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Post-breeding migration of Dutch-breeding Black-tailed Godwits: timing, routes, use of stopovers, and nonbreeding destinations

Jos C.E.W. Hooijmeijer[1], Nathan R. Senner[1,*], T. Lee Tibbitts[2], Robert E. Gill, Jr[3], David C. Douglas[4], Leo W. Bruinzeel[5], Eddy Wymenga[5] & Theunis Piersma[1,6]

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Conservation of long-distance migratory shorebirds is complex because these species use habitats spread across continents and hemispheres, making identification of critical habitats and potential bottlenecks in the annual cycle especially difficult. The population of Black-tailed Godwits that breeds in Western Europe, *Limosa limosa limosa*, has declined precipitously over the past few decades. Despite significant efforts to identify the root causes of this decline, much remains unclear. To better understand the migratory timing, use of stopover and nonbreeding sites, and the potential impact of breeding success on these parameters, we attached 15 Argos satellite transmitters and 10 geolocation tracking devices to adult godwits nearing completion of incubation at breeding sites in southwest Friesland, The Netherlands during the spring of 2009. We successfully tracked 16 adult godwits for their entire southward migration and two others for part of it. Three migration patterns and four regions of use were apparent. Most godwits left their breeding sites and proceeded south directly to stopover sites in the Mediterranean – e.g. Spain, Portugal, and Morocco – before flying on to non-breeding sites in West Africa. Other individuals spent the entire nonbreeding season in the Mediterranean. A third pattern included a few individuals that flew nonstop from their Dutch breeding sites to nonbreeding sites in West Africa. Tracking data from this study will be immediately useful for conservation efforts focused on preserving the dispersed network of sites used by godwits during their southward migration.

Key words: shorebirds, waders, long-distance migration, migratory bird conservation, satellite telemetry, geolocation tracking, migratory connectivity

[1]Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands;
[2]U.S. Geological Survey, 4210 University Drive, Anchorage, AK 99508, USA;
[3]3014 Knik Avenue, Anchorage, AK 99501, USA; [4]U.S. Geological Survey, Alaska Science Center, 250 Egan Drive, Juneau, AK 99801, USA;
[5]Altenburg en Wymenga Ecological Consultants, P.O. Box 32, 9269 ZR Feanwâlden, The Netherlands; [6]Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands;
*corresponding author (n.r.senner@rug.nl)

Long-distance migratory shorebirds are a compelling group: the past two decades have brought a wealth of new information regarding the capability of shorebirds to sustain flight over many thousands of kilometers (Gill *et al.* 2009, Battley *et al.* 2012); adjust their phenotypes to meet the strict requirements of their long-distance movements (Buehler *et al.* 2012, Vezina *et al.* 2012); navigate across open oceans and between hemispheres (Gill *et al.* 2009); and precisely time movements between widely spaced stops at which they make use of resources that occur in brief peaks (Baker *et al.* 2004). What makes long-distance migratory shorebirds compelling, however, also makes them complex. Accordingly, the past few decades have also seen an increasing recognition that much remains unknown about the life cycles of these organisms (Buehler & Piersma 2008). For instance, what kinds of resources do these species require to enable such extreme flights (van Gils *et al.* 2005) and what cues do they use to time their precise movements (Senner 2012)? Unfortunately, what makes long-distance migratory shorebird life cycles complex may also make them vulnerable. Across all avian taxa, populations of migratory shorebirds are among those most uniformly and dramatically in decline (International Wader Study Group 2003). For instance, of 85 North American taxa, 40 have populations that are declining (Andres *et al.* 2012).

European-breeding Black-tailed Godwits, *Limosa l. limosa* (hereafter 'godwits'), are in many respects emblematic of long-distance migratory shorebirds. We know they are able to fly great distances, moving between northwestern Europe and the river deltas of West Africa (Meltofte 1996, Beintema & Drost 1986, Zwarts *et al.* 2009). We know they are able to time these movements, with high repeatability, year after year (Lourenço *et al.* 2011). We also know they are declining precipitously – continental populations are half of what they were 30 years ago (Gill *et al.* 2007, Sovon 2013). The decline itself is emblematic in that extensive study has yet to explain its cause(s), especially potential cross-seasonal interactions (Schroeder *et al.* 2012, Kentie *et al.* 2013).

To better understand the flight behaviour and use of stopover sites by godwits, as well as to obtain more precise information on the contemporary use of wintering areas, we used two remote tracking methods – satellite telemetry and geolocation – to track adult Black-tailed Godwits of the *limosa* subspecies captured on their breeding grounds in The Netherlands. Specifically we wanted to understand the southward migration of godwits by asking the following questions. How soon do adult godwits leave the breeding area after successful and failed breeding attempts? When do they depart the breeding areas? Where do they stop during migration? And, where are their final nonbreeding destinations? We discuss our findings in the context of life-history theory and the current conservation situation.

METHODS

We studied the post-breeding migration of godwits using adults from an intensively studied breeding population in an 8480 ha area of southwest Friesland, The Netherlands, between Makkum (53°02.41'N, 05°23.14'E) in the north and Laaksum (52°50.59'N, 05°25.16'E) in the south (Schroeder *et al.* 2008, Groen *et al.* 2012). This area predominantly consists of grasslands (88.5%) and arable land (11%; mostly maize fields), most of which is intensively managed for dairy farming (Groen *et al.* 2012). About 10% of the grasslands exist as nature reserves that are specially managed for godwits and other meadow-bird species.

