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Individual Black-tailed Godwits do not stick to single routes: a hypothesis on how low population densities might decrease social conformity

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The miniaturization of tracking devices is now rapidly increasing our knowledge on the spatiotemporal organization of seasonal migration. So far, most studies aimed at understanding within- and between-individual variation in migratory routines focus on single populations. This has also been the case for continental Black-tailed Godwits *Limosa l. limosa* (hereafter Godwits), with most work carried out on individuals from the Dutch breeding population, migrating in relatively large numbers in the westernmost part of the range. Here we report the migratory timing and routes of four adult individuals of the same subspecies from the low-density population in eastern Poland and compare this with previously published data on Godwits breeding in The Netherlands. During northward migration, the birds from Poland departed and arrived later from their wintering and breeding grounds. However, on southward migration the Polish breeding Godwits departed earlier, but arrived one month later than the Dutch birds on their wintering grounds in sub-Saharan Africa. Despite the small sample size of tracked birds from Poland, we find a significantly higher between-individual variation in timing during southward migration in Polish Godwits as compared to the Dutch Godwits. Furthermore, not only did migratory routes differ, but the few Polish Godwits tracked showed a higher level of between- and within-individual variation in route choice during both southward and northward migration. To explain this remarkable discrepancy, we propose that the properties of transmission of social information may be different between Godwits from a high-density population (i.e. the one in The Netherlands) and a low-density population (in Poland) and that this leads to different levels of canalization. To examine this hypothesis, future studies should not only follow individuals from an early age onwards, but also quantify and experimentally manipulate their social environments during migration.

Key words: long-distance seasonal migration, population exchange, satellite tracking, Black-tailed Godwit, social learning

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In the past two decades, the development of new and smaller tracking devices created the possibility to describe the, very often surprising, migrations of an increasing number of bird species (e.g. Wikelski *et al.* 2007, Gill *et al.* 2009, Bridge *et al.* 2011). As a result, we now have a better understanding of when and

where migrating birds are throughout the annual cycle (e.g. Bauer & Hoye 2014, Winkler *et al.* 2016). At the same time, the increasing number of repeated individual tracks reveal an intriguing palette of intraspecific variation in the spatial and temporal consistency of migration, which continues to develop our understanding of the various factors influencing the spatial and temporal patterns of migration (Bairlein 2003, Conklin *et al.* 2013, Kölzsch *et al.* 2019, Verhoeven *et al.* 2019).

Depending on the costs and benefits of being consistent in timing and route during migration, individuals and populations are expected to vary in the consistency of their itineraries (Alerstam *et al.* 2003, Drent *et al.* 2003). For instance, in shorebirds and geese, birds which are often assumed to rely on resources that are exclusively available at specific sites and/or moments, we often observe rather high consistency in migratory routing and or timing (Fox *et al.* 2003, Eichhorn *et al.* 2009, Senner *et al.* 2014, Ruthrauff *et al.* 2019). In contrast, for birds such as songbirds and seabirds, which often feed on prey that are available across wide geographical ranges and/or fluctuate strongly between years, opposite patterns are seen (Dias *et al.* 2010, Winkler *et al.* 2014, Weimerskirch *et al.* 2015, van Wijk *et al.* 2016). However, as extrinsic and intrinsic selection pressures differ between populations, comparative population-specific variation can serve as an additional source of inference to understand spatiotemporal variation in migration (Piersma 2007, Webster *et al.* 2002).

Continental Black-tailed Godwits *Limosa l. limosa* (hereafter Godwits) are long-distance migratory shorebirds breeding across much of lowland Europe and rely on a distinct number of staging sites during migration (Beintema & Drost 1986, Hooijmeijer *et al.* 2013, Verhoeven *et al.* in prep.). Wintering birds can be found on the Iberian Peninsula, Greece, the Black Sea coast, North Africa and in sub-Saharan Africa (Beintema & Drost 1986, Zwarts *et al.* 2009, Gerritsen *et al.* 2015). Recent work on the migration ecology of Godwits has focused on staging populations at the Iberian Peninsula and a breeding population in southwest Friesland, The Netherlands (Hooijmeijer *et al.* 2013, Kentie *et al.* 2017, Senner *et al.* 2015, 2018, 2019, Verhoeven *et al.* in prep., 2018, 2019). Briefly, this work revealed a

A flock of Black-tailed Godwits staging in the Tagus Estuary where they prepare for their northward migration (photo Jan van de Kam, Tagus Estuary; Portugal, 19 February 2015).

large, but yet unexplained, amount of within- and between-individual variation in the *temporal* organization of migration (Verhoeven *et al.* 2019). In contrast, *spatial* characteristics, such as the use of migratory routes, staging sites and wintering sites, were found to be rather consistent within individuals of this population (Verhoeven *et al.* 2018, in prep.).

