

Densities of individually marked migrants away from the marking site to estimate population sizes: a test with three wader populations

BERNARD SPAANS^{1*}, LAURENS VAN KOOTEN¹, JENNY CREMER¹, JUTTA LEYRER¹ and THEUNIS PIERSMA^{1,2}

¹Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands and ²Animal Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

Capsule Population estimates based on the mark–resighting method can be a useful alternative to population-wide counts.

Aims To investigate whether the mark–resighting method can be used as an alternative to counts to estimate the size of wader populations.

Methods Individual colour-marking and subsequent resightings allowed accurate estimates of annual survival for three populations of waders, on which basis we could estimate the actual number of marked birds alive. Densities of marked birds were determined on sites away (2000–4300 km) from the ringing locations expecting marked birds to be randomly distributed among non-marked conspecifics. Population sizes are estimated by combining these densities with the number of marked birds alive.

Results We found indications that the distribution of marked birds was indeed random in the locations away from the site of marking. The estimated population size of Red Knot *Calidris canutus canutus* was in accordance with the most recent estimates based on counts. Our estimate of the *Calidris c. islandica* population was somewhat lower, and that of the Bar-tailed Godwit *Limosa lapponica taymyrensis* population was considerably lower than the latest estimates based on counts.

Conclusion Population estimates based on the mark–resighting method can be a useful alternative for, or addition to, population-wide counts, as long as the assumption of random distribution of marked birds at the reading sites is taken into account. We conclude that the Afro-Siberian Bar-tailed Godwit population has recently decreased in size or has been substantially overestimated during the counts.

During the non-breeding seasons, coastal waders (or shorebirds) have the helpful habit of congregating at a relatively small number of sites where they can be counted. The summations of such counts are then taken to represent estimates of the population size of that subspecies or species. On this basis, Wetlands International and the International Wader Study Group have issued a series of summary reports on the status of many of the world's waterbird populations (Delany *et al.* 2009, Wetlands International 2002, 2006, Stroud *et al.* 2004). However, such estimates of population size still suffer from systematic counting errors (Rappoldt *et al.* 1985, Rogers *et al.* 2006), as well as gaps in coverage that may (or may not) partly be

taken care of by statistical ‘imputing’ techniques (Underhill & Prys-Jones 1994, Atkinson *et al.* 2006).

An alternative to the determination of total population sizes by large-scale counting efforts would be the marking of samples of birds, and the subsequent measurement of the densities of marked birds, i.e. the mark–resighting method (Krebs 1989, Ganter & Madsen 2001, Gunnarsson *et al.* 2005, Lourenço *et al.* 2010). If the number of surviving marked birds can be estimated, total population size could actually be approximated from that number multiplied by the measured dilution (ratio unmarked to marked), including confidence intervals around the estimate (Krebs 1989, White 1996). This is all valid if one important assumption is met: the marked birds randomly disperse within the population. This is unlikely to be the case in the

*Correspondence author. Email: Bernard.spaans@nioz.nl

location where birds are marked (Warnock & Takekawa 1996, Burton & Evans 1997, Leyrer *et al.* 2006). However, migrant waterbirds move between locations, and if the population structure is not maintained during such moves (i.e. that birds are distributed randomly among conspecifics away from the marking site), then this assumption could be met.

Here we present population estimates based on the mark-resighting technique for three wader populations in the East Atlantic Flyway: (1) the Afro-Siberian Red Knot *Calidris canutus canutus*, (2) the Nearctic Red Knot *Calidris c. islandica* and (3) the Afro-Siberian Bar-tailed Godwit *Limosa lapponica taymyrensis* (Engelmoer & Roselaar 1998). *Canutus* Knots were individually marked in their wintering area on the Banc d'Arguin in Mauritania, *islandica* Knots during autumn, winter and spring in the Dutch Wadden Sea and individuals of the *taymyrensis* Bar-tailed Godwit population during spring stopover in The Netherlands and in Germany. Over the course of 6–9 years, sufficient numbers of individuals of each population were resighted to get an accurate estimate of annual survival. These survival rates allow us to estimate the total number of colour-marked birds present in the population at any moment that we determined ring densities. To avoid effects of site-faithfulness resulting in a relatively high ring-density in the ringing location (Leyrer *et al.* 2006, Spaans *et al.* 2009), densities of marked individuals were determined in locations far away (2000–4300 km) from the ringing sites. To some extent we were able to verify the assumption of a random distribution of marked individuals among conspecifics.

METHODS

Colour-ringing the populations

Calidris c. canutus

The Afro-Siberian Knots were all caught and marked near the village of Iwik on the Banc d'Arguin in Mauritania (19°53'N, 16°18'W) (Fig. 1, location 2) (Leyrer *et al.* 2006). They are, by definition, of the *canutus* subspecies, because *islandica* does not occur there (Piersma *et al.* 1992).

