Revisiting the proposed leap-frog migration of Bar-tailed Godwits along the East-Atlantic Flyway

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Two populations of Bar-tailed Godwits *Limosa lapponica* occur along the East-Atlantic Flyway. The European population (*L. l. lapponica*) is supposed to breed in northern Scandinavia and has been suggested to only winter in Europe. The Afro–Siberian population (*taymyrensis*) is supposed to breed in Northern Siberia and is thought to winter exclusively in West Africa. An analysis of 946 metal ring recoveries accumulated by EURING (with data going back to 1935), in combination with an analysis of over 13,000 resightings of almost 4000 individuals marked with colour-rings in 2001–2010, enabled us to examine whether there is evidence for overlap of the populations in summer and winter. Nearly all marked individuals behaved according to the previously suggested leap-frog migration pattern. On the basis of the present sample, only 0.8% of (colour) ringed birds that were recovered and/or resighted on the wintering grounds in Europe or West-Africa made a change between the two supposed wintering areas. This is far less than was previously estimated on the basis of biometric data. The distinct migratory behaviour of the two populations makes them near-completely separated in summer and winter. The Bar-tailed Godwit along the East-Atlantic Flyway thus exhibits a clear leap-frog migration, in which the Siberian breeders winter south of the European breeders.

Key words: Banc d'Arguin, biometry, bird ringing, colour-marking, dispersal, migration, morphology, subspecies, Wadden Sea, *Limosa lapponica*

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Shorebirds provide excellent opportunities to study migration strategies. They occur in open landscapes and often rely on relatively few wetlands (Piersma 2007) where they can be captured, marked and resighted with relative ease (Piersma & Spaans 2004, Spaans *et al.* 2011). Not surprisingly then, shorebirds have their 'connectivity' well resolved (van de Kam *et al.* 2004, Delany *et al.* 2009).

In many migrating birds, populations breeding in northerly areas migrate to wintering areas south of populations from more southerly breeding ranges (Newton 2008). This so-called leap-frog migration occurs in several species of shorebirds (Salomonson 1955, Alerstam & Högstedt 1980, Alerstam 1990) and is thought to occur in Bar-tailed Godwits *Limosa lapponica* wintering in Europe and West-Africa (Drent & Piersma 1990, Scheiffarth 2001). The European population breeds and winters in Europe (breeding from Scandinavia to the Kanin peninsula and resides around the North Sea and Irish Sea in winter), and the Afro–Siberian population breeds in north-central Siberia (from Yamal peninsula in the west to the delta of Anabar river in the east) and winters along the west coast of Africa, with large concentrations on the Banc d'Arguin, Mauritania, and in Guinea-Bissau (Scott & Scheiffarth 2009).

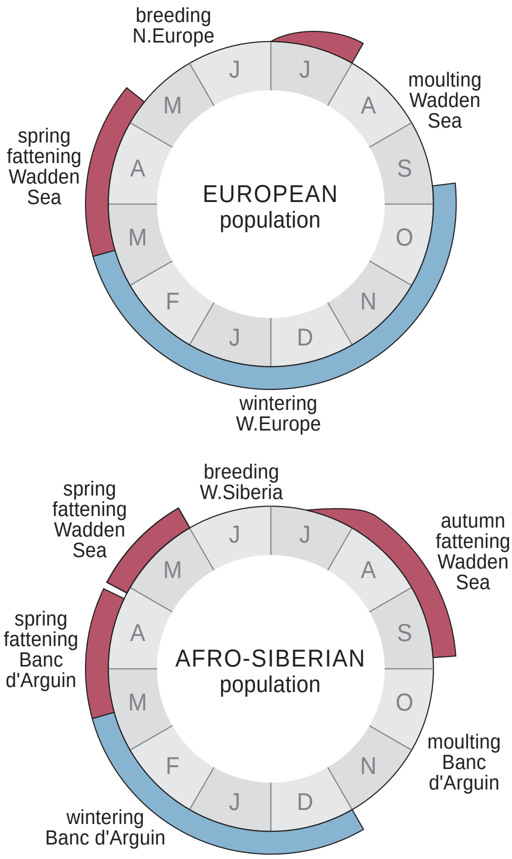

Figure 1. The seasonal itinerary of the two populations of Bar-tailed Godwits (European and Afro–Siberian) indicating the sequence of phases experienced by the two populations in the course of the year (from Drent & Piersma 1990).