Here we explore the migration of Godwits across a larger range by comparing individuals from two breeding populations which are quite distant (1200 km), yet genetically indistinguishable on the basis of neutral markers (Trimbos *et al.* 2014). In total we tracked four Godwits breeding in eastern Poland during three consecutive southward and two northward migrations. We compare the timing and orientation of these migrations with those of individuals from the mentioned Dutch breeding population.

METHODS

Study area and capture of birds

For this study, Godwits were captured in a relatively small breeding population (30–40 breeding pairs) in Gródek valley, eastern Poland (53°05'N, 23°40'E) during the breeding season of 2016. Using automated drop-cages, we captured Godwits on the nest. Following capture, Godwits were marked with a unique combination of colour-rings and a metal ring. Subsequently we measured wing length, tarsus length, tarsus-toe length, bill length and total head length, and we weighed the bird to the nearest gram using an electronic scale. In order to determine the molecular sex of each captured bird, we took a small blood sample from the brachial vein (see van der Velde *et al.* 2017 for method).

To investigate the timing of migration, migratory routes and staging sites during south- and northward migration and the wintering sites of these Godwits, we deployed four 5-g solar platform transmitting terminals (PTT; Model 100, Microwave Telemetry, Columbia, MD, USA). Transmitters were pre-programmed 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 that consisted of Dynemaa-rope (Lankhorst Ropes, Sneek). The weight of the PTT and harness represented c. 2.3% of the total body mass at capture (mean body mass: 270 g). 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 (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, while retaining location classes with quality 3, 2, 1, 0, A, B. On average this resulted in 0.71 ± 0.25 (SD) locations per duty cycle. Locations used for this study are stored on www.movebank.org.

Data analysis

To summarize the timing of migration during south- and northward migration, we determined for each individual when it crossed one of the nine chosen latitudinal boundaries (52°N, 48°N, 44°N, 40°N, 36°N, 32°N, 28°N, 24°N, 20°N). Subsequently, we used the calculated standard deviation of the population in timing at all these boundaries during south and northward migration as a measure of between-individual variation in timing. The within-individual variation in timing at a boundary was determined by calculating the largest timing difference within an individual across years at that boundary. The chosen arbitrary boundaries are the same as Verhoeven *et al.* (2019) and enable us to compare the timing of migration during southward and northward migration between Godwits breeding in The Netherlands and eastern Poland at all crossings except 36°N (unfortunately, in Verhoeven *et al.* 2019 we could not distinguish stops below and above this boundary; see Table 1 for more details).

To visualize and compare the migratory routes and orientation during south- and northward migration, we determined the east-west movement in kilometres within all eight consecutive latitudinal segments (Verhoeven *et al.* in prep.; see Table 1 for more details). Based on these movements, we calculated the standard deviation within the population within a segment and used this as our between-individual variation measure. Within-individual variation in migratory routes was determined by calculating the difference between the two largest east-west movements within an individual per latitudinal segment.

To test for statistical differences in the absolute difference and within-individual differences between both populations in both timing and orientation we used a Mann-Whitney U test in the Program R v. 3.4.3 (R Core Development Team 2018). The between-individual differences in timing and orientation between both populations were compared using the Levene's test which is part of the package 'car' (Fox & Weisberg 2019).

RESULTS

Of the four tracked Godwits (three males and one female) breeding in eastern Poland, the number of southward and northward migrations per individual were: 1/0, 2/1, 2/2 and 3/2 (S/N; Figure 1).