Calidris c. islandica

Islandica Knots were caught in the Dutch Wadden Sea (53°15'N, 5°15'E) (Fig. 1, location 1). The maximum distance between the 10 different catch sites was less

than 90 km. When caught between October and March these birds are, per definition, *islandica* (Davidson & Wilson 1992). However, from the end of July until the end of September and in May, *canutus* Knots use the same location as a stopover site, and we cannot distinguish these two subspecies on the basis of plumage (Nebel *et al.* 2000). We did not catch birds in May, but in July, August and September we did. At this time, the majority of adults are moulting the primaries. As *canutus* Knots do not start wing-moult until they have reached the wintering area (Piersma *et al.* 1992), we assumed that the adults in wing-moult are *islandica*. More problematic are the second calendar year birds recognizable by their basic plumage and advanced wing-moult when captured in July–August, and the non-wing-moulting adults caught during this time. When birds of the latter category were heavier than 155 g, indicating that they were preparing for long-distance migration, we assumed that they were *canutus* (Nebel *et al.* 2000); note that we never caught adults in wing-moult (= *islandica*) that were that heavy. All marked Red Knots of which it was uncertain whether they were *islandica* (29% of the catch) were left out of consideration here.

Limosa l. taymyrensis

Bar-tailed Godwits of the *taymyrensis* subspecies were all caught in The Netherlands and Germany (Fig. 1, locations 1 and 3) between 20 April and late May. The maximum distance between catch sites was 335 km. From late April onwards, the birds arrive from their West African wintering areas and use the Wadden Sea as their main spring fattening area (Piersma & Jukema 1990, Duijns *et al.* 2009). In July and August these birds use the Wadden Sea again as a stopover during their return migration to West Africa (Drent & Piersma 1990, Engelmoer 2008). Resightings show that some individuals caught between 20 April and the end of May and some more birds caught in July and August were actually wintering in Europe. We assume that these birds belong to the *lapponica* subspecies (see Engelmoer 2008, Duijns *et al.* 2009). From extensive ring-reading during the winter months in the western part of the Dutch Wadden Sea, we estimated that 6.7% of the birds caught between 20 April and late May were *lapponica* (B. Spaans *et al.* unpubl. data). However, for July and August this fraction was 41%. Here we have left out birds caught in late July and August.

All birds were individually marked with four colour-rings (two on each tarsus, four different primary



Figure 1. The position of the various ringing and ring-reading locations. 1, Dutch Wadden Sea; 2, Banc d'Arguin, Mauritania; 3, German Wadden Sea, and 4, Iceland. See also Table 3.

colours) and a flag (colour-ring with an extension) on eight different positions (Brochard *et al.* 2002, Piersma & Spaans 2004, see also www.nioz.nl: and then navigate the site via research, scientific departments, marine ecology and projects to Colour Rings). In this

way, we are able to make 2048 different combinations per flag colour. The numbers of individually marked birds per year on which our analysis is based are listed in Table 1 (years run from 1 July to 30 June). The total number of accumulated resightings, the total number

Table 1. The number of individually marked birds of the three wader populations per year. * Number not relevant here.

Year	<i>C. c. canutus</i>	<i>C. c. islandica</i>	<i>L. l. taymyrensis</i>
98/99	0	158	0
99/00	0	405	0
00/01	0	287	128
01/02	0	356	170
02/03	244	93	374
03/04	196	244	295
04/05	201	201	189
05/06	164	360	434
06/07	178	361	313
07/08	107	*	*

of resighted individuals and the fraction observed in the main area of observation are listed per population in Table 2. The observations also yielded information on the distribution of the marked birds over the wintering and/or staging areas and some relevant results are presented here to verify the assumption of random mixing of marked birds away from the ringing sites.

Determining densities of marked birds

Ring densities were mainly determined at the foraging areas (intertidal mudflats) by scanning all individuals for which both legs could be seen. When a colour-ringed individual was found, the number of scanned individuals counted up until that point was noted and the combination was read. We always tried to check as many different individuals as possible. When we found large concentrations of Red Knots of which the legs of a large fraction could not be seen during one scan, for instance when feeding on mudflats with a variation of dry parts and shallow pools of water, we had to make multiple scans through the flock. In those situations every new scan consists of newly controlled birds and birds that were already controlled during the previous scans. So the final number of controlled birds is not the sum of the numbers controlled during each scan, but had to be estimated. By counting the total number of

birds in the flock, the final number of controlled birds (X) was estimated with the following formula, representing the probability of being controlled multiplied by the total number in the flock. Here we assume that the probability of seeing particular individuals within the flock is random.

$$X = \{1 - ((T - C_1)/T) * ((T - C_2)/T) * ((T - C_3)/T) * \dots * ((T - C_i)/T)\} * T$$

where T = the total number in the flock, and C_i = the number controlled at scan i .

Although high-tide roosts have the advantage that many birds are concentrated, it appeared that scanning for colour-rings of birds on high-tide roosts was usually impossible because birds were standing too close together, or on one leg, or in shallow water. Only in a few situations where we gained a clear view could we get reliable ring density estimates at high-tide roosts.