We captured 15 adults on nests between 10 and 17 May 2009 using walk-in traps set during the final few days of incubation or as eggs were hatching. We implanted satellite transmitters into the coelom of these birds following the protocol of Mulcahy *et al.* (2011) and as presented in detail in Hooijmeijer *et al.* (2013). Briefly, captured birds were transported to a three-person surgical team (veterinarian, anaesthetist, and scribe) that performed the 30 min procedure in a mobile surgery unit. During the initial recovery period following surgery, we ringed birds with a unique combination of colour rings, measured morphological features, and took a blood sample for molecular determination of sex (details in Schroeder *et al.* 2010). The remainder of the recovery period took place in a closed holding box in a quiet area and was closely monitored. All birds were released successfully. The total time elapsed from capture until release averaged 108 min (SD = 11, range = 90–135) with about 20%, 30%, and 50% of the total time spent in transport, surgical implantation, and recovery, respectively.

We implanted godwits with the lightest internal satellite transmitter available (Microwave Telemetry, Inc.; 25–26 g; ~54 × 18 × 17 mm) with a duty cycle of 4-h-on and 31-h-off during migration. Sensors on the transmitters also recorded activity (moving or not moving), battery voltage, and either the internal temperature of the bird ($n = 11$) or the external air temperature ($n = 4$). The sensor data allowed us to determine the fate of a bird in the majority of cases (alive or dead). For this study, we selected only the largest female godwits (>300 g) for surgical implantation. This resulted in an average load factor of 7.8% (SD = 0.24, range = 7.50–8.30%) at time of implantation; this load factor is likely lower during the remainder of the year when godwits maintain a higher mass (Gunnarsson *et al.* 2010). All locations were retrieved via the CLS tracking system (www.argos-system.org) and managed and filtered using the Douglas Argos-filter (DAF) algorithm (Douglas *et al.* 2012). We retained all standard class locations (i.e. LC 3, 2, 1) and used the hybrid filtering method in the DAF to exclude auxiliary locations (i.e. LC 0, A, B, Z) that did not meet our prescribed thresholds for maximum movement rate (120 km/h) and spatial redundancy (10 km). This resulted in a dataset of 2465 locations of which 46% were standard class and 54% were auxiliary class.

On 23 April 2009, we also placed British Antarctic Survey (BAS) Mk-14 (1.4 g) geolocation tracking devices on a cohort of adult godwits (8 females and 2 males) captured in conjunction with the satellite-tagging effort. Geolocation tracking devices (hereafter, 'geolocators') were attached to flags on the upper tibia (Figure 1). More detailed discussion of these attachment methods can be found in Conklin & Battley 2010 and Senner *et al.* in press. The combination of flags, glue, and geolocators totalled ~4 g, a load factor of 1.36% (SD = 0.15, range = 1.20–1.65%). We recaptured geolocator-bearing godwits in subsequent years on nests within the study site. Geolocators record ambient light levels and these, in turn, are used to model daily light-dark cycles and estimate the timing of sunrise and sunset. Using software from BAS (version 2, 2010), we analyzed sunrise/sunset times to create location estimates for individuals twice each day. We applied a basic two-step filter that discarded sunrises not preceded by at least 4 h of darkness and location estimates taken ±10 days surrounding the autumn equinox on 21 September.

For the purposes of our analysis, we combined migration tracks taken from both satellite transmitters and geolocators. For the satellite transmitter data, we defined a stopover as the lack of movement of ≥25 km between two consecutive satellite duty cycles. In geolocators, we identified an individual as having made a stopover if two consecutive location estimates were not separated by more than 1° of latitude or longitude. We identified the location of stopovers by taking the mean latitude and longitude from all location estimates recorded during the period that an individual was stopped. See Senner *et al.* (in press) for a more complete discussion of the analysis of geolocation tracking data in migrating shorebirds.

Figure 1. (A) Godwit "Skarl", a week after her satellite transmitter had been implanted, exhibiting 'alarming behaviour' while guiding her chicks (photo by K. Trimbos). (B) Attachment of geolocators on Black-tailed Godwits tracked during southward migration in 2009. Geolocators were attached to flags on the tibia of adult godwits using glue and zip ties (Photo by R. Kentie).

We monitored nests daily and recorded the reproductive success of each individual prior to its southbound migration and the date on which the fate of its nest was known – either a depredated/abandoned nest or depredated/fledged chicks (see Schroeder *et al.* 2012). Renests may occur if a nest is depredated or abandoned early during the incubation cycle, but is unlikely once an individual has reached >22 days of incubation (Piersma *et al.* unpubl. data) and indeed we recorded no occurrences of renesting among our tracked individuals. We considered an individual to have bred successfully if it was observed with a brood after the brood had reached an age of 15 d (Kentie *et al.* 2013). Departure was defined as the last date an individual was recorded on the study area or the first date it had moved >25 km from its nesting location. Following departure, we recorded the dates and locations of each subsequent stop until arrival at each individual's final nonbreeding destination. Because some tracking devices did not collect data for the entire duration of an individual's southbound migration, we only denoted an individual as having reached its final destination if it arrived at a known wintering location in West Africa or if its tracking device recorded information until at least 1 October. This date was chosen *post-hoc* after analyzing the tracks of individuals for which we have movement data lasting past 1 January (n = 6); none of these individuals switched geographic regions after 20 September. Stopover duration was calculated as the number of days between first and last location at a site and thus are minimum estimates of time spent there; given the reporting periods of the transmitters and geolocators, most dates are within 1–2 d of actual events.