Migratory timing
Southward migration from the breeding grounds in

eastern Poland started on 18 May and the last bird left the breeding area on 11 June, yielding in a 34-d time window for the start of migration (Figure 2). Even though this was two weeks earlier than for Godwits breeding in The Netherlands, the long stopover of all Polish Godwits between 44°N and 48°N caused them to arrive on average more than a month later at sub-Saharan wintering grounds than the Dutch birds (Table 1A, Figure 2). The amount of within-individual varia-
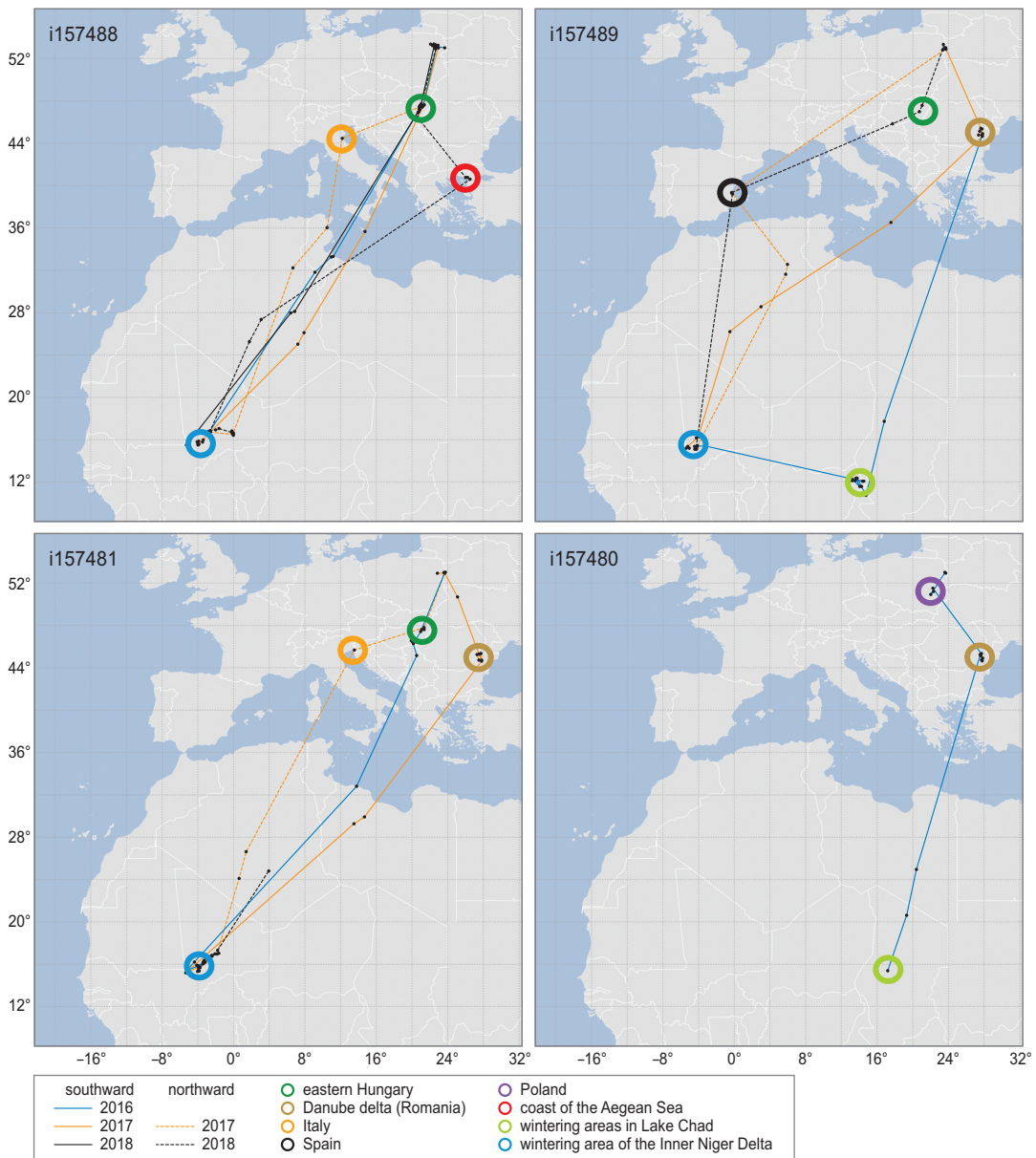
Figure 1. Southward (2016, 2017, 2018; solid lines) and northward (2017, 2018; dashed lines) migration routes of the four Godwits that were tracked from their breeding areas in eastern Poland. Circles show stops and wintering areas. Due to the duty cycle (24 h off, 8 h on) we only report stops longer than 32 h (circles).
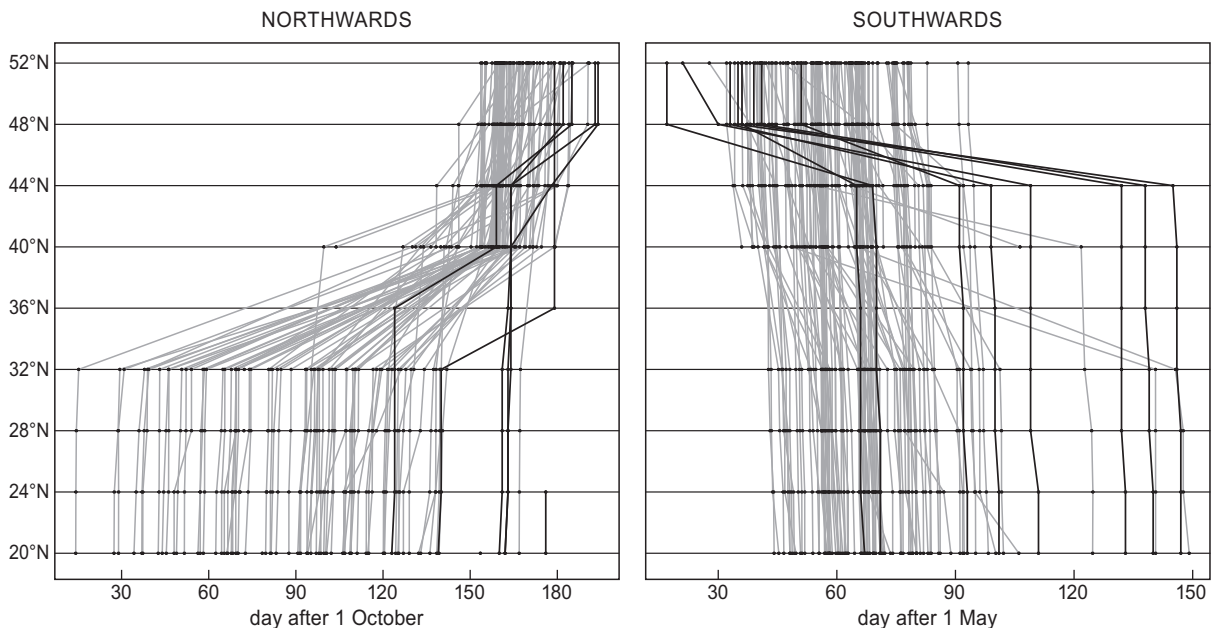
Figure 2. Timing of migration of four Polish adult Godwits (black lines) compared with adult Godwits breeding in The Netherlands (grey lines; after Verhoeven *et al.* 2019). Note that the timing of crossing the boundary at 36°N is excluded for Godwits breeding in The Netherlands.