The locations where ring densities were determined

Calidris c. canutus

Ring densities of *canutus* Knots caught on the Banc d'Arguin, Mauritania were determined from 21 to 28 May 2006, from 22 May to 3 June 2007 and from 22 May to 4 June 2008 in the Schleswig-Holstein part of the German Wadden Sea, between the river Elbe in the south (53°52'N, 08°52'E) to the town of Husum in the north (54°29'N, 09°03'E) (Fig. 1, location 3). The Schleswig Holstein area is known as the single most important spring staging area for this population (Prokosch 1988, Piersma *et al.* 1992). Although *islandica* Knots do occur in this area, adults of this population would have left the German Wadden Sea before 20 May (Prokosch 1988, Dick *et al.* 1987). Only juvenile *islandica* Knots stay there but, in spring, they are easily recognizable by their winter plumage while adults are in summer plumage then. Juvenile *canutus* Knots do not come to these staging areas in May and the

Table 2. The number of resightings of the three wader populations (between brackets: during x years) and number of resighted individuals on which the survival analysis is based, including the fraction that was observed in the main location of observation.

	Total number marked	Number of individual resightings	Number of individuals resighted	Fraction (%) in main resighting location
<i>C. c. canutus</i>	1090	3746 (6)	713	95% on Banc d'Arguin
<i>C. c. islandica</i>	2465	3723 (9)	1385	72% in Dutch Wadden Sea
<i>L. l. taymyrensis</i>	1903	5064 (7)	1040	88% in Dutch Wadden Sea

majority remains in the wintering areas in West Africa (van Dijk *et al.* 1990). Thus, ring density estimates here were only made among Red Knots in summer plumage.

Calidris c. islandica

The ring densities of the Nearctic *islandica* Knots were determined from 9 to 28 May 2007 at a number of coastal areas in Iceland (65°N, 22°W) (Fig. 1, location 4). These areas are known to be an important spring staging area for *islandica* Knots (Gudmundsson & Gardarsson 1993). *Canutus* Knots do not occur at all there (Piersma *et al.* 1992). As juvenile Knots tend to remain on the winter grounds during their first summer, very few, if any, juvenile *islandica* Knots will occur in Iceland at this time.

Limosa l. taymyrensis

To determine ring densities of Bar-tailed Godwits marked during stopover in the Netherlands and Germany, we went to their main wintering areas in West Africa, the Banc d'Arguin in Mauritania (19°50'N, 16°23'W) (Fig. 1, location 2), making observations from 6 to 13 December 2007. This area is known to be the most important wintering area for this population (Altenburg *et al.* 1993, Engelmoer *et al.* 1984, Hagemeyer *et al.* 2004).

For comparison, ring densities were also determined in the areas of ringing for all three populations. The locations of ringing and ring density determination are summarized per population in Table 3, including the (great circle) distance between them.

Numbers of marked birds and the estimation of population size

To be able to estimate the total number of marked birds present in the population at the moment we determined the ring density, we need an estimate of the

Table 3. Locations where birds were ringed and where ring-densities were determined per population. See Fig. 1 for the global position of the numbered locations.

Population	Ringing location	Location where ring-densities were determined	Great circle distance (km) between ringing and sighting locations
<i>C. c. canutus</i>	2	3	4400
<i>C. c. islandica</i>	1	4	2000
<i>L. l. taymyrensis</i>	1 (3)	2	4150

annual survival. Our survival analysis is based on the resightings of the marked birds (Tables 1 & 2). We calculated annual survival by using the Cormack-Jolly Seber model in the MARK software package and use the estimates of the most parsimonious model (White & Burnham 1999). For all three populations, the model with a year-dependent survival in the first year after catch and a (higher) constant survival in the following years, and a year-dependent resighting probability appeared to be the best model. Finding lower survival in the first year after catch than afterwards is common in wader studies (Sandercock 2003), and has been attributed to a fraction of birds being 'transient' (i.e. accidentally passing through the catching and monitoring locations) and enhanced mortality just after catch. Thus, we used the variable $\Phi_{\text{year } 1}$ to estimate the number of surviving individuals during the first year after catch and the constant $\Phi_{\text{after year } 1}$ for the following years. The average overall estimate of $\Phi_{\text{year } 1}$ was 0.79 for *canutus* Knots, 0.80 for *islandica* Knots, and 0.57 for *taymyrensis* Godwits. The estimate of $\Phi_{\text{after year } 1}$ (\pm se) for *canutus* Knots was 0.85 ± 0.03 , for *islandica* Knots 0.87 ± 0.01 and for *taymyrensis* Godwits it was 0.81 ± 0.02 . We calculated the number of marked birds in the population in year (T + 1) by multiplying the cohort from year T (Table 1) by the annual survival as given above. By repeating this until the season in which we determined ring densities, we end up with the estimated number surviving in that season.

Finally, the latter number was corrected by inter-seasonal mortality rates. As the period between midwinter and May is about half a year, we assumed the mortality between midwinter and May to be half (50%) of the annual mortality for *canutus* Knots as well as the *taymyrensis* Godwits. For the *islandica* Knots, the time between the period of observation (ring-reading) on the wintering grounds (mainly Wadden Sea) and spring-fattening on Iceland in May is shorter than half a year. That is why we assumed the mortality between wintering and spring-fattening in 2007 to be 25% of the annual mortality. The Red Knots caught as juveniles are supposed not to migrate to the spring-staging sites in their first year and are therefore not taken into account.