We compared departure and arrival dates among adults within a set of pre-defined candidate models, using a linear regression analysis and all potential combinations of standardized parameters (Gelman 2008). The model with the lowest AIC$_c$ score was chosen as the most well supported model (Burnham and Anderson 2002). Because no single candidate model in any analysis had a model weight (w_i) greater than 0.90 (Grueber *et al.* 2011), we employed model averaging to identify the relative importance (RI) and w_i of each individual parameter. All candidate models included a categorical variable denoting nesting success, where nests that hatched, but did not successfully fledge young (reference), nests that were depredated/abandoned before hatch, and nests that successfully fledged young were each coded separately. All models also included a categorical variable identifying the type of tracking device carried by each individual – satellite transmitter (reference) or geolocator. Models explaining an individual's arrival date in the Mediterranean also included a categorical variable denoting whether or not an individual had previously stopped in Western Europe (we chose no stopover as the reference). Finally, models explaining arrival dates in West Africa included a continuous variable for the

Table 1. Migration histories for satellite-tagged (n = 13) and geolocator-tagged (n = 5) Black-tailed Godwits from their breeding grounds in southwest Friesland, The Netherlands, in 2009. Individuals tracked with satellite transmitters are named; those with geolocation tracking devices are numbered. Individuals are divided into one of four groups (Figure 2): Pattern 1, Pattern 2, Pattern 3, and indeterminate (because of transmitter failure). Nest result abbreviations are: hatched (H), depredated (D), abandoned (A). Country abbreviations are: Belgium (BE), France (FR), Guinea-Bissau (GB), Ivory Coast (IC), Mali (ML), Mauritania (MU), Morocco (MA), The Netherlands (NL), Portugal (PT), Senegal (SE), Spain (ES). If a migration stage is marked as unknown, it is because the tracking device had failed.

Name	Nest fate date	Nest result	Fledged chicks?	Last date breeding Area	Stopover W. Europe?	Med. stopover location	First date in Med.	First date in West Africa	Non-breeding site	Date of last location
Heidenskip	13 May	D	No	20 Jun	No	None		24 Jun	GB	30 Jul 2009
Nijhuzum	15 Jun	H	Yes	27 Jun	NL	None		11 Aug	GB,SE	9 Jun 2010
Warkum	21 May	D	No	20 Jun	No	None		26 Jun	GB,SE	22 Sep 2009
8664	7 Jun	H	Yes	20 Jun	NL	None		3 Jul	MU	20 Jan 2010
8670	6 May	A	No	15 Jun	No	None		17 Jun	SE	19 Nov 2009
Himmelum	14 May	D	No	4 Jun	NL		18 Jun		ES	16 May 2010
Hylpen	7 Jun	H	Yes	24 Jun	FR	ES	7 Jul		PT	28 Dec 2009
Parrega	18 May	H	No	24 Jun	No		30 Jun		PT	3 Jun 2010
Bakhuzen	23 May	H	No	15 Jun	No	ES	21 Jun	28 Jun	SE	27 Jul 2009
Ferwâlde	2 Jun	H	Yes	14 Jun	NL	ES	1 Jul	13 Jul	GB	18 Oct 2009
Gaast	18 May	H	No	22 Jun	No	ES	2 Jul	29 Jul	SE,GB,ML	1 Nov 2009
Molkwar	21 May	H	No	3 Jul	NL,BE	MA	30 Jul	8 Aug	SE	23 Aug 2009
Skarl	27 May	H	Yes	9 Jul	No	ES	12 Jul	24 Jul	MU,SE, ML	22 May 2010
8667	14 May	H	No	4 Jun	NL	ES	13 Jun	23 Jun	SE	16 Mar 2010
8668	14 May	H	No	13 Jun	No	ES	14 Jun	21 Sep	GB	19 Nov 2009
8672	20 Jun	H	Yes	4 Jul	No	MA	7 Jul	18 Jul	ML, IC	13 Dec 2009
Starum	21 May	A	No	14 Jun	NL	ES	25 Jun	Unknown	Unknown	10 Aug 2009
Skuzum	18 May	H	No	5 Jun	FR	ES	22 Jun	Unknown	Unknown	5 Jul 2009

