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High Migratory Survival and Highly Variable Migratory Behavior in Black-Tailed Godwits

Nathan R. Senner^{1,2*}, Mo A. Verhoeven¹, José M. Abad-Gómez³, José A. Alves^{4,5},
Jos C. E. W. Hooijmeijer¹, Ruth A. Howison¹, Rosemarie Kentie^{1,6,7}, A. H. Jelle Loonstra¹,
José A. Masero³, Afonso Rocha⁸, Maria Stager⁹ and Theunis Piersma^{1,7}

¹ Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, Netherlands, ² Department of Biological Sciences, University of South Carolina, Columbia, SC, United States, ³ Conservation Biology Research Group, Department of Anatomy, Cell Biology and Zoology, Faculty of Sciences, University of Extremadura, Badajoz, Spain, ⁴ DBIO/CESAM Centre for Environmental and Marine Studies, University of Aveiro, Campus Universitário de Santiago, Aveiro, Portugal, ⁵ South Iceland Research Centre, University of Iceland, Fjölheimar, Selfoss, Iceland, ⁶ Department of Zoology, University of Oxford, Oxford, United Kingdom, ⁷ NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems and Utrecht University, Den Burg, Netherlands, ⁸ Department of Life Sciences, Marine and Environmental Research Centre, University of Coimbra, Coimbra, Portugal, ⁹ Division of Biological Sciences, University of Montana, Missoula, MT, United States

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*Correspondence:

Nathan R. Senner
nathan.senner@gmail.com

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Few studies have been able to directly measure the seasonal survival rates of migratory species or determine how variable the timing of migration is within individuals and across populations over multiple years. As such, it remains unclear how likely migration is to affect the population dynamics of migratory species and how capable migrants may be of responding to changing environmental conditions within their lifetimes. To address these questions, we used three types of tracking devices to track individual black-tailed godwits from the nominate subspecies (*Limosa limosa limosa*) throughout their annual cycles for up to 5 consecutive years. We found that godwits exhibit considerable inter- and intra-individual variation in their migratory behavior across years. We also found that godwits had generally high survival rates during migration, although survival was reduced during northward flights across the Sahara Desert. These patterns differ from those observed in most other migratory species, suggesting that migration may only be truly dangerous when crossing geographic barriers that lack emergency stopover sites and that the levels of phenotypic flexibility exhibited by some populations may enable them to rapidly respond to changing environmental conditions.

Keywords: repeatability, phenotypic flexibility, seasonal survival, migration, annual cycle

INTRODUCTION

Many migratory species are experiencing rapid and dramatic population declines (Wilcove and Wikelski, 2008). These declines have been linked with a variety of anthropogenic changes, including habitat loss (Rushing et al., 2016), and land-use (Gill et al., 2007) and climatic change (Both et al., 2006). Nonetheless, linking a species' or population's decline with specific environmental drivers remains difficult given the vast distances that separate areas occupied during different phases of the annual cycle (Piersma et al., 2016). The advent of new tracking technologies over the past two decades has begun to bridge this gap, but these new technologies remain expensive—meaning that

many studies of migration are carried out over short timescales or with small sample sizes—and thus a plethora of questions about migration and the causes of declines in migratory species still remain (Hebblewhite and Haydon, 2010). This is especially true in regards to our understanding of how migratory behaviors may change over the course of an individual's lifetime and how migration itself may influence the population dynamics of migratory species (Piersma, 2011).

Recent work, however, has begun to deepen our understanding of the degree of variation in migratory behavior that individuals can be expected to display over the course of their lives. For instance, a number of studies have shown that individual migratory birds can exhibit highly repeatable migratory timing (Stanley et al., 2012; Gill et al., 2014). In some cases, individuals may vary their departure dates from non-breeding sites by as little as 3 days over 4 consecutive years (Conklin et al., 2013). In contrast, other studies have found that individuals of some species can exhibit marked improvement and flexibility in their migratory timing and performance, enabling them to adjust their behaviors to prevailing environmental conditions (Sergio et al., 2014; Pedler et al., 2018). What remains unclear, though, is how flexible migratory behaviors are generally and how both historical and contemporary selection pressures may mold the levels of flexibility exhibited by individuals within a population.

Similarly, our understanding of the location and timing of mortality events during the annual cycles of migratory species has developed rapidly over the past two decades. While most efforts to determine the seasonal survival rates of migratory species have relied on color-marking schemes and mark-recapture analyses to infer when and where individuals die (Sillett and Holmes, 2002; Lok et al., 2015), some recent studies have used satellite tracking devices to monitor the survival of individuals continuously throughout their annual cycles (Hebblewhite and Merrill, 2011; Klaassen et al., 2014; Hewson et al., 2016; Watts et al., 2019). In general, these studies have identified migration as the period during the annual cycle with the highest mortality rates. Nonetheless, work with two different sub-species of red knots (*Calidris canutus islandica* and *C. c. canutus*) has found the opposite—higher survival during migration than in stationary periods—indicating that migration may not be universally dangerous (Leyrer et al., 2013; Rakhimberdiev et al., 2015). As a result, the seasonal survival patterns of a larger number of migratory species still need to be documented in order to more fully understand how migration may influence a species' population dynamics.