The estimates of the number of marked birds alive obtained as described above are listed in Table 4. For the Bar-tailed Godwit the numbers originally caught (Table 1) were corrected for the small fraction (6.7%) of *Limosa l. lapponica* in the catches. To give an idea of the variation associated with the estimated numbers alive, we calculated the lower and upper limit of the

Table 4. The estimated numbers of marked individuals in the population at a particular point in time. In the third column these estimates are given using the lower and upper limits of the 95% confidence intervals of the survival estimates.

	Number of marked birds alive	Lower – Upper with 95% CI of Φ
<i>C. c. canutus</i> in May 2006	533	445–605
<i>C. c. canutus</i> in May 2007	598	481–699
<i>C. c. canutus</i> in May 2008	617	477–744
<i>C. c. islandica</i> in May 2007	1296	1025–1550
<i>L. l. taymyrensis</i> in Dec. 2007	779	656–912

number of marked birds alive using the upper and lower limits of the 95% confidence intervals of the survival estimates (Table 4).

With the ring densities determined at independent resighting occasions as input, we used the NOREMARK freeware package to compute the population sizes and its 95% confidence limits, using the joint hypergeometric maximum likelihood estimator (JHE) of population size (White 1996).

For both Red Knot populations, the estimates apply for the adult population only (because ring density is determined in areas rarely, if ever, used by juveniles in May). For comparison with the population estimates based on counts, our estimates need to be corrected for the fraction of juveniles. We assumed that the average proportion of juveniles is comparable to the annual mortality and therefore used 15% juveniles in *canutus* and 13% juveniles in *islandica* Knots for this correction. Population estimates were rounded off to the nearest 1000.

RESULTS

Evidence for random distribution of the marked birds

In case our marked birds would concentrate in the locations where we determined ring densities (Fig. 1), the assumption of random distribution is not met. Showing that our marked birds use many sites along their migration routes is at least an indication that these birds are more widely distributed.

For *canutus* Knots no other important spring staging area besides the Wadden Sea in Schleswig-Holstein is known (Dick *et al.* 1987). However, individuals marked on the Banc d'Arguin were resighted in May in the Netherlands (three), France (five) and Spain (two).

Besides Iceland, the other well-known spring staging area for *islandica* Knots is situated in northern

Table 5. The origin (site of ringing) of all marked Bar-tailed Godwits that were seen on the Banc d'Arguin (BdA) between 2002 and 2007. The expected number was calculated as: (number of birds caught per site/total number caught) \times 100. The distance to the first site (Castricum, furthest southwest) is also given. The latter three sites are pooled for the Chi² analysis.

Catching site	Distance to Castricum (km)	Observed on BdA	Expected number	Chi ²
Castricum (NL)	0	27	27	
Texel (NL)	60	32	27	
Terschelling (NL)	104	34	41	
Frisian coast (NL)	114	2	2	
Schiermonnikoog (NL)	150	2	1	
Westerhever (D)	335	3	2	
Total		100	100	3.27 (ns)

Norway, mainly around the Porsanger Fjord, about 2200 km away from the Dutch Wadden Sea (Davidson *et al.* 1986, Wilson *et al.* 2007). In this location, at least 77 different individuals of *islandica* Knots, marked in the Wadden Sea, were observed (Wilson *et al.* 2007).

Taymyrensis Godwits marked during northward migration in the Netherlands and Germany were resighted on the Banc d'Arguin (100 different individuals), and elsewhere in West Africa: one in Senegal, one in the Gambia, one in South Africa and five in Namibia. In Namibia, three of our ringed Bar-tailed Godwits were found among 1190 individuals in January 2009 (B. Spaans, unpubl. data). When we compare the distribution over the catching sites of all marked Bar-tailed Godwits observed on the Banc d'Arguin during 6 years (100 individuals) with the expected distribution on the basis of random distribution, there appeared to be no significant difference (Table 5).

Ring densities and population estimates

Table 6 lists by population the number of birds that were checked for markings in and far away from the ringing locations, the number of marked birds found, the ratios of unmarked to marked and the dilution factor. The dilution factor D indicates how much lower the ring densities were in the far-away locations than in the ringing locations, the ratio being highest (14–18) in *canutus* Knots and lowest (2) in *islandica* Knots (Table 6).

The population estimates, including the 95% confidence intervals, are listed in Table 7. These estimates apply for both the Red Knot subspecies for the adult population only.

Table 6. The number of individuals controlled for colour-rings (Nc), the number of marked individuals (M) and the ratio unmarked to marked (Nc/M) in the far-away and in the ringing locations. D, the dilution factor = (Nc/M in far-away location)/(Nc/M in ringing location). See Fig. 1 and Table 3 for the ringing and far-away locations per population.