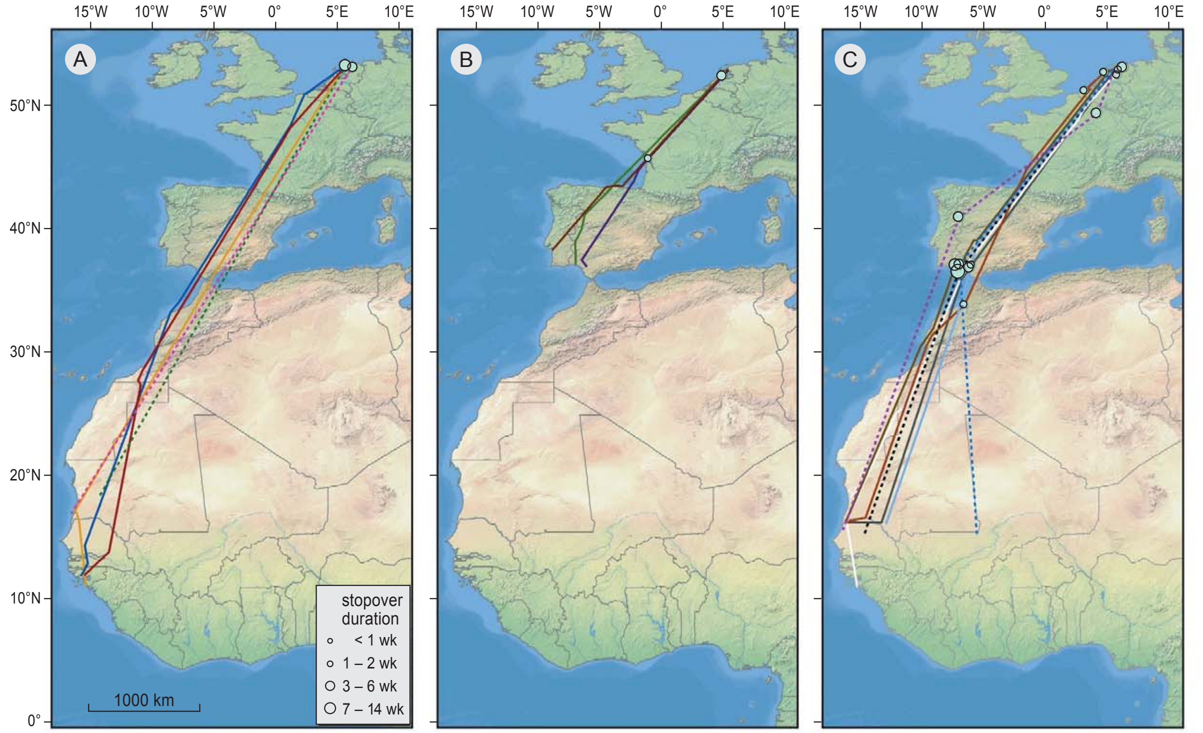

Figure 2. Complete southbound migration tracks of satellite-tagged (solid lines, $n = 11$) and geolocator-tagged (dotted lines, $n = 5$) Black-tailed Godwits in 2009. Birds exhibited three migration patterns: (A) direct flights to West Africa, (B) direct flights to Mediterranean, and (C) journeys to West Africa with a stopover in the Mediterranean. Circles indicate stopover locations and durations.

number of stops made during the preceding portion of the migration. We similarly compared the likelihood that an individual used specific stopover and nonbreeding sites using generalized linear models and a binomial error distribution within an information theoretic framework. Candidate models for logistic regression analyses mirrored those for linear regression analyses; for instance, the decision to stopover in the Mediterranean included the same candidate model set as did the linear regression analysis for arrival date in the Mediterranean. The decision to stopover in Western Europe included the same candidate models as did the analysis of the departure date from the breeding grounds. We carried out all analyses using the “AICcmodavg” package in Program R (version 2.15.2, R Development Core Team 2012). Errors reported are standard errors.

RESULTS

We recovered 5 of 10 (50%) geolocators, all of which provided complete southward migration tracks. Thirteen of 15 (87%) satellite transmitters yielded tracks as far south as the Mediterranean and 11 of 15 (73%) yielded complete southward migration tracks, with an average tracking period of 144 ± 34 d (Table 1). Combined, this yielded 16 complete southward migration tracks for adult godwits (Figure 2).

All godwits took a southwestern route from The Netherlands towards their nonbreeding destinations in Spain, Portugal, or West Africa (Figure 2). We observed three broad patterns of migration: 5 individuals flew directly to West Africa from The Netherlands (Figure 2A), 3 individuals flew directly to the Mediterranean from The Netherlands and spent the entire nonbreeding season there (Figure 2B), and 8 individuals staged in the Mediterranean before continuing on to Africa (Figure 2C). Across all individuals, the average departure date from the breeding grounds was 19 June ± 2 d and average arrival at final nonbreeding sites was 27 June ± 6 d for those spending the nonbreeding season in the Mediterranean and 16 July ± 7 d for those spending the nonbreeding season in Africa (Figure 3, Table 2). On average, individuals made 1.2 ± 0.17 stops before arriving at the final nonbreeding site.

The model with the lowest AIC_c score explaining the departure date of adults from the breeding grounds

Table 2. Dates of migratory movements and stopovers for Black-tailed Godwits grouped by breeding success. All data represent movements of adults captured on nests in southwest Friesland, The Netherlands, using either satellite transmitters or geolocation tracking devices. Arrival dates and percentage of individuals using Africa as a wintering destination are based on 16 birds and not 18 because of transmitter failure. All errors presented are standard errors. Abbreviations: Med. = Mediterranean, NA = Not available.

	Nest fate date	Departure date from breeding grounds	% Stopped W. Europe	Stopover duration W. Europe (d)^1	% Stopped in Med.	Med. arrival date	Stopover duration Med. (d)^{1,2}	% Stopped W. Africa	Arrival date in W. Africa
All (n = 18)	24 May ±3 d	19 Jun ±2 d	50.0	14.9 ±3.4	72.2	29 Jun ±4 d	23.9 ±11.1	81.3	16 Jul ±7 d
Depredated or Abandoned (n = 4)	14 May ±3 d	13 Jun ±3 d	50.0	8.5 ±1.5	50.0	21 Jun ±4 d	NA^3	50.0	19 Jun ±2 d
Hatched, but Not Successful (n = 8)	18 May ±1 d	17 Jun ±4 d	37.5	15.3 ±4.9	87.5	26 Jun ±6 d	31.6 ±17.6	85.7	23 Jul ±14 d
Successful (n = 6)	7 Jun ±4 d	27 Jun ±4 d	66.7	17.8 ±6.8	66.7	6 Jul ±2 d	11.0 ±0	83.3	18 Jul ±6 d

[1] Only includes those individuals that actually stopped over at these sites. [2] Does not include those individuals that spent the entire boreal winter at these sites. [3] Of these two individuals, one is missing data due to transmitter failure, the other spent the entire nonbreeding season in the region.