The nominate subspecies of the black-tailed godwit (*Limosa limosa limosa*) breeds predominantly in The Netherlands and spends the non-breeding season disjunctively in sub-Saharan West Africa and the southern Iberian Peninsula (Hooijmeijer et al., 2013; Kentie et al., 2016). Previous work has indicated that individuals exhibit significant repeatability in the timing of their departure from staging sites during northward migration ($r = 0.30\text{--}0.42$; Lourenço et al., 2011) and arrival at the breeding grounds ($r = 0.24$; Kentie et al., 2017), irrespective of their non-breeding location. Individuals can also exhibit marked flexibility in their migratory behaviors, however. For instance, in response

to a recent early spring snowstorm, many godwits were able to alter their arrival timing and use of stopover sites in order to avoid the most inclement conditions (Senner et al., 2015a). Similarly, recent work has found little evidence that godwits migrating longer distances incur costs that carry-over to affect reproduction, indicating the possibility that migration may not be the limiting event during the godwit annual cycle (Kentie et al., 2017). Godwits thus represent an intriguing opportunity to assess levels of flexibility in migratory timing across an individual's life, as well as to broaden our understanding of how mortality events are spread across migratory annual cycles.

To address these knowledge gaps, we used three types of tracking devices to monitor godwit migration timing and seasonal survival over the course of 6 years, from 2012 to 2017. Given their ability to flexibly respond to conditions encountered mid-migration and the lack of reversible state effects linking migration to reproductive success (Senner et al., 2015a; Kentie et al., 2017), we predicted that godwits would exhibit high levels of flexibility and high survival during migration. By broadening the spectrum of species for which seasonal survival estimates and measures of migratory repeatability have been determined, we aim to improve our understanding of the ways in which migratory species may be able to respond to environmental change.

METHODS

Study Species

Godwits of the nominate subspecies breed across much of Western Europe, but nearly 80% of their population now breeds in The Netherlands (Kentie et al., 2016). Historically, the entire population was thought to spend the non-breeding season in West Africa and then migrate northward via stopover sites in Italy, Morocco, Portugal, and France (Beintema and Drost, 1986). However, coinciding with shrinking populations and the creation of fish ponds and seasonally flooded rice fields in Spain and Portugal in the 1980s, godwits have altered both their non-breeding distribution and migration routes (Lourenço and Piersma, 2008). Currently, nearly a quarter of the population spends the non-breeding season in and around Doñana Natural and National Parks in southern Spain (Márquez-Ferrando et al., 2014). Together with staging sites in Extremadura, Spanish sites now host approximately half of the population during northward migration as well (Masero et al., 2011), with the remainder using Portuguese staging sites (Lourenço et al., 2010; Verhoeven et al., 2018). Moreover, Italy is now rarely visited and the use of French and Moroccan stopovers has declined dramatically (Lourenço and Piersma, 2008; Alves and Lourenço, 2014).

In general, godwits spending the non-breeding season in West Africa depart from January to February and then join the remainder of the population in Iberia, where they can stage for as long as 4–5 weeks (Masero et al., 2011). Godwits begin leaving Iberia in early March and can fly directly to their breeding sites or stopover as many as four times *en route* (Senner et al., 2015a). Breeding ground arrival then spans a period from early March to mid-May. Once on the breeding grounds, a period of 5 weeks can elapse between arrival and

clutch initiation (Senner et al., 2015b). Finally, adult godwits depart breeding areas on southward migration from mid-June onwards (Hooijmeijer et al., 2013).

General Methods and Tracking Devices

We employed three different tracking technologies: solar geolocation devices (“geolocators”), satellite transmitters, and GPS trackers. Geolocators and GPS trackers were both deployed during the breeding season (Apr–Jun) at our long-term demographic study area in southwest Friesland, The Netherlands (Senner et al., 2015a). This area encompasses 10,280 ha spanning from 53.0672°N, 5.4021°E in the north, to 52.8527°N, 5.4127°E in the south, 52.9715°N, 5.6053°E in the east, and 52.8829°N, 5.3607°E in the west. Satellite transmitters were deployed during northward migration (Jan–Feb) at staging sites in Extremadura, Spain (39.0364°N, 5.9112°W; Masero et al., 2011) and Santarém, Portugal (38.8525°N, 8.9695°W; Lourenço et al., 2011).

We deployed geolocators from Migrate Technology, Ltd. on adults captured on nests using walk-in traps or mist-nets placed over the nest ($n = 126$; 2012–2013: 0.65 g W65A9, 2014: 1 g Intigeo C65). Geolocators were attached to colored flags placed on the upper tibia; the combination of the geocator and flag weighed ≤ 3.3 g, which was $\leq 1.5\%$ of an individual’s mass at the time of capture. In subsequent years, we then attempted to recapture geocator-carrying individuals using similar methods as during the initial capture. We also attached 9.5 g solar-powered PTT-100s satellite transmitters from Microwave Technology Inc. ($n = 60$; 2013–2015) and 7.5 g solar-powered UvA-Bits GPS trackers ($n = 20$; 2013) developed by the University of Amsterdam (Bouten et al., 2013) using a leg-loop harness made of 2 mm nylon rope (see Senner et al., 2015a for more details). Because of the weight, we deployed these devices only on individuals weighing > 300 g, meaning the majority were placed on females ($n = 1$ male). In total, the tracking device and harness weighed ~ 12 and 10 g, respectively, representing 3.43 ± 0.22 and $2.86 \pm 0.19\%$ of an individual’s mass at the time of capture.