The characterization of the leap-frog migration pattern (Drent & Piersma 1990) was based on Prokosch (1988), who found morphological differences in time and space suggestive of subspecific differentiation. Engelmoer & Roselaar (1998) proposed that the two Bar-tailed Godwit populations should be recognized as distinct subspecies. They named the birds with smaller body dimensions breeding in north-central Siberia *taymyrensis* and proposed to retain the larger-bodied European population as the nominate subspecies *lapponica*. When reviewing Engelmoer & Roselaar (1998), Tomkovich & Serra (1999) argued about some of their subspecies assignments, but not about the distinction between *lapponica* and *taymyrensis*. In later studies the two populations appeared to be not only morphologically, but also ecologically distinct (Scheiffarth *et al.* 2002, Duijns *et al.* 2009).

Based on morphological measurements of birds captured in the Wadden Sea, and discrimination functions based on museum specimens from the breeding grounds, Engelmoer (2008) estimated that about 20% of the Bar-tailed Godwits wintering in the Wadden Sea belong to the Afro–Siberian population. This implies that of the 120,000 birds wintering in the Wadden Sea (the European population; Scott & Scheiffarth 2009), no fewer than 24,000 individuals represent Afro–Siberian birds that were supposed to all winter in West-Africa. If so, this would mean that the leap-frog migration pattern is partial at best.

In this paper we aim to reconsider all available evidence using historical ringing, recovery and colour-ring resighting information of Bar-tailed Godwits along the East-Atlantic Flyway. Based on seasonal itineraries (Figure 1), we derived three criteria to assign individuals to either population at capture and ringing: (1) individuals (re)captured and/or resighted between November and March in Europe belong to the European breeding population, (2) individuals captured and/or resighted in West-Africa belong to the Siberian breeding population, and (3) individuals captured in the Wadden Sea during autumn in active primary moult are also expected to belong to the European population, as wing-moulting individuals tend to winter in Europe (Atkinson 1996). We use then the recoveries and resighting data to establish whether the suggested leap-frog migration pattern of the two subspecies holds up.

METHODS

Bar-tailed Godwits were captured at various sites in the Dutch and German Wadden Sea and on the Banc d'Arguin, Mauritania, West-Africa. Birds were processed immediately after capture, length of bill (exposed culmen, from tip of bill to base of feathers), wing (flattened and straightened; Prater *et al.* 1977) and tarsus being measured on most individuals using standard methods. The primary moult score was given according to Newton (1966); old: 0; growing: 1–4; new: 5. A bird that had completed moult of all 10 primaries had a primary moult score (PMS) of 50.

Each Bar-tailed Godwit was marked individually with four colour-rings (blue, red, white and yellow), combined with one yellow or red flag, and a metal ring. There were two colour-rings on the left and two on the right tarsus, and the metal ring was placed on one of the tibiae, but was not part of the code. The flag was the marker of the scheme and was placed on the tarsus or on one of eight different positions. In this way 2048 combinations were possible per flag colour. The colour-