tion did not differ between Godwits breeding in The Netherlands and eastern Poland (Table 1A). However, the amount of between-individual variation in timing differed between the two populations and was larger for Godwits from Poland at the last six boundaries (44°N–20°N; Table 1A).

Northward migration from the wintering area in the Inner Niger Delta took place over a 53-d period, ranging from 31 January to 25 March, and was on average two months later than the departure of Godwits breeding in The Netherlands (Table 1B, Figure 2). Average arrival on the breeding grounds occurred only one month later than the Dutch birds (Table 1B; Figure 2). The two populations had similar within- and between-individual variation in timing of migration at all crossings (Table 1B, Figure 2).

Migration routes

During southward migration, three routes could be distinguished for Godwits breeding in eastern Poland: route 1 via the delta of the Danube in Romania to Lake Chad (and subsequently moving to the Inner Niger Delta for the rest of winter), route 2 with a similar stopover in the Danube delta, but with a direct migration to the Inner Niger Delta, and route 3 going to eastern Hungary with a direct migration to the Inner Niger Delta (Figure 1). While all individuals (*n* = 3)

stayed at least part of the winter in the Inner Niger Delta, one individual (i157489) performed an additional 'westward' migration at the end of October, i.e. from Lake Chad to the Inner Niger Delta in 2016 (great circle distance: 1851 km). This did not happen in 2017 when she flew straight to the Inner Niger Delta (Figure 1).

During northward migration, we could also distinguish three different routes, with all birds (*n* = 3) on these routes converging in eastern Hungary before reaching the breeding grounds in eastern Poland (Figure 1). Route 1 went from the Inner Niger Delta to the Iberian Peninsula and then to eastern Hungary; route 2 went from the Inner Niger Delta to the coast of the Adriatic Sea in northern Italy and then to eastern Hungary; route 3 went from the Inner Niger Delta to the north-eastern coast of the Aegean Sea in Greece and/or Turkey and then to eastern Hungary (Figure 1).

The three Godwits tracked for more than one migration were not faithful to a single route during south- or northward migration (Figure 1). During both south and northward migration, Polish Godwits oriented differently from Dutch Godwits during multiple parts of the migratory trajectories (Table 1C, 1D). Also, Godwits breeding in eastern Poland showed a higher within- and between-individual variation in the directions taken at various points along the route (Table 1C, 1D).

DISCUSSION

By comparing the migratory routes and timing of two distant breeding populations of the Continental Black-tailed Godwits, we revealed significant population differences in the route use during, and the timing of, migration. Despite the small sample size of individuals tracked from Poland, we found a higher within- and between-individual variation in migratory routes of Polish compared with Dutch Godwits. While we did not find differences in the within-individual variation in timing of migration between the two populations, the amount of between-individual variation differed significantly: on southward migration between-individual

variation was larger among the Polish birds for the last six boundary crossings (Table 1).