Tracking Data

Geolocators measure ambient light levels in order to identify the timing of sunrise and sunset, and, ultimately, estimate an individual’s position on the globe. To transform our raw light data into twice-daily position estimates, we first passed it through the program *IntiProc* (v. 1.03; Migrate Technology, Ltd.) and then processed our transformed light data using the “BAStag” package (Wootherspoon et al., 2013) in the R software environment (R Development Core Team, 2016). We used a light threshold of 1.5 to demarcate all sunrises and sunsets and discarded sunrises/sunsets that had non-random shading events, such as when a geocator was shaded during either the beginning or end of a twilight period. Finally, we processed our light data using the R package “FLightR” (Rakhimberdiev et al., 2017) following Rakhimberdiev et al. (2016). In FLightR, we used the period during which an individual was known to be on the breeding grounds (from resighting data) as a calibration period. We then analyzed the data without land or behavioral masks or automated outlier exclusion, but with movements constrained to

the region between 18°W–13°E and 11–57°N (Hooijmeijer et al., 2013). All models were optimized with 1 million particles.

We programmed satellite transmitters to collect locations for 10 h and recharge for 48 h, which allowed us to identify locations used for ≥ 2 d. We retrieved all location fixes via the CLS tracking system (www.argos-system.org) and passed them through the Douglas Argos-filter (DAF) algorithm (Douglas et al., 2012). We retained all standard class locations (i.e., LC 3, 2, 1) and excluded all auxiliary class locations that did not meet our predefined threshold for maximum movement rate (120 km h^{-1}). On average, this resulted in 8 ± 1 locations per 10-h duty cycle for each individual.

We programmed the GPS trackers to record an individual’s location once every 5 min when the tracker’s battery was fully charged and once every 15 min in all other instances (see Senner et al., 2018 for more details). Although GPS trackers generate many fewer erroneous locations than satellite transmitters, spurious locations are recorded. We thus also filtered our GPS tracker data with the DAF and used the same movement thresholds as those imposed on our satellite transmitter data.

Statistical Analysis

To detail the temporal flexibility of godwit annual cycles, we first characterized the timing of all movements made by tracked individuals. Because both the spatial and temporal resolution of the three types of tracking devices differed (Bouten et al., 2013; Boyd and Brightsmith, 2013; Rakhimberdiev et al., 2016), we took a conservative approach to identifying movements in order to make the data comparable across devices. Therefore, given that the average location estimates generated by FLightR have a deviation of $\pm \sim 40$ km from an individual’s true location and that our satellite transmitters were only able to detect stopovers lasting ≥ 2 d, we defined a migratory movement as a direct flight of ≥ 80 km and a stopover as a stationary period lasting ≥ 2 d. Additionally, geolocators have difficulty estimating latitude—but not longitude—within a week of the equinoxes (Rakhimberdiev et al., 2016). Unfortunately, the spring equinox coincides with godwit northward migration and the period of their arrival at their breeding sites. However, godwits migrate in both a northerly and easterly direction during this period, enabling us to document each individual’s arrival date by identifying the date on which they crossed a longitude of 5°E, which corresponds to The Netherlands when arriving from the west (see Verhoeven et al., 2019 for more details).

Given these “decision rules” for identifying migratory movements, following our previously published studies (e.g., Hooijmeijer et al., 2013), we delineated the godwit annual cycle into 10 separate annual cycle events that are performed by most godwits—the breeding season, post-breeding season, southbound migration over Europe, Iberian stopover period, southbound migration over the Sahara Desert, the non-breeding season, northbound migration over the Sahara Desert, Iberian staging period, northbound flight over Europe, and European stopover period. Briefly, we defined non-breeding sites as the site where an individual was located on 20 September, while breeding sites were those sites where an individual was located on 15 May. We defined the post-breeding period as beginning for

geolocator-carrying individuals the day they were last resighted in our study area (see Loonstra et al., 2019 for detailed information about our hemisphere-wide resighting efforts); for all other individuals, the post-breeding period began when they moved >25 km away from their breeding site. Finally, not all individuals migrate to sub-Saharan Africa. As a result, we only made comparisons among individuals performing the same event (e.g., northbound flight over Europe).

We then calculated: the repeatability (r) of the timing and number of movements with the R package “rptR” (Stoffel et al., 2017) using the linear mixed model method and including individual as a random-effect; the amount of variation exhibited by an individual in their migratory behavior across years (difference in the timing of an event between consecutive years; “intra-individual” variation); and the amount of population-level variation across all tracked individuals (difference in timing between earliest and latest individual within a single year \pm SD; “inter-individual” variation). To ensure that the observed levels of intra-individual variation were not a byproduct of stochastic environmental conditions or the type of transmitter an individual carried, we used linear mixed models with individual included as a random effect, and year and type of tracking device as predictor variables. Additionally, as an anecdotal comparison, we obtained data on the amount of intra-individual variation in northward migratory timing exhibited by two other species of godwits—Hudsonian (*L. haemastica*) and bar-tailed godwits (*L. lapponica baueri*)—from the published literature (Conklin et al., 2013; Senner et al., 2014).