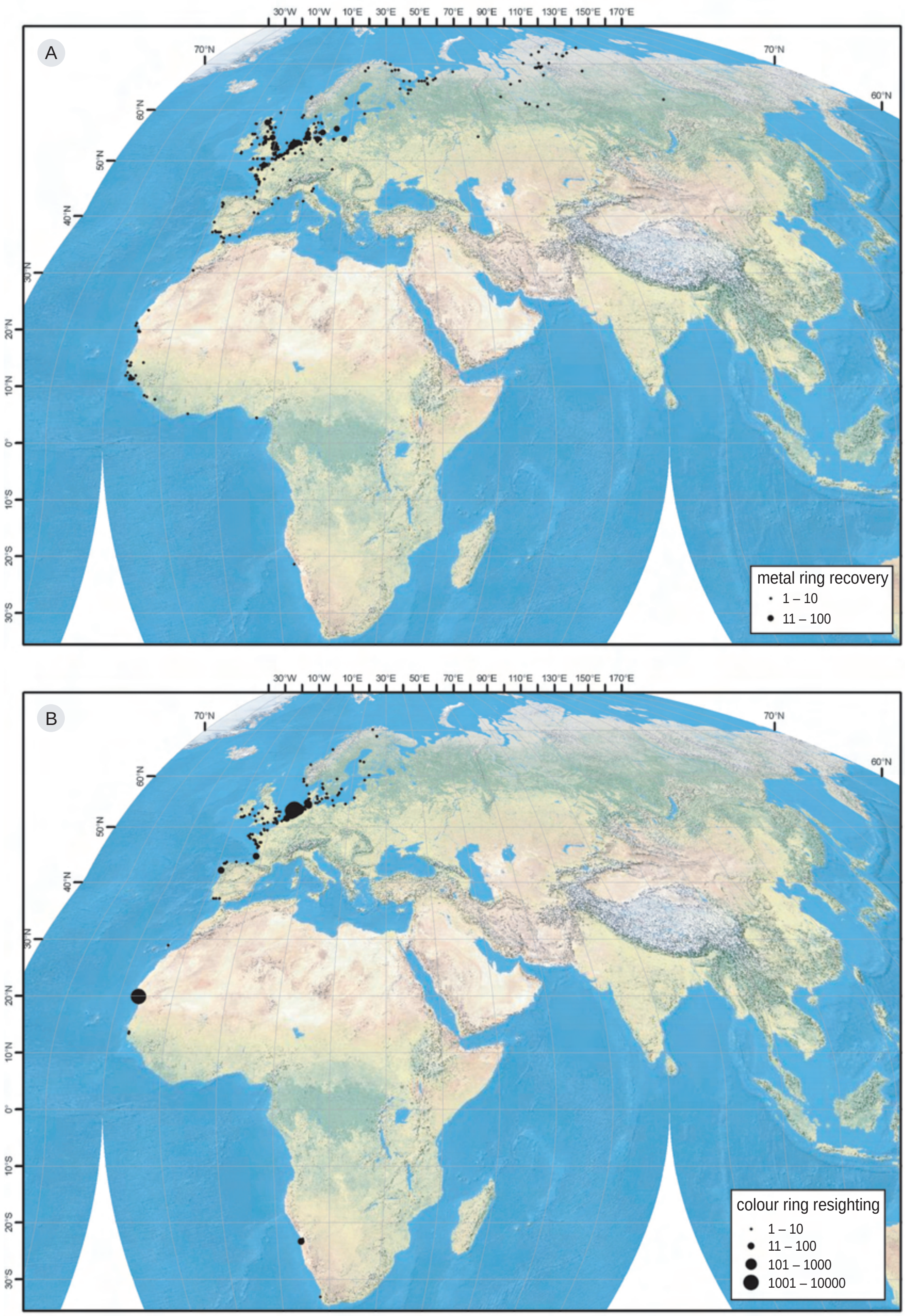

Figure 2. Recoveries and resightings of Bar-tailed Godwits along the East-Atlantic Flyway. (A) Metal ring recoveries (n = 946) from 1935–2010; (B) colour-ring resightings (n = 13,326) from 2001–2010.