Table 3. Highest-ranked models (with lowest AIC$_c$) in candidate sets for effects of covariates on departure and stopover decisions of southward migrating Black-tailed Godwits tracked with satellite telemetry and geolocation tracking devices from their breeding grounds in southwest Friesland, The Netherlands, in 2009. Only models with model weight (w_i) > 0.10 are reported. K indicates number of parameters in each model.

Response variable	Candidate models	K	Deviance	AIC$_c$	ΔAIC$_c$	w_i
Departure date from breeding grounds	Null	1	4.3	29.9	0.0	0.42
	Nest success	3	3.0	30.1	0.2	0.39
	Type of tracking device	2	4.2	32.5	2.6	0.11
Decision to stop in Western Europe	Null	1	25.0	27.2	0.0	0.68
	Type of tracking device	2	24.7	29.5	2.3	0.22
Decision to stopover in the Mediterranean	Null	1	21.3	23.5	0.0	0.49
	Type of tracking device	2	20.8	25.6	2.1	0.17
	Stopover in Western Europe	2	21.0	25.8	2.3	0.16
Arrival date in Mediterranean	Null	1	2077.7	108.1	0.0	0.60
	Type of tracking device	2	1896.3	110.3	2.3	0.19
	Stopover in Western Europe	2	2066.8	111.5	3.4	0.11
Decision to migrate to Africa	Null	1	15.4	17.7	0.0	0.27
	Type of tracking device	2	12.9	17.8	0.1	0.26
	Number of stopovers	2	12.9	17.8	0.1	0.26
	Number of stopovers + Type of tracking device	3	13.43	18.7	1.0	0.16
Arrival date in Africa	Null	1	8418.8	126.2	0.0	0.61
	Number of stopovers	2	7757.3	128.7	2.4	0.18
	Type of tracking device	2	8416.8	129.7	3.5	0.11

was the null model (w_i = 0.42; Table 3); however, it was statistically indistinguishable from the model with the second lowest AIC_c, which included a variable for an individual's nest success (ΔAIC_c = 0.2, w_i = 0.30). Among the variables considered, nest success was the most important predictor (RI = 0.46), with nests that fledged young having the largest effect size in the model (β = 0.47, SE = 0.24; Table 4). The dates of final nest fates of adults fledging young were 20 d later than those not fledging young (Table 2) and successful adults departed from the breeding grounds more than 10 days later (27 Jun ± 4 d, n = 6) than did individuals not fledging young (17 Jun ± 3 d, n = 12; Figure 3, Table 2).

After departure, 9 birds (50%) stopped in Western Europe at sites extending from The Netherlands south to France (Figure 2) for an average of 15 ± 3 d (Tables 1 and 2). Sample sizes were too small to statistically analyze stopover duration, but durations ranged from 9 ± 2 d for individuals whose nests were depredated/abandoned to 18 ± 7 d for individuals successfully fledging young (Table 2). The most well supported model explaining whether or not an individual stopped in Western Europe was the null model (w_i = 0.68; Table 3). There was weak support (ΔAIC_c = 2.3, w_i = 0.22) for a competing model that included the effect of tracking device, with individuals carrying geolocators being less likely to stop (β = –0.57, SE = 1.07; Table 4).

Thirteen individuals (72%) stopped over in Spain, Portugal, and Morocco for an average of 24 ± 11 d (Tables 1 and 2). These individuals stopped in the

Table 4. Model-averaged coefficients for factors affecting stopover, departure, and arrival decisions in southward migrating Black-tailed Godwits tracked with satellite telemetry and geolocation tracking devices from their breeding grounds in southwest Friesland, The Netherlands, in 2009. RI = relative importance of variable.