We also used satellite transmitter data to calculate event-specific survival rates. Retrieving data from both the GPS trackers and geolocators was dependent upon an individual returning to the breeding grounds, meaning we could not pinpoint when mortality occurred in individuals carrying those types of devices that did not return to The Netherlands. To calculate the event-specific survival rates, we first determined which type of annual-cycle event an individual was engaged in on each day that its transmitter provided location estimates using an individual’s location and movement patterns (see above). Then, we identified on which day each individual died via its transmitter’s activity sensor. Although the death of a transmitter does not necessarily imply that the individual carrying that transmitter also died, in all but five cases in which we documented the death of a transmitter, we also failed to subsequently observe the associated individual. In those cases in which we did observe the individual after the transmitter had stopped functioning, two birds had lost their transmitters, while the transmitters of the other three individuals had failed. These individuals were removed from our analyses in the season during which their transmitter failed or was lost; our estimates of godwit survival rates may therefore be biased low. Finally, to test for differences in daily survival rates among years and annual cycle events, we used an Andersen-Gill model—a type of hazards model—in the R package “survival” (Therneau and Lumley, 2015). In these models, we included the annual cycle event as the (categorical) predictor variable, survival between consecutive time steps as the dependent variable, year as the strata, and individual as a random effect. Because the hazards calculated by the model depend on which event of the annual

cycle was used as the reference/baseline level, we reran the model with each separate event as the reference and then used model averaging in the R package “AICcmodavg” (Mazerolle, 2013) to determine their model-averaged coefficients.

For our linear regression model testing the effects of year and type of tracking device on intra-individual variation, we compared models including predictor variables to an intercept-only “null” model within an AIC_c framework, where the model with the lowest AIC_c score was considered the most well-supported model (Burnham and Anderson, 2002). Predictor variables whose 95% confidence intervals did not include zero were considered biologically relevant (Grueber et al., 2011). The regression models were run using the R package “lme4” (Bates et al., 2014); the statistical significance of random effects was tested using the R package “lmerTest” (Kuznetsova et al., 2015). All results are reported as mean \pm SD unless otherwise noted.

RESULTS

Return Rates and Migration Routes

We deployed 60 satellite transmitters, 20 GPS trackers, and 126 geolocators from 2012 to 2015 (Figure 1). Three satellite transmitters were inadvertently placed on Icelandic-breeding black-tailed godwits (*L. l. islandica*) and not included in our analyses; the remaining 57 individuals were tracked for ≤ 4 southward and ≤ 5 northward migrations per individual. Fourteen individuals with GPS trackers returned the following year, of which 4 provided data and 1 eventually provided two complete annual cycles. One-hundred and eighteen individuals with geolocators returned to the breeding grounds at least once, 43 of those individuals were recaptured, 28 of those geolocators provided data for at least one full migration period, and 2 individuals were tracked for two complete annual cycles.

Among the individuals with satellite transmitters, all but 10 bred in The Netherlands ($n = 47$); the remaining individuals bred in Germany ($n = 3$), Belgium ($n = 2$), and Poland ($n = 1$), or were not tracked long enough to determine their breeding location ($n = 4$). Across all individuals tracked to their non-breeding grounds ($n = 64$), irrespective of tracking device type, all but eight spent the non-breeding season in sub-Saharan West Africa, with the remainder spending that period either on the Iberian Peninsula ($n = 7$) or in Morocco ($n = 1$); 13 individuals died before reaching their non-breeding grounds. All individuals exhibited broad fidelity to both their breeding and non-breeding sites, as no individual changed either the province in which they bred nor whether they spent the non-breeding season north or south of the Sahara Desert (Figure 1; see also Kentie et al., 2017; Verhoeven et al., 2019).

Repeatability

The repeatability of migratory timing and behavior ranged from $r = 0.78$ (95% CI = 0.55, 0.91; Table 1) for the date of departure from the non-breeding grounds to $r = 0.00$ (95% CI = 0.00, 0.40) for the number of stops made during southward migration. In only three cases were aspects of migration not repeatable—the