Population	Ringing location			Far-away location			
	Nc	M	Nc/M	Nc	M	Nc/M	D
<i>C. c. canutus</i> 2006	23,413	587	40	13,589	19	715	17.9
<i>C. c. canutus</i> 2007	28,757	725	40	14,965	24	624	15.6
<i>C. c. canutus</i> 2008	22,008	539	41	12,664	22	576	14.0
<i>C. c. islandica</i>	12,917	107	121	13,475	57	236	2.00
<i>L. l. taymyrensis</i>	2,831	52	54	11,699	38	308	5.7

Table 7. Population estimates and 95% confidence interval (in thousands) based on the mark-resighting technique. For the Red Knots, these estimates refer to the adult population only. The numbers in the third column are the population estimates based on the lower and upper estimates of the number of marked birds alive from Table 4.

	Population estimate	95% CI	Lower – Upper
<i>C. c. canutus</i> (2006)	381	251–443	318–432
<i>C. c. canutus</i> (2007)	373	257–435	300–436
<i>C. c. canutus</i> (2008)	355	241–417	274–428
<i>C. c. islandica</i> (2007)	306	239–368	242–366
<i>L. l. taymyrensis</i> (2007)	240	177–302	202–281

Our estimates, now corrected for the fraction of juveniles for both the Knot populations, are presented together with the most recent estimates based on counts (Delany *et al.* 2009) in Fig. 2.

DISCUSSION

Do the marked birds distribute randomly away from the marking site?

Our marked Bar-tailed Godwits were resighted all along the western shores of Africa as far as South Africa, showing that these birds do not exclusively go to a certain part of the wintering area but distribute themselves more widely. The observation of three of our marked birds among 1190 Bar-tailed Godwits in Namibia (Nc/M = 397) is an indication that ring-density in this very southern part of their wintering range is not very different from the ring density of Nc/M = 308 on the Banc d'Arguin, suggesting random distribution over the whole wintering range.

Many of our marked *islandica* Knots were seen in northern Norway (Wilson *et al.* 2007), showing that *islandica* Knots caught in the Dutch Wadden Sea use the Icelandic as well as the Norwegian spring staging sites.

The fact that we see dilution in the far away locations (Table 3) shows that ring densities obtained at the catching location cannot be used to estimate population size. The differences in dilution factor between the species reflect their degree of site-faithfulness to the catching location, varying from a factor of 18 for the extreme site-faithful *canutus* Knots in their wintering area on the Banc d'Arguin (Leyrer *et al.* 2006) to a factor 2 for the *islandica* Knots in the Dutch Wadden Sea with their very large home-ranges (Piersma *et al.* 1993, van Gils *et al.* 2005). However, dilution only shows that, away from the location of ringing, there is at least a certain degree of mixing among conspecifics. The best evidence for random mixing is the comparison of the catching-site origin of all the Bar-tailed Godwits ever resighted on the Banc d'Arguin (Table 5), where catching origin did not differ from the predicted origin based on randomness. Thus, we have no indication that away from their ringing-site the marked birds are not randomly distributed, although it is clear that the assumption of randomness needs more investigation in the near future.

Population size estimates

Calidris c. canutus

The most recent population estimate for the *canutus* Knots based on counts made in 2001 is 400 000 (Delany *et al.* 2009), which is higher than the 340 000 in the 1990s but down from earlier estimates of up to 550 000 in the 1980s (Stroud *et al.* 2004, Wetlands International 2002, Smit & Piersma 1989). Our estimate including the fraction of juveniles will be around 435 000 (three years averaged) with a 95% CI of 294 000–508 000 (Fig. 2). As the most recent estimate based on counts lies well within this range, our results are in accordance with it.

