA *112*, 184–189.
25. Piersma, T., and Baker, A.J. (2000). Life history characteristics and the conservation of migratory shorebirds. In Behaviour and Conservation, L.M. Gosling, and W.J. Sutherland, eds. (Cambridge University Press), pp. 105–124.
26. Davidson, N.C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. Mar. Freshw. Res. *65*, 934–941.
27. Douglas, D.C., Weinzierl, R., Davidson, S.C., Kays, R., Wikelski, M., and Bohrer, G. (2012). Moderating Argos location errors in animal tracking data. Methods Ecol. Evol. *3*, 999–1007.
28. Fox, J., and Weisberg, S. (2019). An R Companion to Applied Regression, Third Edition (Sage).
29. Halekoh, U., and Højsgaard, S. (2014). Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models – the R package "pbkrtest". J. Stat. Soft. *59*, 1–30.
30. Stoffel, M.A., Nakagawa, S., and Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol. Evol. *8*, 1639–1644.
31. Hijmans, R.J. (2017). geosphere: spherical trigonometry. R package version 1.5-7. http://cran.nexr.com/web/packages/geosphere/index.html.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw tracking data of experimental birds	This paper	https://doi.org/10.5281/zenodo.7954455
Location data of adult Black-tailed Godwits	Verhoeven et al.,[1] Loonstra et al.,[10] and Verhoeven et al.[11]	N/A
Software and algorithms		
R statistical Software	R Project	https://www.r-project.org
Contributed R packages	Comprehensive R Archive Network (CRAN)	https://www.r-project.org

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed to and will be fulfilled by the lead contact, Theunis Piersma (theunis.piersma@nioz.nl).

Materials availability

This study did not make use of any off-the-shelf materials.

Data and code availability

Tracking data on juvenile Black-tailed Godwits are available at https://www.zenodo.org/ (ID: 7954455), raw tracking data on adult Black-tailed Godwits are available at Verhoeven et al.,[1] Loonstra et al.,[10] and Verhoeven et al.[11] DOIs are listed in the key resources table. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

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. 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 6.25m^2 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 groups every day. Indoor day lengths were similar to the conditions outside. With all nights spent indoors, the chicks were never exposed to nighttime skies before being released. From ages greater than seven days, all chicks spent every other day outside in 2500m^2 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 an aviary with a ground surface of 82 m^2 and a height of 3.5 m. In this aviary birds were able to fly and had *ad libitum* access to food and water.

METHOD DETAILS

Tracking and translocation

At an average age of 35.7 ± 2.3 SD days in 2016 and 35.6 ± 3.3 SD 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) on the same date. The other two groups were delayed by 28 days and then released at the same two 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 car ride 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 until the temperature sensor started to follow a day-night rhythm (indicating the death of a bird).[14] Locations were retrieved via the CLS tracking system (https://www.argos-system.org/) and passed through the "Best Hybrid-filter" algorithm to remove unrealistic locations that exceeded 120 km h^{-1}, while retaining location-classes with quality 3, 2, 1, 0, A, B.[27] On average this resulted in 2.56 ± 0.85 SD locations per duty cycle.

QUANTIFICATION AND STATISTICAL ANALYSIS

Data analysis

All statistical analyses were performed using R (v. 3.4.3; R Core Development Team 2018).[28] In all models the statistical significance of fixed effects was assessed with parametric bootstrapping tests, using the 'pbkrtest' package.[29] The adjusted repeatability of the random intercepts was computed using the package "rptR".[30] All calculated great circle distance were computed using the function "distHaversine" in the package "geosphere".[31] Maps were constructed using background maps from Natural Earth (https://www.naturalearthdata.com/).

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 previously published for the Dutch population (n=70)[9] and the Polish population (n=6).[10] Unfortunately, we lack information on the timing of migration of Dutch adult godwits at the 36°N crossing, so we were not able to test for differences between Dutch adults and juveniles at this crossing during north- and southward migration. 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).[1,10]

To evaluate potential differences in timing during southward migration of juveniles for release location (The Netherlands or Poland), release timing (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 (Figure S1), we included FamilyID as a random effect if the number of families exceeded three (in such cases we constructed a generalized linear mixed model). In a second step, we used a generalized linear model to compare the timing during southward migration of hand-raised juvenile birds released in The Netherlands vs. Dutch adults, and hand-raised juvenile birds released in Poland vs. adults in Poland.

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 (there were no siblings from the same family in this dataset; Data S1B).

Orientation

To assess 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 the same segments was obtained and compared with published data on the Polish population (n=6)[8] and the Dutch population (n=26).[1]

Differences in orientation during southward migration between juveniles released in The Netherlands and Poland, release timing (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 (there were 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, i.e. the date of the last southward migratory movement >100 km made by a juvenile (in this case, 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), for 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 a standard set of diagnostics.[14] Mortalities north of 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 for north- and southward migrations of 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'.[28]