Model	Variable	β	Unconditional SE	Confidence interval	RI
Departure date from breeding grounds	Intercept	2.49	0.12	–0.76, 0.97	NA
	Nest success (Depredated/Abandoned)	–0.19	0.28	–0.73, 0.36	0.46
	Nest success (Fledged)	0.47	0.24	–0.01, 0.95	0.46
	Type of tracking device (Geolocator)	–0.15	0.26	–0.66, 0.36	0.19
Decision to stop in Western Europe	Intercept	0.00	0.47	–1.18, 1.18	NA
	Nest success (Depredated/Abandoned)	0.51	1.24	–1.92, 2.95	0.10
	Nest success (Fledged)	1.22	1.14	–1.01, 3.45	0.10
	Type of tracking device (Geolocator)	–0.57	1.07	–2.68, 1.53	0.24
Decision to stopover in Mediterranean	Intercept	0.96	0.53	–1.60, 0.81	NA
	Nest success (Depredated/Abandoned)	–1.99	1.48	–4.90, 0.91	0.14
	Nest success (Fledged)	–1.31	1.40	–4.06, 1.45	0.14
	Type of tracking device (Geolocator)	–0.79	1.14	–3.02, 1.44	0.24
	Stopover in W. Europe (Stopped)	0.59	1.10	–1.56, 2.74	0.23
Arrival date in Mediterranean	Intercept	59.15	3.65	–15.15, 31.85	NA
	Nest success (Depredated/Abandoned)	–5.71	10.41	–26.11, 14.70	0.07
	Nest success (Fledged)	10.85	8.00	–4.83, 26.53	0.07
	Type of tracking device (Geolocator)	–8.96	8.71	–26.03, 8.11	0.23
	Stopover in W. Europe (Stopped)	1.65	7.72	–13.48, 16.79	0.14
Decision to migrate to Africa	Intercept	1.47	0.64	–1.83, 0.64	NA
	Nest success (Depredated/Abandoned)	–1.53	2.00	–5.44, 2.38	0.05
	Nest success (Fledged)	–0.10	1.63	–3.29, 3.09	0.05
	Type of tracking device (Geolocator)	18.5	4668.26	–9131.12, 9168.12	0.44
	Number of Stops	–2.52	1.87	–6.18, 1.15	0.44
Arrival date in Africa	Intercept	77.31	7.34	–29.31, 66.69	NA
	Nest success (Depredated/Abandoned)	–34.89	21.43	–76.89, 7.11	0.07
	Nest success (Fledged)	–5.65	15.62	–36.26, 24.97	0.07
	Type of tracking device (Geolocator)	0.89	15.79	–30.05, 31.82	0.13
	Number of Stops	15.08	16.20	–16.68, 46.83	0.21

Parque Nacional Doñana, Spain (n = 6); the mouth of the Rio Tinto, Spain (n = 2); near Rabat, Morocco (n = 2); the mouth of the Rio Guadiana, Spain (n = 1); the mouth of the Rio Tejo, Portugal (n = 1); and the rice fields of Extremadura, Spain (n = 1; Figure 2). The lowest AIC_c model explaining whether or not an individual made a stopover in the Mediterranean was the null model (w_i = 0.49; Table 3); again there was weak support (ΔAIC_c = 2.1, w_i = 0.17) for a model that included an effect of tracking device, with individuals carrying geolocators being less likely to stop. Similarly, for arrival date in the Mediterranean the null model received the strongest support (w_i = 0.60) and a model with effect of tracking device (birds with geolocators arriving earlier) had weak support (ΔAIC_c = 2.3, w_i = 0.19; Table 3).

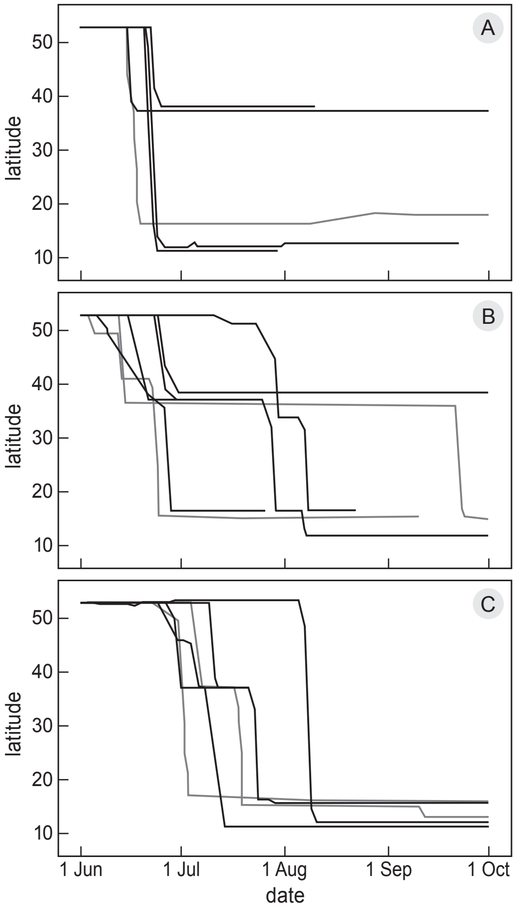

Figure 3. Latitude of satellite-tagged (black lines, n = 13) and geolocator-tagged (grey lines, n = 5) Black-tailed Godwits by date, from 1 June to 1 October 2009. (A) Individuals that did not hatch a nest (n = 5); (B) individuals that hatched a nest, but did not fledge young (n = 7); (C) individuals that fledged young (n = 6).

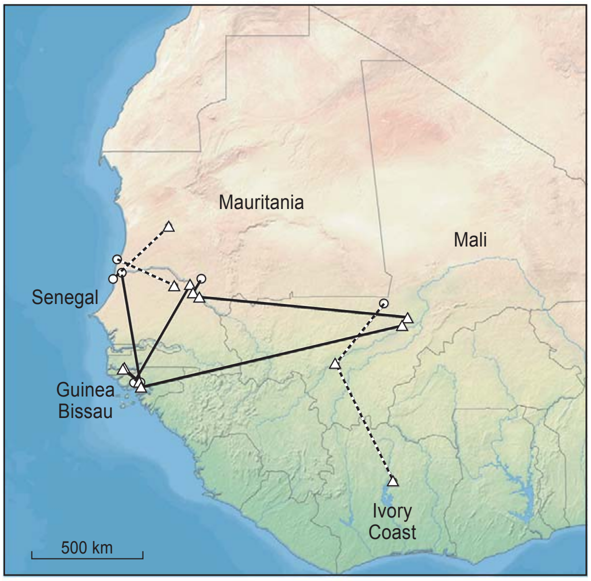

Figure 4. Generalized winter movements in West Africa by satellite-tagged (solid lines, n = 4) and geolocator-tagged (dotted lines, n = 3) Black-tailed Godwits in 2009/10. Circles denote initial landfalls and triangles show subsequent locations. Not all birds that wintered in West Africa were tracked for the entire season. Locations were determined by averaging all positions acquired between movements. In two cases with geolocator tags, averaged locations occurred slightly offshore; to compensate we mapped those locations at the closest landfall to that point.