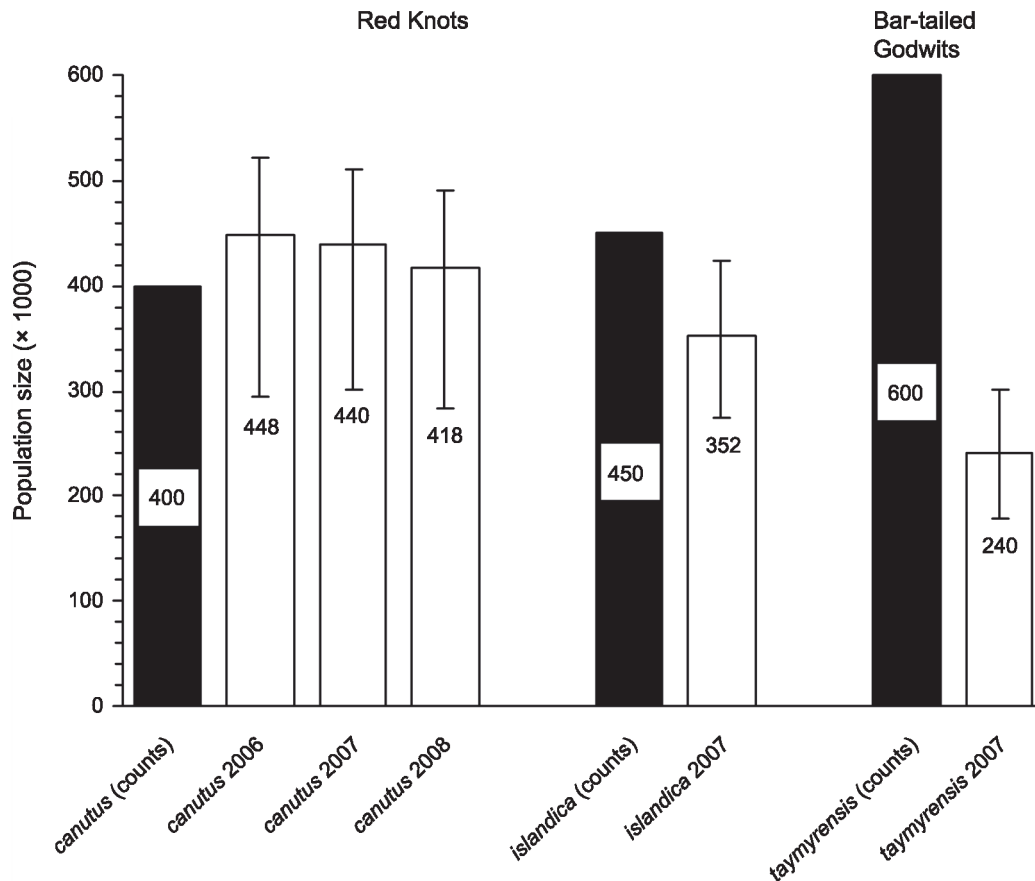


Figure 2. The total population sizes of Red Knots (*canutus* and *islandica* populations) and Bar-tailed Godwits (*taymyrensis* population) based on counts (black bars) according to Wetlands International (2006) followed by the total population estimates and 95% confidence intervals (error bars) based on the mark-resighting technique (white bars).

Calidris c. islandica

Based on counts, the most recent estimate of the size of the *islandica* Knot population is 450 000 (Delany *et al.* 2009, Stroud *et al.* 2004), which represents a higher number than the 345 000 in the early 1980s (Smit & Piersma 1989). Correcting our estimate for the fraction of juveniles, we end up with total population 352 000 and a 95% CI of 276 000–423 000. The most recent estimate based on counts is about 28% higher than our estimate and lies just outside the CI. Taking the variation around the survival estimates used into account (Table 4), the upper limit of the number of marked birds alive is 1550. This is almost 20% higher than the 1296 marked individuals used here to estimate the population size. Using this upper limit of 1550 marked individuals would yield a population of 420 000 (juveniles included), very close to the 450 000 based on counts. Summarizing, we can say that our results slightly indicate a somewhat smaller population than

assumed. A real recent population decline would not be unlikely as a consequence of shellfish dredging-related declines in the food stocks for Red Knots in the Dutch Wadden Sea that have been shown to negatively affect the population (van Gils *et al.* 2006, Kraan *et al.* 2009).

Limosa l. taymyrensis

The size of the *taymyrensis* Bar-tailed Godwit population, based on counts, is estimated to be 600 000 (Delany *et al.* 2009), a rise from an earlier estimate of 520 000 (Wetlands International 2002, Stroud *et al.* 2004). Both figures are much higher than our estimate of 240 000 and are far outside the 95% CI limits (Fig. 1). Even if we take the possible variation around our survival estimates into account (Table 4) and use the upper limit as the number of 912 marked birds alive, we would end up with a population size of 281 000

(Table 6), still far beyond the estimate based on counts.

Has there been a real decline of the Bar-tailed Godwit *taymyrensis* population?

When Bar-tailed Godwits which spring-stage in the Netherlands concentrate on the Banc d'Arguin in winter, we would measure a high ring density there and find therefore a low population estimate. The fact that we received resightings from our marked birds from Senegal, The Gambia, Namibia and as far south as South Africa indicates that *taymyrensis* Godwits marked in the Netherlands and Germany utilize the whole West African coastline as a wintering area, not just the Banc d'Arguin.

It is well established that the vast majority of the *taymyrensis* population uses the international Wadden Sea in May as a fuelling area where birds stage there at least three weeks to accumulate sufficient energy stores (Scheiffarth *et al.* 2002, Piersma & Jukema 1990). Consistent with our low population size estimate of 240 000, the numbers counted there are also considerably lower than the total population estimate of 600 000 based on counts in the wintering areas (Delany *et al.* 2009). Between 1993 and 2000 May numbers in the entire Wadden Sea ranged between 100 000 and 150 000. Only in May 1995 was a total of 348 000 birds counted there (Blew & Südbeck 2005). Assuming a population of about 600 000, only a high turnover rate could explain these low actual counted numbers in May in the Wadden Sea. However, as the birds need to increase body mass by almost 200 g in May at a rate of 6.5 g per day (Piersma & Jukema 1990), they will need the full month to do so. Therefore a high turnover rate seems unlikely. If the current population size is indeed smaller than hitherto assumed, either the birds were over-estimated during the counts in West Africa or the population has declined recently.