ring combination could easily be observed in the field by telescope. Unfortunately, mistakes were sometimes made as ring colours deteriorated through time (Burton 2000, Ward 2000). One should keep this in mind in the case of exceptional life-histories based on single ring-reading occasions. From spring 2001 to the end of 2010 a total of 3996 individuals were colour-ringed and 13,326 individual resightings from 2373 individual birds (59% of birds marked) were received from 311 different locations. The majority of the colour-ringed birds were caught in the Wadden Sea (91%), followed by Mauritania (7%). The colour-ring resightings show the same geographic bias, as most of the birds were resighted in the Wadden Sea (87%) followed by West-Africa (11%). A similar pattern is observed for the metal rings. Most birds were captured in Western Europe (85%; i.e. United Kingdom, The Netherlands, and Germany), and recovered in Western Europe (85%; Appendix 1).

From the EURING database 946 recoveries of metal rings were obtained, with the earliest recovery dating from 1935 and the latest from 2010. A preliminary analysis showed no spatial or temporal difference between earlier (<1980) and later records, so all recoveries were used. In total 790 catching or recovery locations were identified. From only 35% of the individuals, relevant biometric (age and sex) information was available. To avoid reducing the sample size, all individuals were therefore included in the analysis.

Capture and resighting data were used to create a map with a resolution of 0.25 degrees (Figure 2). Resighting colour-ringed individuals is highly dependent on volunteers, and therefore the data were skewed towards locations where volunteers were active. To

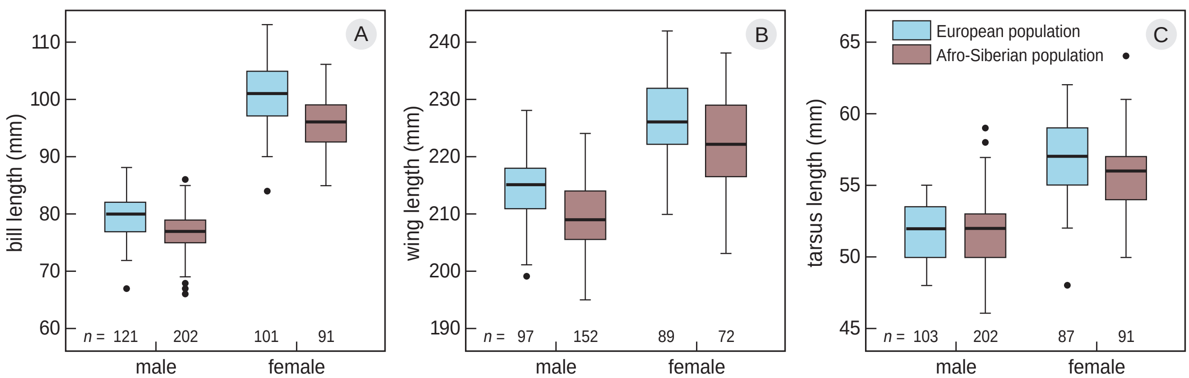

Figure 3. Morphological characteristics of Bar-tailed Godwits, by sex and population. The box-and-whisker plots show median (line in box), interquartile range (box), range (bars), and outliers (small dots) of: (A) bill length (B) wing length and (C) tarsus length.

Table 1. Assignment criteria of ringed and colour-marked Bar-tailed Godwits to the two populations and the verifications testing the leap-frog migration hypothesis based on resighting and recovery locations: the eight exceptions are listed in Appendix 2. The *n* values refer to the total number of individuals. Individuals may feature in different categories (e.g. an individual was caught and resighted), and therefore the totals differ from the sum of the separate categories.