Even though breeding started at rather similar dates in Poland and The Netherlands (average initiation of breeding in The Netherlands 21 April vs. 22 April in Poland; Verhoeven *et al.* 2019, in prep., P. Chylarecki unpubl. data), Godwits breeding in eastern Poland arrived over a shorter interval and significantly later in the season than birds breeding in The Netherlands. This difference might hint at population-specific strategies of nutrient accumulation for breeding (cf. Piersma *et al.* 2005). Perhaps Godwits breeding in Poland accumulate more nutrient stores along the way than Dutch Godwits (Drent *et al.* 2006); and/or the arrival of Godwits in

Table 1. Observed timing and between- and within-individual variation in timing of migration for Godwits breeding in The Netherlands[1] and eastern Poland (A) during southward migration (mean ± SD) and (B) during northward migration (mean ± SD). Observed orientation and between- and within-individual variation in orientation of migration for Godwits breeding in The Netherlands[2] and eastern Poland (C) during southward migration (mean ± SD) and (D) during northward migration (mean ± SD). [1]after data from Verhoeven *et al.* 2019; [2]after data from Verhoeven *et al.* in prep. [3]First significance measure relates to the significance of absolute difference in timing or orientation and second significant measure to between-individual difference in timing or orientation.

Table 1A. Timing – Southward migration.

Latitudinal crossing	Population	Absolute timing and between-individual variation (NL vs. PL)[3]	Within-individual variation (NL vs. PL)
52°	NL	June 26 ± 13 days ($n = 117$)	17 ± 10 days ($n = 36$)
	PL	June 2 ± 11 days ($n = 8$)	14 ± 7 days ($n = 3$)
		($P < 0.001$; $P = 0.10$)	($P = 0.85$)
48°	NL	June 26 ± 13 days ($n = 117$)	16 ± 9 days ($n = 36$)
	PL	June 3 ± 10 days ($n = 8$)	14 ± 7 days ($n = 3$)
		($P < 0.001$; $P = 0.10$)	($P = 0.79$)
44°	NL	June 28 ± 13 days ($n = 117$)	16 ± 9 days ($n = 36$)
	PL	August 13 ± 31 days ($n = 8$)	8 ± 5 days ($n = 3$)
		($P < 0.001$; $P < 0.01$)	($P = 0.09$)
40°	NL	June 30 ± 15 days ($n = 117$)	19 ± 10 days ($n = 36$)
	PL	August 13 ± 31 days ($n = 8$)	9 ± 5 days ($n = 3$)
		($P < 0.001$; $P = 0.04$)	($P = 0.09$)
36°	NL	—	—
	PL	August 14 ± 30 days ($n = 8$)	9 ± 5 days ($n = 3$)
32°	NL	July 7 ± 18 days ($n = 93$)	15 ± 8 days ($n = 29$)
	PL	August 14 ± 30 days ($n = 8$)	9 ± 5 days ($n = 3$)
		($P < 0.001$; $P = 0.04$)	($P = 0.22$)
28°	NL	July 7 ± 18 days ($n = 93$)	15 ± 8 days ($n = 29$)
	PL	August 14 ± 30 days ($n = 8$)	9 ± 5 days ($n = 3$)
		($P < 0.001$; $P = 0.04$)	($P = 0.22$)
24°	NL	July 8 ± 18 days ($n = 93$)	15 ± 8 days ($n = 29$)
	PL	August 15 ± 31 days ($n = 8$)	9 ± 5 days ($n = 3$)
		($P < 0.001$; $P = 0.04$)	($P = 0.20$)
20°	NL	July 9 ± 19 days ($n = 93$)	15 ± 9 days ($n = 29$)
	PL	August 15 ± 30 days ($n = 8$)	9 ± 5 days ($n = 3$)
		($P < 0.001$; $P = 0.04$)	($P = 0.20$)

Poland is constrained by a later onset of spring and resource availability (Briedis *et al.* 2016).

Interestingly, during southward migration, Godwits breeding in eastern Poland departed significantly earlier from the breeding grounds than Godwits from The Netherlands. This may have been caused by early nest or chick loss (across all years, none of the birds tracked from Poland successfully fledged chicks) or by a lack of high-quality habitat that would allow them to initiate primary moult at the breeding grounds (van Dijk 1980). After this early departure from the breeding grounds, all Polish Godwits staged for a considerable time at staging areas between 48°N and 44°N. Perhaps, Polish Godwits use this period to moult their flight feathers, whereas Dutch birds start primary moult already on the breeding grounds (van Dijk 1980, Márquez-Ferrando *et al.* 2018).