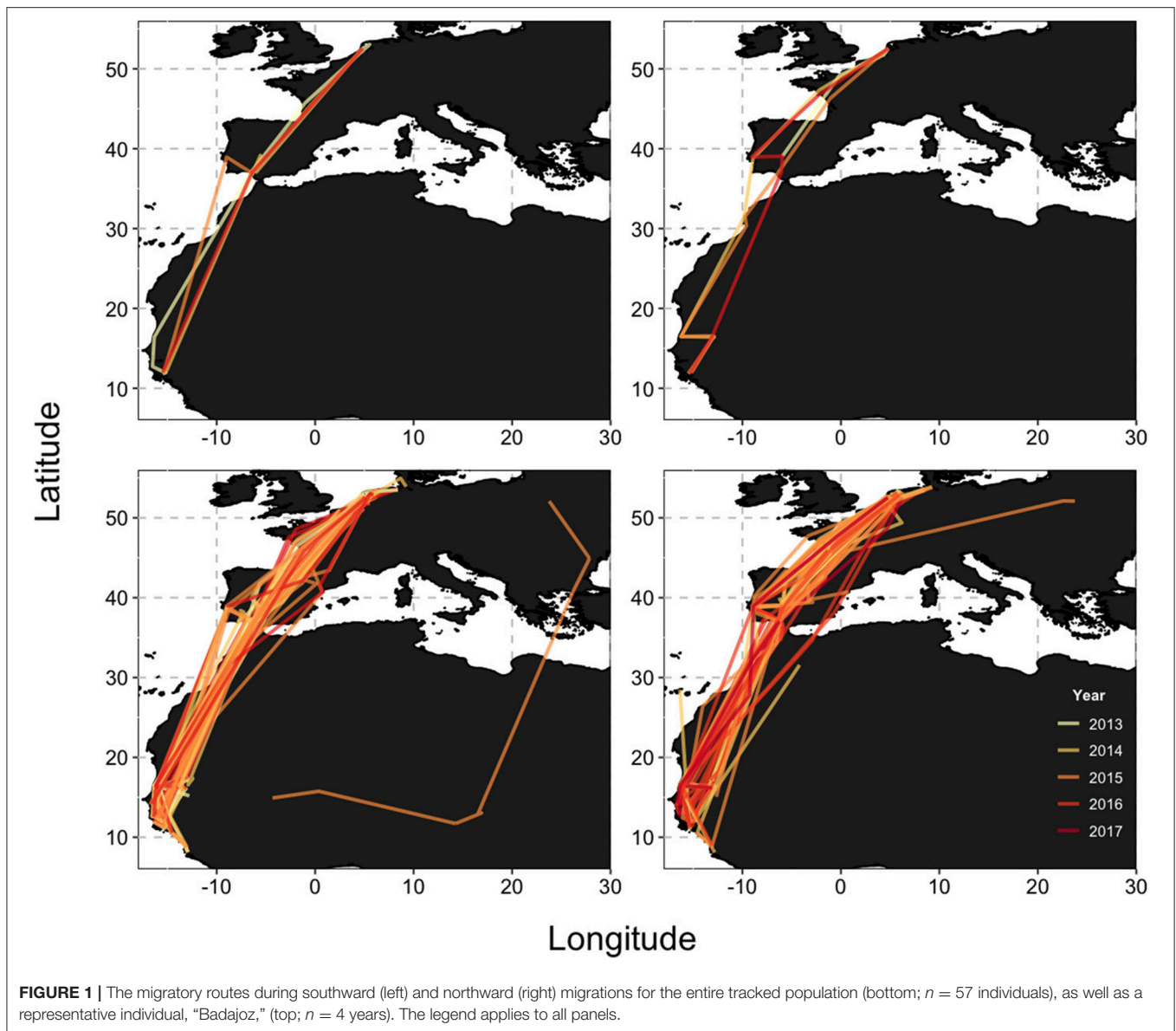


FIGURE 1 | The migratory routes during southward (left) and northward (right) migrations for the entire tracked population (bottom; $n = 57$ individuals), as well as a representative individual, “Badajoz,” (top; $n = 4$ years). The legend applies to all panels.

number of stops made during southward migration (see above), number of stops made during northward migration ($r = 0.20$, 95% CI = 0.00, 0.52), and duration of northward migration ($r = 0.21$, 95% CI = 0.00, 0.52).

Inter-individual Variation

Levels of inter-individual variation for the timing of migratory events ranged from an average of 96 ± 29 d ($n = 6$ years; **Table 1**) for the timing of departure from the non-breeding grounds to an average of 47 ± 9 d ($n = 6$ years) for the timing of departure from the breeding grounds. Inter-individual variation in the number of stops made was 4 ± 2 stops ($n = 6$ years) during northward migration and 4 ± 2 stops during southward migration ($n = 5$ years), while for the duration of migration, it was 25 ± 11 d ($n = 6$ years) for northward migration and 63 ± 23 d ($n = 5$ years) for southward migration.

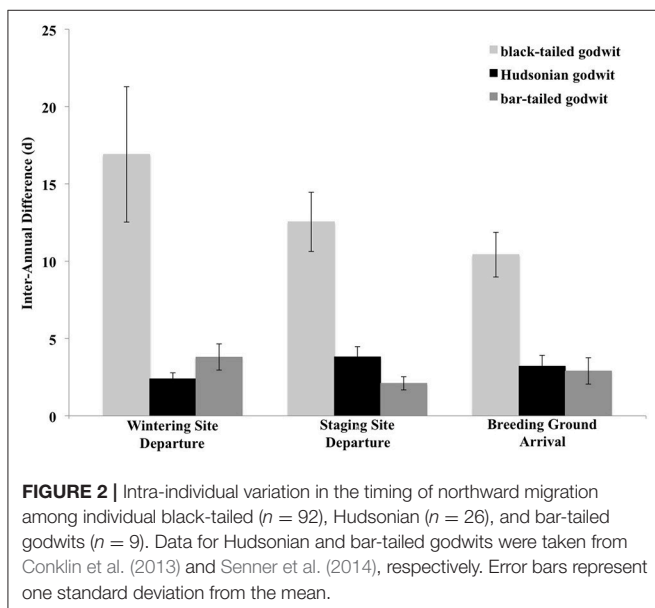
Intra-individual Variation

Levels of intra-individual variation in the timing of migratory events ranged from an average of 17 ± 12 d ($n = 17$ individuals; **Table 1**) for the timing of arrival at non-breeding sites following southward migration to an average of 10 ± 11 d ($n = 22$ individuals) for the timing of arrival at the breeding grounds. Intra-individual variation in the number of stops made was 1 ± 1 stops ($n = 33$ individuals) during northward migration and 2 ± 1 stops during southward migration ($n = 19$ individuals), while, for the duration of migration, it was 6 ± 8 d ($n = 33$ individuals) for northward migration and 15 ± 9 d ($n = 19$ individuals) for southward migration. These levels of intra-individual variation did not vary across years or with the type of tracking device an individual carried (**Supplementary Information Tables 1, 2**). Additionally, black-tailed godwits exhibited qualitatively more flexibility than did

TABLE 1 | Repeatability (*r*), and inter- and intra-individual variation in migratory timing and behavior of continental black-tailed godwits tracked with satellite transmitters, GPS trackers, and solar geolocation devices, 2012–2017.