Thirteen individuals (81%, n = 16) either spent the remainder of the year in West Africa based on continuous tracking data (n = 6) or were tracked to West Africa before their devices failed, and were presumed to spend the winter there based on our knowledge of the behaviour of the species (n = 7). Three of the remaining individuals (19%, n = 16) either spent the entire boreal winter in the Mediterranean (n = 2) or made it to the Mediterranean and remained until after 1 October and were presumed to spend the rest of the winter in the region (n = 1). Tracking devices of two other individuals stopped working during their time in the Mediterranean, but before 1 October, and we were unable to determine their final nonbreeding sites (Table 1).

Three models explaining the decision to migrate to West Africa received nearly equal support, the null model (w_i = 0.27), and models containing the variable for the type of tracking device carried (ΔAIC_c = 0.1, w_i = 0.26) and the number of stopovers made during migration (ΔAIC_c = 0.1, w_i = 0.26). The null model was also the minimum AIC_c model explaining arrival date in West Africa (w_i = 0.61; Table 3). For both sets of models, sample sizes were insufficient to distinguish among potential explanatory factors, as evidenced by large standard errors of parameter estimates (Table 4).

After arriving in West Africa, the majority of individuals made subsequent movements within the region (n = 7, Figure 4). In total, godwits spent time in five countries in West Africa – Senegal (n = 8), Guinea-Bissau (n = 6), Mali (n = 3), Mauritania (n = 2), and the Ivory Coast (n = 1). The three areas supporting the largest numbers of birds were the Rio Geba Delta, Guinea-Bissau (n = 6); the Senegal River Delta, Senegal and Mauritania (n = 6); and the Inner Niger River Delta, Mali (n = 3). Most tracking devices failed (n = 9) during this period, however, and a complete characterization of godwit movements in the region was not possible.

DISCUSSION

We successfully tracked 18 adult Black-tailed Godwits (16 for the complete season) during their southward migration. Our tracking data highlight the links between Dutch breeding sites, stopover sites in Western Europe, stopover and nonbreeding sites in the Mediterranean, and nonbreeding sites in West Africa. Differential use of these sites suggests three patterns of migration. While these migration patterns were not clearly linked with reproductive effort or contingent upon an individual's use of other sites, our data do suggest that the duration of reproductive investment may influence the timing of migration and the amount of time spent at stopover sites. The existence of these different migratory patterns suggests that the conservation of disparate areas is likely critical to the long-term conservation and rehabilitation of this rapidly declining population.

Adult godwits, regardless of breeding duration or success, staged (*sensu* Warnock 2010) inside, or close to, the study area for nearly one month following the completion of the breeding season. Half of all birds subsequently migrated southward to areas in the Mediterranean, where they stayed for an average of three weeks and relied upon coastal marshes such as Parque Nacional de Doñana and the mouth of the Rio Guadiana, Spain, before continuing on to West Africa (Guinea-Bissau, Ivory Coast, Mali, Mauritania, and Senegal). In contrast, the other half of the birds made an initial stop of 1–2 weeks in Western Europe, mostly in agricultural areas near to the coast in The Netherlands and France and then continued onto the Mediterranean where they were more likely to spend the entire nonbreeding season instead of migrating further south to West Africa. Finally, a few individuals migrated rapidly to West Africa and either did not stop in Western Europe or the Mediterranean (or both).

Life-history theory predicts a trade-off between reproductive effort in the current year and future years (Charnov & Krebs 1974). This trade-off is thought to lead adults to balance their reproductive effort to maximize their lifetime fitness. In long-lived species for which the costs of reproduction are especially high, those individuals that successfully fledge young can exhibit reduced fitness during the following year (Inger *et al.* 2010). It thus would not be surprising if successfully breeding godwits migrated later or spent more time at stopover sites in route, so as to balance the costs of a long breeding season (c.f. Alves *et al.* 2013). On the other hand, individuals with a shortened breeding season resulting from nest depredation or clutch abandonment may be able to rapidly transition to migratory readiness and benefit from moving quickly to as-of-yet largely unoccupied nonbreeding sites.

Such flexibility in migration timing during the southbound migration is not rare amongst long-lived, long-distance migratory waterbirds (Conklin & Battley 2012, Senner *et al.* in press). While some other species are able to dissipate such delays during the nonbreeding season, we do not know if that is the case for Continental godwits or whether such discrepancies in timing may carry over to affect future fitness in this population, as has been suggested for Icelandic Black-tailed Godwits (Gunnarsson *et al.* 2006). Our low sample size and single year of tracking data did not permit such a detailed assessment of our results or allow us to disentangle such potentially confounding variables as breeding habitat quality (Schroeder *et al.* 2012) or individual schedules (Lourenço *et al.* 2011).