Because they rely on distinct and widely dispersed food-rich freshwater or coastal mudflats, long-distance migratory shorebirds like Godwits are expected to exhibit high consistency in migratory routes (Newton 2008, Ruthrauff *et al.* 2019). The flexibility to switch between routes observed in Polish Godwits during both southward and northward migration, contradicts this expectation and suggests that Godwits either (1) have an innate map of different suitable migratory routes, (2) continuously learn through the use of social information, or (3) discover and switch routes through a form of asocial learning (Kendal *et al.* 2005, Creswell 2014, Flack *et al.* 2012, Mueller *et al.* 2013, Berdahl *et al.* 2018, Mouritsen 2018, Kölzsch *et al.* 2019). Unfortunately, we only tracked experienced adult birds and in the absence of information on the composition of migratory flocks, we are unable to assess whether the conditions for individual learning and social knowledge sharing existed.

Nevertheless, we hypothesize that when social information is lacking, inexperienced individuals are

Table 1B. Timing – Northward migration.

Latitudinal crossing	Population	Absolute timing and between-individual variation (NL vs. PL)[3]	Within-individual variation (NL vs. PL)
52°	NL	14 March ± 9 days (*n* = 72)	9 ± 6 days (*n* = 25)
	PL	4 April ± 7 days (*n* = 5)	4 ± 4 days (*n* = 2)
		(***P* < 0.001**; *P* = 0.51)	(*P* = 0.16)
48°	NL	12 March ± 8 days (*n* = 71)	9 ± 6 days (*n* = 24)
	PL	4 April ± 7 days (*n* = 5)	4 ± 4 days (*n* = 2)
		(***P* < 0.001**; *P* = 0.69)	(*P* = 0.16)
44°	NL	10 March ± 9 days (*n* = 71)	8 ± 5 days (*n* = 24)
	PL	17 March ± 9 days (*n* = 5)	11 ± 4 days (*n* = 2)
		(*P* = 0.07; *P* = 0.80)	(*P* = 0.06)
40°	NL	3 March ± 14 days (*n* = 71)	10 ± 10 days (*n* = 24)
	PL	14 March ± 8 days (*n* = 5)	10 ± 14 days (*n* = 2)
		(***P* = 0.03**; *P* = 0.28)	(*P* = 0.78)
36°	NL	—	—
	PL	7 March ± 21 days (*n* = 5)	28 ± 38 days (*n* = 2)
32°	NL	30 Dec ± 33 days (*n* = 81)	11 ± 6 days (*n* = 25)
	PL	27 Feb ± 18 days (*n* = 5)	10 ± 9 days (*n* = 2)
		(***P* < 0.001**; *P* = 0.10)	(*P* = 0.89)
28°	NL	29 Dec ± 33 days (*n* = 80)	11 ± 6 days (*n* = 24)
	PL	27 Feb ± 18 days (*n* = 5)	9 ± 9 days (*n* = 2)
		(***P* < 0.001**; *P* = 0.10)	(*P* = 0.85)
24°	NL	28 Dec ± 33 days (*n* = 79)	10 ± 7 days (*n* = 24)
	PL	3 Mar ± 19 days (*n* = 6)	10 ± 7 days (*n* = 2)
		(***P* < 0.001**; *P* = 0.10)	(*P* = 0.96)
20°	NL	28 Dec ± 33 days (*n* = 79)	10 ± 6 days (*n* = 24)
	PL	2 Mar ± 15 days (*n* = 6)	11 ± 8 days (*n* = 2)
		(***P* < 0.001**; *P* = 0.10)	(*P* = 0.91)

more likely to develop more individual routes on their very first southward and/or northward migration, i.e. routes that are more different from one another than when birds are able to fly with many experienced conspecifics. Subsequently, if individuals from low density populations survive, and if the spatial environment allows these alternative strategies, every year this mechanism generates more between-individual differences in migratory routes within the low-density population. If information about different routes and goals can be shared with other individuals during overlapping occurrences in space and time (Berdahl *et al.* 2018), these individuals are likely to switch between routes (higher within-individual variation). Thus, the degree of between-individual overlap in space and time and the amount and strength of social information will ultimately determine the extent of social canalization, which will be reflected in the amount of within- and between-individual variation in migratory routes that is shown by a population.

Following this, we argue that social canalization may play a larger role in the relatively large and concentrated Dutch population (c. 33,000 breeding pairs; Kentie *et al.* 2016), than in the small and scattered Polish population (c. 2000 breeding pairs; Ławicki *et al.* 2011). After the first southward migration, in both populations young and experienced older individuals overlap in their occurrence on wintering sites and are able to share information during the nonbreeding season. However, as different Polish individuals are more likely to have knowledge on different possible routes, these individuals have a higher probability to switch between routes and thus exhibit a higher within-individual variation in migratory routes.