Migratory stage	Inter-individual variation	Intra-individual variation	<i>r</i>
Non-breeding site departure	107 ± 29 d (<i>n</i> = 6)	17 ± 20 d (<i>n</i> = 16)	0.78 (0.55, 0.91)
Iberian stage site departure northward migration	40 ± 22 d (<i>n</i> = 6)	13 ± 12 d (<i>n</i> = 37)	0.33 (0.03, 0.57)
Number of stopovers during northward migration	4 ± 2 stops (<i>n</i> = 6)	1 ± 1 stops (<i>n</i> = 33)	0.20 (0.00, 0.52)
Duration of northward migration	23 ± 21 d (<i>n</i> = 6)	6 ± 8 d (<i>n</i> = 33)	0.11 (0.00, 0.52)
Breeding ground arrival	39 ± 12 d (<i>n</i> = 6)	11 ± 8 d (<i>n</i> = 33)	0.47 (0.18, 0.69)
Breeding ground departure	42 ± 22 d (<i>n</i> = 5)	10 ± 11 d (<i>n</i> = 22)	0.37 (0.02, 0.65)
Iberian stopover site departure southward migration	55 ± 34 d (<i>n</i> = 5)	16 ± 14 d (<i>n</i> = 16)	0.39 (0.00, 0.71)
Non-breeding site arrival	66 ± 40 d (<i>n</i> = 5)	17 ± 12 d (<i>n</i> = 23)	0.52 (0.18, 0.74)
Number of stopovers during southward migration	3 ± 2 stops (<i>n</i> = 5)	2 ± 1 stops (<i>n</i> = 19)	0.00 (0.00, 0.40)
Duration of southward migration	54 ± 35 d (<i>n</i> = 5)	15 ± 9 d (<i>n</i> = 19)	0.69 (0.47, 0.85)

Intra-individual variation is the difference in migratory timing for an individual between consecutive years; inter-individual variation is the time span between the first and last individual performing an event. The standard deviation is presented for the inter- and intra-individual variation in migratory timing and the 95% confidence interval for r.



either Hudsonian or bar-tailed godwits (Figure 2) over the course of northward migration.

Seasonal Survival

Across all years and periods of the annual cycle, daily survival rates for godwits carrying satellite transmitters averaged 0.998 ± 0.001 (*n* = 57 individuals and 24,366 days), leading to an annual survival rate of 0.52 ± 0.12. Hazard rates were highest during the flight from non-breeding areas in sub-Saharan West Africa to staging areas in Spain and Portugal ($\beta = 18.97$, 95% CI = 11.75, 26.19; Table 2; Supplementary Information Tables 3, 4). In contrast, hazard rates were lowest during the post-breeding staging period ($\beta = -15.6$, 95% CI = -27.29, -3.91). No other portion of the annual cycle had hazard rates that differed significantly from the baseline (Table 2). Finally, the breeding season accounted for 29.8 ± 20.1% (*n* = 5 years; Table 2) of all

mortality events, while northward flights over Africa accounted for 12.8 ± 16.0% (*n* = 5 years), and the post-breeding period 0.0 ± 0.0% (*n* = 4 years).

DISCUSSION

We found that black-tailed godwits breeding in northwestern Europe exhibited high-levels of inter- and intra-individual variation in migratory timing—but also high repeatability of departure and arrival dates—and generally high survival rates during migratory flights. Nonetheless, survival rates were lower during migratory flights over the Sahara Desert. Our results thus suggest that the relative danger of migration may be context dependent and that, under the right circumstances, some migratory species may be readily capable of responding to contemporary environmental changes.

Seasonal Survival in Migratory Species

Given the difficulty of tracking migrants throughout their annual cycles, few studies have explored their seasonal survival. The majority of studies that have succeeded in developing such estimates have identified migration as the period with the lowest daily (and seasonal) survival rates of the annual cycle (Sillett and Holmes, 2002; Hebblewhite and Merrill, 2011; Klaassen et al., 2014; Romer et al., 2015; Watts et al., 2019). Our results are not entirely consistent with these findings: migratory flights over Europe during both north- and southward migration were consistently characterized by hazard rates that were equivalent to those exhibited during other, stationary, portions of the godwit annual cycle. Nevertheless, hazard rates during the northward flight traversing the Sahara Desert were significantly higher—and thus survival rates lower—overall than during other periods of the annual cycle. Our results thus suggest that the relative danger of migration is likely context dependent and migration may only be truly dangerous during flights over geographic barriers that lack potential emergency stopover sites (see also Lok et al., 2015).

Two potential caveats, however, should also be noted: First, even after accounting for the potential biases in our survival estimates resulting from transmitter failures, the overall survival

TABLE 2 | The duration, model-averaged β coefficients from an Andersen-Gill model, and total proportion of mortality events observed during each annual cycle event.