Locality	European population	*n*	*n* total	Afro–Siberian population	*n*	*n* total
Assignment criteria						
Wintering area	Captured in Europe in Nov–March	55	224	Captured in Africa	200	385
Wintering area	Resighted in Europe in Nov–March	94		Resighted in Africa	309	
Autumn staging area	Active primary moult when caught in Wadden Sea in July–Sept	132		Non-moulting when caught in Wadden Sea in July–Sept	250	
Verifications in different seasons and locations						
Breeding area	Recovered in Northern Scandinavia and White Sea area	29		Recovered in North Central Siberia	23	
Wintering area	Subsequent field observations of moulting individuals in Wadden Sea in Nov–March	83		Subsequent field observations of non-moulting individuals in Africa	19	

reduce the effect of identification errors, only individuals that were resighted twice in their wintering areas (i.e. West-Africa or Western Europe) were included in the analysis (n = 1399). Most Bar-tailed Godwits were caught and/or resighted during spring migration in the Dutch Wadden Sea in May when both populations occur in the Wadden Sea (Drent & Piersma 1990, Duijns *et al.* 2009), and therefore 790 (56%) of the colour-ringed birds could not be assigned to any population. Furthermore, only adult birds were included in the analysis as juvenile Bar-tailed Godwits may migrate differently to adults (B. Spaans *et al.* unpubl. data) and they are known to be scarce at Western European staging sites in spring (Prokosch 1988). This age-differential migration is not uncommon in migrating birds (e.g. Cristol *et al.* 1999, Lok *et al.* 2011).

To test for differences in morphological variables between the two populations, we performed an ANOVA with population and sex as fixed factors and date of catch as a covariate. Basic assumptions of parametric tests were examined by testing for normality with a Kolmogorov–Smirnov test, and the application of the Levene's test for equality of variances.

RESULTS

Despite a large overlap in morphological variables (Figure 3), bill and wing length (but not tarsus) confirmed that birds of the European population are larger-bodied than birds assigned to the Afro–Siberian population (ANOVA, $F_{1,381} = 39.21$, $P < 0.001$, $F_{1,278} = 15.8$, $P < 0.001$ and $F_{1,372} = 0.5$, $P = 0.481$, respectively).

Of the assigned individuals, 224 (16%) colour-ringed birds wintered in Western Europe, or were in active primary moult in autumn; 385 (28%) wintered in West-Africa. Of the 946 metal ring recoveries, 291 (31%) individuals wintered in Europe and 68 (7%) individuals wintered in West-Africa. Most of the marked individuals that were recovered or resighted behaved as predicted on the basis of the previously inferred leap-frog migration pattern (Table 1). As predicted, the two colour-ringed individuals that were observed in the breeding range in Northern Scandinavia were resighted in Europe in winter, and the 27 metal-ringed individuals assigned to the European population were recovered in Northern Scandinavia (Figure 4A). Of the metal-ringed birds, 23 African-winterers were recovered in the Northern Siberian breeding range (Figure 4B), thus confirming the links between wintering areas and breeding grounds. Of the 992 assigned birds (i.e. European or Afro–Siberian), only eight (0.8%) individuals did not follow the predictions. This included four colour-ringed birds and four metal-ringed birds (Appendix 2).

DISCUSSION

Due to the low density of breeding birds and the very low ring-reading efforts on the breeding grounds, we received only two resightings in the breeding areas. Yet, the recoveries from the Scandinavian and north-central Siberian areas support a leap-frog migration system, with little evidence for overlap of the breeding populations in winter. The leap-frog migration hypothesis is further supported by the observation that of 1009 birds caught in May and resighted more than once, only 3.8% were resighted in Europe during winter (Spaans *et al.*, unpubl. data). Similarly, Wilson *et al.* (2007) found "low levels" of exchange for two other populations of Bar-tailed Godwit (*menzbieri* and *baueri*) with a comparable migration system. The eight exceptions (Appendix 2) were in fact all quite peculiar in terms of age (at the time of capture less than 2 years old), recovery dates (i.e. mid-April and mid-May when such individuals should still be in Europe), or ring colour (white and yellow may have been confused). Even if correct, these individuals switching wintering areas represent a small proportion of the population, and this suggests that the estimate by Engelmoer (2008) of 20% of the wintering population in the Wadden Sea as north-central Siberian-breeding (Afro–Siberian), is an overestimate. Our results thus suggest almost complete separation of the wintering and breeding grounds of the two populations of Bar-tailed Godwits along the East-Atlantic Flyway, and confirm that the two populations represent a clear example of a leap-frog migration system as Drent & Piersma (1990) suggested it to be.