Additionally, our data set may be biased by our use of only individuals that have successfully incubated their nests to the age of 22–23 d. Early failed breeders may time their migration differently and anecdotal evidence in West Africa suggests that godwits are arriving increasingly early there, leading to disruptions (and changes) in rice farming practices in the region (Zwarts *et al.* 2009). The individuals tracked in this study did not arrive in West Africa earlier than historical arrival dates (Zwarts *et al.* 2009), suggesting that our sample was likely biased and such early arriving individuals missed.

We cannot entirely discount, either, that tracking devices influenced an individual's migratory timing and use of stopover sites. While across all models only one variable was identified as biologically relevant based on its 95% CI – nest success in the model explaining departure date from the breeding grounds – the variable denoting the type of tracking device that an individual carried was the most well supported variable in 4 out of 6 models. In none of these models did the variable have the largest effect size, but parameter estimates consistently suggested that individuals carrying geolocators stopped over less frequently and for a shorter length of time than individuals carrying satellite transmitters.

Regardless of what created them, three distinct migration patterns are apparent among Dutch-breeding godwits and this complicates an already difficult and deteriorating conservation scenario. Agricultural intensification in Dutch meadows has been widely identified as playing a significant role in the reduction of breeding success and overall population declines in Dutch-breeding Black-tailed Godwits (Kentie *et al.* 2013). It also could play a significant, but as yet unknown, role in the ability of adults to obtain sufficient fuel resources before their southward migration given their apparent use of agricultural habitats during this period (Piersma *et al.* unpubl. data). The extent of available habitat at major spring stopover sites in France has declined in recent years – one of the two sites used by individuals in this study (Baie de l'Aiguillon, France) has lost more than 50% of its wet grasslands to the cultivation of corn – and when combined with continued late-summer hunting pressure may mean that these sites do not provide sufficient resources for adult godwits during this period (Kuijper *et al.* 2006). Coastal sites in Spain, Portugal, and Morocco are facing similar fates as more and more freshwater is diverted to agriculture, reducing both overall habitat quantity and quality, as the freshwater wetlands required by *L. l. limosa* are turned brackish (Kuijper *et al.* 2006). Inland sites, such as the rice fields of Extremadura, Spain, and the estuarine ricefields of the Sado and Tejo rivers, Portugal, are currently more stable and artificially maintained (Lourenço & Piersma 2009). However pressure from illegal hunting, potential changes in agricultural practices, and the lack of alternatives makes reliance on these sites unsatisfactory in the long-term (Lourenço & Piersma 2009, N.R. Senner pers. obs.). Finally, the rice fields and wetlands in West Africa that provide wintering habitat for the majority of Dutch-breeding godwits are changing. Coastal rice fields and natural wetlands in the Senegal River Delta – which were used by 10 of the 13 godwits that spent the winter in West Africa in this study – have been reduced in size by more than half since the 1980s (Wymenga & Zwarts 2010). Wetlands in the Inner Niger Delta – the nonbreeding site of the three other individuals from this study wintering in West Africa – are still present, but conversion for agricultural uses (irrigation) is planned (Wymenga & Zwarts 2010).

When combined, these anthropogenic changes may be creating feedback loops that interact to influence migration patterns in novel and unforeseen ways (as in Ruffs *Philomachus pugnax*, Rakhimberdiev *et al.* 2011, Verkuil *et al.* 2012). It is possible that the increasingly short windows of time during which adequate resources are available at the sites frequented by godwits determine their migration patterns as much as does their breeding success or other environmental variables such as wind (Shamoun-Baranes *et al.* 2010, Wymenga & Zwarts 2010). At the very least, the interplay between migration, reproductive success, and habitat quality and quantity as mediated by humans creates a complex story that demands more attention in the face of the rapid decline of the Dutch-breeding population. Future efforts should focus on tracking adult godwits across seasons and years in order to determine the possible linkages between these various factors and events. Further work elucidating the migratory habits of juvenile godwits is also critical, as previous work has shown that poor recruitment into the breeding population is, in large part, driving the population decline and little is known about their habitat use once they leave their natal breeding sites (Gill *et al.* 2007). Tracking data in this paper demonstrates that Dutch-breeding godwits use a network of sites and habitats in Western Europe, the Mediterranean, and West Africa. This information will be useful for conservation efforts aimed at improving reproductive success and stabilizing important habitats of this near-threatened population.

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SAMENVATTING

De populatie van de in West-Europa broedende Grutto *Limosa limosa limosa* is de afgelopen decennia ingestort. De oorzaak van de afname is ondanks alle onderzoek hieraan nog steeds niet helemaal duidelijk. Om meer te weten te komen over de trekroutes en overwinteringsplekken werden 15 Grutto's uitgerust met een Argos satellietzender en 10 met een 'geolocator'. De vogels werden aan het einde van het broedseizoen van 2009 gevangen in het zuidwesten van Friesland. We slaagden erin de trekroute naar het zuiden van 18 vogels vast te leggen. In 16 gevallen betrof het de volledige route tot in het overwinteringsgebied. De meeste Grutto's vlogen direct van de broedplaatsen naar pleisterplaatsen in het Middellandse Zeegebied (Spanje, Portugal, Marokko), waarna ze doorvlogen naar de overwinteringsgebieden in West-Afrika. Sommige vogels bleven in het Middellandse Zeegebied overwinteren. Daarnaast waren er enkele individuen die non-stop van de broedplek in Friesland naar het overwinteringsgebied in Afrika vlogen. De resultaten van dit onderzoek kunnen gebruikt worden bij de bescherming van pleisterplaatsen die de Grutto's aandoen tijdens hun reis naar het zuiden.

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