With respect to over-counting we can say the following. At the numerically most important wintering area of *taymyrensis* Godwits, the Banc d'Arguin, the total number is determined to a large extent by a few very large concentrations. Altenburg *et al.* (1983) counted 364 000 Godwits (= 67% of their total) in only four concentrations ranging from 56 000 to 170 000 and Hagemeyer *et al.* (2004) counted 245 000 Godwits (= 61% of their total) in four concentrations ranging from 41 000 to 104 000 Bar-tailed Godwits. Moreover, these large flocks are mixtures of Bar-tailed Godwits and Red Knots and a number of smaller species and counters are

often time-stressed because they have to count a large area during the same high tide (Altenburg *et al.* 1983). Given these circumstances large but unknown mistakes may be possible.

Concerning a possible recent population decline, this is in fact measured in May on the spring staging sites in the Wadden Sea (Blew & Südbeck 2005). Moreover, the average annual survival of 0.81 found by us over the period 2001–2007 is remarkably low for a wader of this size. In Icelandic Black-tailed Godwits *Limosa limosa islandica*, for instance, survival values of 0.87 and 0.94 were found (Gunnarsson *et al.* 2005). The low survival found by us in the *taymyrensis* Godwits could thus indicate a period of higher than normal mortality and this could result in a population decline if the reproduction did not compensate the increased mortality (Boyd & Piersma 2001). Unfortunately we do not have any reliable measurements of the reproductive success in the *taymyrensis* Godwit population. However, even if we would use the high survival values as found in the Icelandic Black-tailed Godwits (also during the first year after catch), our estimated populations sizes would be 371 000 (using $\Phi = 0.87$) and 456 000 (using $\Phi = 0.94$), values still far away from the 600 000 estimate based on counts. Thus we think that our data indicate that the recent population size of *taymyrensis* could well be remarkably smaller than assumed.

CONCLUSIONS

The mark–resighting approach to estimate total population size used previously by Gunnarsson *et al.* (2005) and Lourenço *et al.* (2010) in two subspecies of Black-tailed Godwits is not only a very useful addition to the traditional counts, but potentially a superior way to estimate population size because of the ability to derive confidence limits and the fact that not all locations have to be visited and counted. The latter is an obvious advantage and holds even more for species that occur more widespread than those described in this paper, Ruffs *Philomachus pugnax*, for example (Stroud *et al.* 2004). Nevertheless, the approach warrants considerable investment because a colour-marking program needs to be established. Once this is done and resighting efforts are maintained, estimations can be repeated each year with much less effort compared to the organization of comprehensive counts. Indeed, the mark–resighting approach is now applied on a worldwide scale to monitor the fate of the many currently endangered long-distance migrating wader populations (Piersma 2007).