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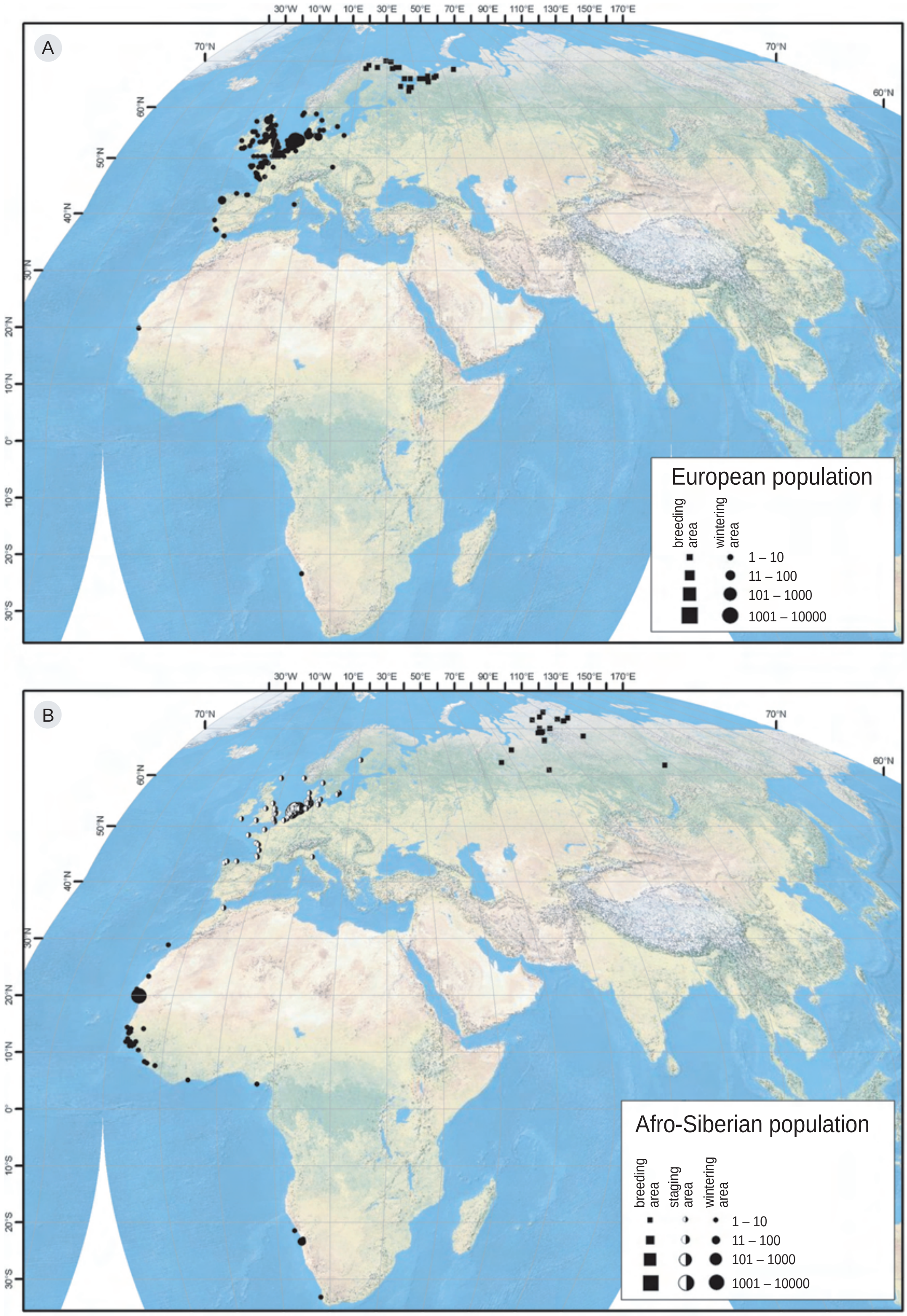