We propose that the rate of information exchange and the rate in which new routes are 'developed' will, together with the relative density of newly generated information within the population, determine how fast individuals from a population canalize and how conformity develops with age. Perhaps, the fast rate of information exchange and canalization of migratory strategy within the Dutch population is also illustrated by the observation of a left-skewed age distribution of Dutch Godwit recoveries in the Po Delta in Italy

Table 1C. Migratory Route – Southward migration.

Latitudinal crossing	Population	Absolute movement and between-individual variation (NL vs. PL)[3]	Within-individual variation (NL vs. PL)
52° > 48°	NL	223.1 ± 94.8 km ($n = 68$)	119.6 ± 93.0 km ($n = 23$)
	PL	–30.1 ± 130.9 km ($n = 8$)	95.0 ± 150.3 km ($n = 3$)
		($P < 0.001$; $P = 0.03$)	($P = 0.35$)
48° > 44°	NL	233.5 ± 102.5 km ($n = 68$)	133.6 ± 101.2 km ($n = 23$)
	PL	50.2 ± 148.5 km ($n = 8$)	105.1 ± 62.8 km ($n = 3$)
		($P < 0.01$; $P = 0.04$)	($P = 0.82$)
44° > 40	NL	229.3 ± 104.9 km ($n = 68$)	136.9 ± 95.9 km ($n = 23$)
	PL	220.1 ± 94.3 km ($n = 8$)	154.4 ± 103.3 km ($n = 3$)
		($P = 0.82$; $P = 0.69$)	($P = 0.54$)
40° > 36°	NL	177.1 ± 132.3 km ($n = 56$)	191.5 ± 134.6 km ($n = 20$)
	PL	233.9 ± 106.8 km ($n = 8$)	163.1 ± 136.0 km ($n = 3$)
		($P = 0.15$; $P = 0.55$)	($P = 0.92$)
36° > 32°	NL	173.7 ± 64.5 km ($n = 56$)	84.5 ± 77.3 km ($n = 20$)
	PL	287.1 ± 166.0 km ($n = 8$)	232.6 ± 241.6 km ($n = 3$)
		($P = 0.02$; $P = 0.02$)	($P = 0.04$)
32° > 28°	NL	182.3 ± 75.4 km ($n = 56$)	78.3 ± 63.4 km ($n = 20$)
	PL	319.4 ± 184.1 km ($n = 8$)	230.7 ± 254.4 km ($n = 3$)
		($P = 0.04$; $P = 0.001$)	($P = 0.04$)
28° > 24°	NL	156.5 ± 86.5 km ($n = 56$)	73.3 ± 73.6 km ($n = 20$)
	PL	325.3 ± 132.0 km ($n = 8$)	119.8 ± 53.3 km ($n = 3$)
		($P < 0.01$; $P = 0.01$)	($P = 0.13$)
24° > 20°	NL	161.2 ± 91.6 km ($n = 55$)	104.0 ± 97.1 km ($n = 20$)
	PL	312.7 ± 164.1 km ($n = 8$)	100.8 ± 81.7 km ($n = 3$)
		($P = 0.03$; $P = 0.001$)	($P = 0.83$)

(Beintema 2015). While this pattern could be explained by the selective disappearance of individuals migrating via Italy, we believe that it is more likely that social information on other routes causes them to use the more common Atlantic route later on in life. Nonetheless, an alternative, but not mutually exclusive, explanation for the larger within- and between-individual variation the Polish Godwits is that the spatial distribution of geographical barriers (e.g. Atlantic Ocean) and favourite ecological conditions may be different between both populations.

In conclusion, our study comparing two Godwit populations revealed remarkable population differences in both the between-individual variation and the within-individual flexibility of migratory strategies that would not have been expected in view of the lower sample size of tracked Polish Godwits. We raise new questions on the role of social environments in the shaping of migratory routines in birds not migrating in family units. To pursue these ideas, and to understand how the innate control of migration interacts with the learning through individuals including the sharing of social information of other individuals, we will have to track individuals from birth into adulthood whilst at the same time quantifying and manipulating the geographical and social environment of migrating birds by displacing and delaying inexperienced individuals.

Table 1D. Migratory Route – Northward migration.