Annual cycle event	Mean duration \pm SD	Cox β coefficient \pm 95% confidence interval	Proportion of mortality events \pm SD
Non-breeding season	21 \pm 33 d ($n = 47$)	-2.90 (-17.19, 11.39)	21.3 \pm 17.0% ($n = 5$)
Northward flight over Africa	2 \pm 1 d ($n = 48$)	18.97 (11.75, 26.19)	12.8 \pm 16.0% ($n = 5$)
Iberian staging period	37 \pm 20 d ($n = 97$)	-0.53 (-14.84, 13.79)	17.0 \pm 16.0% ($n = 5$)
Northward flight over Europe	3 \pm 1 d ($n = 81$)	0.16 (-14.23, 14.55)	2.1 \pm 14.9% ($n = 5$)
European stopover period	12 \pm 10 ($n = 69$)	-0.75 (-15.11, 13.61)	4.3 \pm 14.4% ($n = 5$)
Breeding season	69 \pm 25 d ($n = 77$)	-1.11 (-15.41, 13.18)	29.8 \pm 20.0% ($n = 5$)
Post-breeding season	15 \pm 12 d ($n = 29$)	-15.6 (-27.29, -3.91)	0.0 \pm 0.0% ($n = 4$)
Southward flight over Europe	3 \pm 1 d ($n = 66$)	0.67 (-13.72, 15.05)	2.1 \pm 2.6% ($n = 4$)
Iberian stopover period	34 \pm 39 d ($n = 63$)	-1.94 (-16.20, 12.32)	6.4 \pm 9.5% ($n = 4$)
Southward flight over Africa	2 \pm 4 d ($n = 59$)	2.03 (-12.35, 16.42)	4.2 \pm 11.8% ($n = 4$)

Sample sizes for the mean duration refer to the number of episodes of each event documented across all individuals; for the proportion of mortality events it refers to the number of years included.

rates documented here are considerably lower than those found in other studies with color-marked godwits (Roodbergen et al., 2008; Kentie et al., 2016, 2018; Loonstra et al., 2019). This suggests our use of satellite transmitters weighing 9.5 g may have served as a handicap that reduced survival. Survival was lower than expected across nearly all annual-cycle events, however, indicating that these effects were not just experienced during migration. Second, our sample of godwits carrying satellite transmitters was heavily biased toward females and it is possible that males and females differ in their seasonal survival patterns. Previous godwit studies, though, have suggested that migratory patterns are roughly similar between the two sexes (Lourenço et al., 2011; Kentie et al., 2016), although adult females do have slightly lower annual survival rates (Loonstra et al., 2019). We therefore believe that our results are robust and broadly representative of the seasonal survival rates and migratory patterns exhibited by godwits breeding in northwest Europe.

Given these results and those from recent studies with red knots (Leyrer et al., 2013; Rakhimberdiev et al., 2015), how strongly should migration be expected to determine the population dynamics of migratory species? Previous studies of migratory birds making flights across large geographic barriers, such as the Sahara, have found that mortality events experienced during these flights may result from a suite of potentially interacting and sometimes unpredictable processes, including extremely high temperatures (Schmaljohann et al., 2007), violent sandstorms (Klaassen et al., 2010), poor body condition (Ward et al., 2018), and predation (Gangoso et al., 2013). In some cases, the mortality events experienced during these flights play an important role in determining a species' overall population dynamics (Lok et al., 2013). Many migratory species never cross such barriers, however. For these species, our results suggest that migration should not necessarily be more dangerous than any other activity, so long as high-quality stopover sites exist (Alves et al., 2013).

Even for those species whose migrations do include geographic barriers, it is unclear how strongly migration should generally be expected to regulate population dynamics. For

instance, although hazard rates were highest during trans-Saharan flights in our study, these flights accounted for only a relatively small proportion of the total number of mortality events experienced by godwits across their annual cycle. Instead the breeding season, which is substantially longer in duration than a trans-Saharan flight ($\mu = 75$ and 2 d, respectively), resulted in more than twice the number of mortality events as did trans-Saharan flights. Given that trans-Saharan flights occupy such a short period of time, survival rates during these flights would have to be severely reduced before they become the limiting component of the godwit annual cycle (but see Sillett and Holmes, 2002; Leyrer et al., 2013). Nonetheless, understanding what is influencing mortality rates during trans-Saharan flights, and during flights over geographic barriers more generally (e.g., Ward et al., 2018), is necessary to predict how changing conditions may impact the population dynamics of migratory species.

Flexibility in Migratory Timing

Godwits also exhibited significant inter- and intra-individual variation in their migratory timing within and among years. For instance, individual godwits varied their departure timing from non-breeding sites by an average of 17 days and their arrival on the breeding grounds by an average of 11 days between consecutive years. Furthermore, within a single year, departure dates across the population from non-breeding sites in Africa could span nearly 5 months and arrival dates at breeding sites in The Netherlands could cover almost 2 months (see also Verhoeven et al., 2019). In turn, our previous work has indicated that this variation is neither influenced by an individual's non-breeding site—as godwits spending the non-breeding season in sub-Saharan Africa exhibit similar levels of intra-individual variation and repeatability to those spending it in Iberia (see Kentie et al., 2017; Verhoeven et al., 2019)—nor the length of its life—as godwits do not directionally change the timing of their migrations over the course of their lives (see Verhoeven et al., 2019). To the best of our knowledge, godwits thus display the largest degree of variation in migratory timing yet documented

among obligate migratory birds (Both et al., 2016). For example, in other godwit species, departure and arrival dates can span a period as small as 10 days across entire breeding populations (Senner et al., 2014), while individuals can vary their migratory timing by as little as 4 days over the course of their lifetimes (Figure 2; Conklin et al., 2013; Gill et al., 2014; Senner et al., 2014). More broadly, even among those bird species exhibiting low levels of repeatability in migratory timing, their absolute levels of intra- and inter-individual variation are lower than those observed in godwits (Both et al., 2016).