Figure 4. Wintering, staging, and breeding sites for Bar-tailed Godwits. (A) Recoveries of the European population with the main wintering sites in the Dutch and German Wadden Sea, the NW of Spain and the SE of the United Kingdom. (B) Recoveries of the Afro–Siberian population, with 'hot spots' in the Dutch and German Wadden Sea and the Banc d'Arguin in Mauritania.

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SAMENVATTING

Er komen langs de Oost-Atlantische trekroute twee verschillende populaties van de Rosse Grutto *Limosa lapponica* voor. Een 'Europese' populatie (ondersoort *lapponica*), die in het noorden van Scandinavië broedt en naar wordt aangenomen uitsluitend in Europa overwintert. En een 'Afro–Siberische' populatie (ondersoort *taymyrensis*), die in Noord-Siberië broedt en verondersteld wordt de winter in West-Afrika door te brengen. Als we dit tot op heden theoretische onderscheid kunnen onderbouwen, dan hebben we een mooi voorbeeld van een 'leap-frog' migratiesysteem, waarbij de Afro–Siberische populatie 'over' de Europese populatie heen trekt. Wij analyseerden 946 terugmeldingen van metalen ringen opgebouwd door EURING (met gegevens die teruggaan tot 1935) en meer dan 13.000 waarnemingen van het NIOZ kleurringprogramma uit de afgelopen jaren (2001–2010). Deze analyse stelt ons in staat om te onderzoeken of de Rosse Grutto inderdaad een 'leap-frog' migratie laat zien of dat er tussen beide overwinteringsgebieden uitwisseling plaatsvindt. Bijna alle gemerkte individuen gedroegen zich volgens de gangbare theorie. Slechts acht vogels (0,8%) van de (kleur)ringmeldingen bleken beide overwinteringsgebieden (Europa en Afrika) gebruikt te hebben. Zij vertegenwoordigen dus opmerkelijke uitzonderingen. We kunnen zelfs niet met 100% zekerheid zeggen dat deze vogels inderdaad in beide overwinteringsgebieden geweest zijn, want mogelijk is er sprake geweest van verkleuring van de kleurringen. De mate van overlap in overwinteringsgebied tussen beide broedpopulaties is veel kleiner dan aanvankelijk op grond van de biometrie van de vogels werd gedacht. De verschillen in morfologie tussen de twee populaties zijn echter te klein om individuele vogels in het overwinteringsgebied aan een van de twee broedpopulaties toe te rekenen. De verschillen in trekstrategie en overwinteringsgebied tussen de Europese en Siberische broedpopulatie laten zien dat de populaties ook buiten de broedtijd bijna volledig gescheiden zijn en dat er inderdaad sprake is van een 'leap-frog' migratie.

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Appendix 1. Total number of ringed Bar-tailed Godwits resighted and recovered per country.

Country	Colour rings				Metal rings			
	Caught		Resightings		Caught		Recovered	
	n	%	*n*	%	*n*	%	*n*	%
Russia					1	0.11	57	6.03
Norway			6	0.05	8	0.85	3	0.32
Finland			6	0.05	1	0.11		
Sweden			18	0.14	22	2.33	9	0.95
Estonia			1	0.01			1	0.11
Latvia			1	0.01				
Denmark			17	0.13	22	2.33	43	4.55
United Kingdom			44	0.33	334	35.31	242	25.58
Ireland			19	0.14	5	0.53	1	0.11
Poland			3	0.02	24	2.54	18	1.90
Germany	48	1.20	96	0.72	99	10.47	73	7.72
The Netherlands	3653	91.42	11577	86.88	374	39.53	356	37.63
Belgium			2	0.02	2	0.21	1	0.11
France			51	0.38	17	1.80	91	9.62
Switzerland					1	0.11		
Czech Republic					2	0.21		
Italy					9	0.95	6	0.63
Spain			42	0.32	7	0.74	14	1.48
Portugal			3	0.02	5	0.53	2	0.21
Morocco							3	0.32
Mauritania	295	7.38	1420	10.66	4	0.42	2	0.21
Senegal			3	0.02	1	0.11		
Gambia			1	0.01				
Guinea Bissau					8	0.85	18	1.90
Sierra Leone							3	0.32
Ghana								
Ivory Coast							1	0.11
Nigeria							1	0.11
Namibia			14	0.11			1	0.11
South Africa			2	0.02				
Total	3996	100	13326	100	946	100	946	100