Latitudinal crossing	Population	Absolute movement and between-individual variation (NL vs. PL)[3]	Within-individual variation (NL vs. PL)
48° > 52°	NL	–286,9 ± 97.4 km ($n = 37$)	106.9 ± 116.2 km ($n = 12$)
	PL	–177.3 ± 170.3 km ($n = 5$)	183.1 ± 250.0 km ($n = 2$)
		(***P = 0.04***; $P = 0.60$)	($P = 0.92$)
44° > 48°	NL	–215.8 ± 117.7 km ($n = 37$)	89.1 ± 75.8 km ($n = 12$)
	PL	–532.9 ± 228.7 km ($n = 5$)	474.0 ± 490.6 km ($n = 2$)
		(***P < 0.01***; $P = 0.34$)	(***P < 0.01***)
40° > 44°	NL	–253.7 ± 138.4 km ($n = 38$)	152.0 ± 117.0 km ($n = 12$)
	PL	–381.6 ± 336.9 km ($n = 5$)	291.1 ± 46.5 km ($n = 2$)
		($P = 0.78$; ***P = 0.03***)	($P = 0.24$)
36° > 40°	NL	–178.6 ± 171.4 km ($n = 29$)	139.0 ± 144.9 km ($n = 8$)
	PL	–247.6 ± 275.8 km ($n = 5$)	440.7 ± 129.2 km ($n = 2$)
		($P = 0.67$; $P = 0.97$)	(***P = 0.03***)
32° > 36°	NL	–251.6 ± 159.7 km ($n = 29$)	195.1 ± 154.0 km ($n = 8$)
	PL	–310.7 ± 210.7 km ($n = 5$)	309.9 ± 37.4 km ($n = 2$)
		($P = 0.44$; $P = 0.67$)	(***P = 0.02***)
28° > 32°	NL	–192.0 ± 153.9 km ($n = 33$)	162.3 ± 109.3 km ($n = 10$)
	PL	–269.6 ± 231.9 km ($n = 5$)	327.9 ± 149.7 km ($n = 2$)
		($P = 0.61$; $P = 0.71$)	(***P = 0.03***)
24° > 28°	NL	–136.4 ± 119.5 km ($n = 32$)	157.7 ± 132.4 km ($n = 10$)
	PL	–189.8 ± 90.0 km ($n = 6$)	155.6 ± 23.6 km ($n = 3$)
		($P = 0.25$; $P = 0.70$)	($P = 0.78$)
20° > 24°	NL	–90.8 ± 115.7 km ($n = 33$)	130.9 ± 105.3 km ($n = 10$)
	PL	–192.2 ± 83.9 km ($n = 6$)	127.4 ± 79.2 km ($n = 3$)
		(***P = 0.02***; $P = 0.61$)	($P = 0.83$)

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SAMENVATTING

Dankzij het gebruik van nauwkeurige zenders is onze kennis over de individuele en soortspecifieke variatie in de ruimtelijke en temporele organisatie van vogeltrek sterk gegroeid. Tot dusverre zijn de meeste studies gericht geweest op het documenteren van de variatie in trek tussen en binnen individuen binnen één populatie. Dit is ook het geval voor de continentale ondersoort van de Grutto *Limosa l. limosa*, aangezien het meeste onderzoek is uitgevoerd aan Grutto's die in relatief hoge dichtheden in Nederland broeden. In dit artikel beschrijven wij de trekroute en het moment van de trek van volwassen Grutto's die in het oosten van Polen broeden en vergelijken wij die met eerder gepubliceerde resultaten van Nederlandse broedvogels. Tijdens de noordwaartse trek vertrokken de Poolse Grutto's later uit hun Afrikaanse overwinteringsgebieden dan Nederlandse Grutto's en kwamen ook later in hun broedgebieden aan. De Poolse Grutto's verlieten na de broedtijd hun broedgebied eerder, maar arriveerden gemiddeld een maand na de Nederlandse vogels in hun overwinteringsgebieden. De Poolse vogels verbleven onderweg veel langer op tussenstops tussen hun broed- en overwinteringsbieden. De variatie in de timing van de zuidwaartse trek tussen individuele vogels was bij Grutto's uit Polen groter dan bij Nederlandse Grutto's. Ten slotte vertoonden de Poolse Grutto's zowel op de noord- als de zuidwaartse trek een veel grotere variatie in trekroute tussen individuen en jaren dan Nederlandse Grutto's. Wij postuleren dat een verschil in gruttodichtheid tussen beide populaties (hoog in Nederland, laag in Polen) hieraan ten grondslag ligt. Door het dichtheidsverschil zou de kans op sociale informatie bij de Poolse vogels op hun eerste zuid- en noordwaartse trek kleiner zijn dan bij de Nederlandse vogels met als gevolg dat de Poolse Grutto's vaker op eigen houtje trekken en daardoor vaker verschillende trekroutes ontwikkelen. Als deze informatie vervolgens later in het leven gedeeld wordt met andere individuen, resulteert dit in een grotere variatie binnen en tussen individuen. Om deze hypothese verder te onderzoeken, zullen toekomstige studies niet alleen individuen van jongs af aan moeten volgen, maar ook de sociale omgeving tijdens de trek kwantificeren en experimenteel manipuleren.