Intriguingly, in addition to their high levels of intra- and inter-individual variation, godwits also exhibited significant levels of repeatability in nearly all of their migratory behaviors. As discussed extensively by Conklin et al. (2013), high levels of repeatability can arise for a number of different reasons, as the measure represents the ratio between intra- and inter-individual variation within a population. In godwits, their measures of high repeatability appear to result from the large degree of inter-individual variation exhibited by the population (see Verhoeven et al., 2019 for more details). Thus, individual godwits tend to time their annual cycles differently from one another, yet show significant flexibility in the timing of their movements within their separate migratory windows.

This high degree of individual-level flexibility and population-level variability could mean that godwits are better able to respond to environmental change than other long-distance migrants. For instance, unlike Hudsonian and bar-tailed godwits (Conklin et al., 2010; Senner et al., 2017), black-tailed godwits do not appear to be time constrained during their northward migration. This means that the fitness benefits for an individual of flexibly altering its migration timing, as well as the number of stops it makes during migration, may outweigh those of arriving at a specific site at a specific time. In turn, this may enable them to minimize the initiation of reversible state effects that carry-over the conditions experienced during previous time periods, potentially affecting their survival and fitness (*sensu* Senner et al., 2015c). Accordingly, we have previously shown that many godwits delayed their migrations by arriving more than 20 days later than normal to their breeding sites in response to an early spring snowstorm in northwest Europe, enabling individuals that delayed their migrations to avoid the most inclement storm-related conditions, but also subsequently achieve high reproductive success (Senner et al., 2015a).

Nonetheless, their flexibility does not enable godwits to adequately respond to all types of environmental change. During the past nine decades, for example, godwits have failed to shift the onset of their breeding season earlier (Meltøfte et al., 2018) and have become increasingly mismatched with the local insect phenology on their breeding grounds, leading to reductions in their reproductive success that have compounded the reductions simultaneously incurred by broad-scale agricultural intensification (Kleijn et al., 2010; Schroeder et al., 2012; Kentie et al., 2018). As such, heightened flexibility may enable godwits to respond to some, but not necessarily all, environmental changes.

The Drivers of Migratory Flexibility

More broadly, there is mounting evidence that plasticity can drive advances in migratory timing in response to climate change (Gill et al., 2014), as well as the colonization of novel migratory routes within only a few generations (Eichhorn et al., 2009; Verhoeven et al., 2018). Flexible migratory behaviors are also not unique to godwits, as some ungulates are able to flexibly alter whether or not they migrate in a given year in response to environmental conditions and herd size (Eggeman et al., 2016). Furthermore, the farthest flying migratory birds can fly more than 12,000 km non-stop and maintain annual survival rates among the highest recorded across all bird species, suggesting the ability to flexibly respond to a wide range of conditions in flight (Conklin et al., 2013). These studies thus suggest that under the right circumstances, many migratory populations can exhibit significant levels of plasticity and flexibility. But, what are those circumstances?

We propose that high levels of plasticity and flexibility in migratory behaviors could be related to: (1) high variability in the cues used to time migration (Senner, 2012; Winkler et al., 2014); (2) a relaxation of selection on migratory timing in response to a lack of density dependent selection pressures (Day and Kokko, 2015); or, (3) strong selection on flexibility in migratory behaviors (Nussey et al., 2005). In the case of godwits, we hypothesize that a relaxation of selection on migratory timing resulting from the on-going godwit population decline is the most likely scenario. For instance, if the cues godwits use to migrate were highly variable, we would expect to observe that godwits exhibit low repeatability in addition to their considerable population-level variation in migratory timing (Conklin et al., 2013). Instead, individual godwits, while displaying high flexibility in their migratory behaviors, still appear to time their migrations very differently from each other (Verhoeven et al., 2019). Similarly, if density dependence were acting strongly on godwits, we would expect survival rates to vary with the size of the godwit population (Rakhimberdiev et al., 2015). However, we found little inter-annual variation in survival rates despite the fact that the godwit population size has fluctuated in recent years (Kentie et al., 2016). Furthermore, an individual's migratory timing is not influenced by the number of other godwit pairs breeding nearby and is uncorrelated with their subsequent reproductive success (Senner et al., unpublished data), suggesting that selection on migratory timing has been relaxed. Finally, the creation of new, artificial, wetlands throughout their range has led to an expansion of the amount of habitat available for adult godwits during the non-breeding season and enabled a series of rapid changes to godwit migration patterns (Márquez-Ferrando et al., 2014; Verhoeven et al., 2018).

In combination, density dependent pressures do not currently appear to be influencing godwit survival or migratory timing and this may now mean that adult godwits exist below their carrying capacity throughout the year. Unfortunately, however, we currently lack the data to robustly assess these three possibilities and future studies should therefore endeavor to identify those circumstances that may enable migratory populations to exhibit high levels of flexibility and

plasticity in their migratory behaviors. Developing a deeper understanding of why some populations are more flexible than others will both aid conservation efforts, but also help revise our view of what is normal and possible for migrants (Conklin et al., 2017).

AUTHOR CONTRIBUTIONS

NS, MV, and TP designed the project. All authors carried out the fieldwork. NS and MS carried out the analyses. NS wrote the manuscript. All authors contributed edits.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00096/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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