Appendix 2. (Colour-) ringed individual Bar-tailed Godwits that were unfaithful to their wintering area, or that were reported in Europe in winter where they were expected to be in West-Africa at the time of resighting. If a bird was resighted twice on the same day, this means that the individual was observed by at least two independent observers.

Ind. Code	AC[a]	Sex	PMS	Age	Catching location	Date	Latitude	Longitude	Resighting location	Date	Latitude	Longitude	Caveat
DN44314	CD	F	-	juvenile	UK	5-11-1983	56°10'N	3°03'W	Russia	15-4-1988	55°59'N	92°54'E	Age at catching and questionable recovery date
DS86344	CD	F	-	juvenile	UK	3-1-1977	55°15'N	1°30'W	Russia	20-5-1979	62°13'N	70°38'E	Age at catching and questionable recovery date
DR99482	CD	M	-	full grown	UK	12-3-1983	53°31'N	4°09'E	Guinea-Bissau	6-8-1993	11°20'N	16°00'W	
1098920	CD	-	-	>2nd year	The Netherlands	17-3-1972	53°16'N	5°00'E	Russia	13-5-1972	62°13'N	70°38'E	Age at catching and questionable recovery date
Y2RYBW	CD	M	0	adult	The Netherlands	31-3-2003	53°15'N	5°16'E	The Netherlands	5-5-2003	53°00'N	04°46'E	White and yellow in the colour-ring combination
									The Netherlands	23-3-2004	53°15'N	05°15'E	
									Mauritania	12-12-2004	19°54'N	16°19'W	
									The Netherlands	30-1-2006	53°09'N	04°54'E	
									Mauritania	18-12-2009	19°54'N	16°19'W	
									Mauritania	18-12-2009	19°54'N	16°19'W	
Y5WYRR	PMS	F	29	≥ 2nd year	The Netherlands	30-9-2003	53°28'N	6°15'E	Mauritania	20-12-2006	19°54'N	16°19'W	Age at catching and white and yellow in the colour-ring combination
									Mauritania	12-12-2009	19°52'N	16°17'W	
Y5WYWY	PMS	F	36	≥ 2nd year	The Netherlands	30-9-2003	53°29'N	6°15'E	Mauritania	25-12-2006	19°53'N	16°19'W	Age at catching and white and yellow in the colour-ring combination
									Mauritania	25-12-2006	19°53'N	16°19'W	
Y3YYRR	PMS	M	49	>2nd year	The Netherlands	9-9-2002	53°29'N	6°15'E	The Netherlands	28-3-2006	53°09'N	04°54'E	Age at catching and white and yellow in the colour-ring combination
									The Netherlands	7-5-2006	53°22'N	05°20'E	
									The Netherlands	8-5-2006	53°22'N	05°20'E	
									The Netherlands	9-5-2006	53°22'N	05°20'E	
									The Netherlands	6-1-2008	53°08'N	04°55'E	
									Namibia	23-1-2009	23°22'S	14°30'E	
									Namibia	24-1-2009	23°22'S	14°30'E	
									Namibia	24-1-2009	23°22'S	14°30'E	

[a] Assigment criterion: CD = Catching location and date, PMS = Primary moult score.