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REFERENCES

- Altenburg, W., Engelmoer, M., Mes, R. & Piersma, T. 1983. [Recensement des limicoles et autres oiseaux aquatiques au Banc d'Arguin, Mauritanie.] *Gerfaut* **73**: 243–264 (in French).
- Atkinson, P.W., Austin, G.E., Rehfish, M.M., Baker, H., Cranswick, P., Kershaw, M., Robinson, J., Langston, R.H.W., Stroud, D.A., van Turnhout, C. & Maclean, I.M.D. 2006. Identifying declines in waterbirds: the effects of missing data, population variability and count period on the interpretation of long-term survey data. *Biol. Conserv.* **130**: 549–559.
- Blew, J. & Südbek, P. (eds). 2005. *Migratory Waterbirds in the Wadden Sea 1980–2000*. Wadden Sea Ecosystem No. 20. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Joint Monitoring Group of Migratory Birds in the Wadden Sea, Wilhelmshaven, Germany.
- Boyd, H. & Piersma, T. 2001. Changing balance between survival and recruitment explains population trends in Red Knots *Calidris canutus islandica* wintering in Britain, 1969–1995. *Ardea* **89**: 301–317.
- Brochard, C., Spaans, B., Prop, J. & Piersma, T. 2002. Use of individual colour-ringing to estimate annual survival in male and female Red Knot *Calidris canutus islandica*: a progress report for 1998–2001. *Wader Study Group Bull.* **99**: 54–56.
- Burton N.H.K. & Evans, P.R. 1997. Survival and winter site-fidelity of Turnstones *Arenaria interpres* and Purple Sandpipers *Calidris maritima* in northeast England. *Bird Study* **44**: 35–44.
- Davidson, N.C., Strann, K.B., Crockford, N.J., Evans, P.R., Richardson, J., Standen, L.J., Townshend, D.J., Uttley, J.D., Wilson, J.R. & Wood, A.G. 1986. The origins of Knots *Calidris canutus* in Arctic Norway in spring. *Ornis Scand.* **17**: 175–179.
- Davidson, N.C. & Wilson, J.R. 1992. The migration system of European-wintering Knots *Calidris canutus islandica*. *Wader Study Group Bull.* **64** (Suppl.): 39–51.
- Delany, S., Scott, D., Dodman, T. & Stroud, D. (eds) 2009. *An Atlas of Wader Populations in Africa and Western Eurasia*. Wetlands International, Wageningen, The Netherlands.
- Dick, W.J.A., Piersma, T. & Prokosch, P. 1987. Spring migration of the Siberian Knots *Calidris canutus canutus*: results of a co-operative Wader Study Group project. *Ornis Scand.* **18**: 5–16.
- Drent, R. & Piersma, T. 1990. An exploration of the energetics of leap-frog migration in arctic breeding waders. In Gwinner, E. (ed.) *Bird Migration: Physiology and Ecophysiology*: 399–412. Springer-Verlag, Berlin.
- Duijns S., van Dijk J.G.B., Spaans B., Jukema J., de Boer W.F. & Piersma T. 2009. Foraging site selection of two subspecies of Bar-tailed Godwit *Limosa lapponica*: time minimizers accept greater predation danger than energy minimizers. *Ardea* **97**: 51–59.
- Engelmoer, M. 2008. Breeding origins of wader populations utilizing the Dutch Wadden Sea as deduced from body dimensions, body mass, and primary moult. PhD Thesis, Fryske Akademy, Leeuwarden.
- Engelmoer, M., Piersma, T., Altenburg, W. & Mes, R. 1984. The Banc d'Arguin (Mauritania). In Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds.) *Coastal Waders and Wildfowl in Winter*: 293–310. Cambridge University Press, Cambridge.
- Engelmoer, M. & Roselaar, C.S. 1998. *Geographical Variation in Waders*. Kluwer, Dordrecht.
- Ganter, B. & Madsen, J. 2001. An examination of methods to estimate population size in wintering geese. *Bird Study* **48**: 90–101.
- Gudmundsson, G.A. & Gardarsson, A. 1993. Numbers, geographic distribution and habitat utilization of waders (Charadrii) in spring on the shores of Iceland. *Ecography* **16**: 82–93.
- Gunnarsson, T.G., J.A. Gill, T.G., Pots, P.M., Atkinson, P.W., Croger, R.E., Gélinaud, G., Gardarsson, A. & Sutherland, W.J. 2005. Estimating population size in Black-tailed Godwits *Limosa limosa islandica* by colour-marking. *Bird Study* **52**: 153–158.
- Hagemeijer, W., Smit, C., de Boer, P., van Dijk, A.J., Ravenscroft, N., van Roomen, M.W.J. & Wright, M. 2004. *Wader and Waterbird Census at the Banc d'Arguin, Mauritania, January 2000*. WIWO Report 81. WIWO, Beek-Ubbergen.
- Kraan, C., van Gils, J.A., Spaans, B., Dekinga, A., Bijleveld, A.I., van Roomen, M., Kleefstra, R. & Piersma, T. 2009. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *J. Anim. Ecol.* **78**: 1259–1268.
- Krebs, C. J. 1989. *Ecological Methodology*. HarperCollins Publishers, New York.
- Leyrer, J., Spaans, B., Camara, M. & Piersma, T. 2006. Small home ranges and high site fidelity in Red Knots (*Calidris c. canutus*) wintering on the Banc d'Arguin, Mauritania. *J. Ornithol.* **147**: 376–384.
- Lourenço, P.M., Kentie, R., Schroeder, J., Alves, J.A., Groen, N.M., Hooijmeijer, J.C.E.W. & Piersma, T. 2010. Phenology, stopover dynamics and population size of migrating Black-tailed Godwits *Limosa limosa limosa* in Portuguese rice plantations. *Ardea* **98**: 35–42.
- Nebel, S., Piersma, T., van Gils, J., Dekinga, A. & Spaans, B. 2000. Length of stopover, fuel storage and a sex-bias in the occurrence of Red Knots *Calidris c. canutus* and *Calidris c. islandica* in the Wadden Sea during southward migration. *Ardea* **88**: 165–176.
- Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *J. Ornithol.* **148** (Suppl. 1): 45–59.
- Piersma, T. & Jukema, J. 1990. Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. *Ardea* **78**: 315–337.
- Piersma, T. & Spaans, B. 2004. The power of comparison; ecological studies on waders worldwide. *Limosa* **77**: 43–54.

- Piersma, T., Prokosch, P. & Bredin, D.** 1992. The migration system of Afro-Siberian Knots *Calidris canutus canutus*. *Wader Study Group Bull.*, **64** (Suppl.): 52–63.
- Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P.F. & Wiersma, P.** 1993. Scale and intensity of intertidal habitat use by Knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Neth. J. Sea Res.* **31**: 331–357.
- Prokosch, P.** 1988. [Das Schleswig-Holsteinische Wattenmeer als Frühjahrs-Aufenthaltsgebiet arktischer Watvogelpopulationen am Beispiel von Kiebitzregenpfeifer (*Pluvialis squatarola*, L. 1758), Knutt (*Calidris canutus*, L. 1758) und Pfuhschnepfe (*Limosa lapponica*, L. 1758).] *Corax* **12**: 273–442 (in German).
- Rappoldt, C., Kersten, M. & Smit, C.** 1985. Errors in large-scale shorebird counts. *Ardea* **73**: 13–24.
- Rogers, D.I., Rogers, K.G., Gosbell, K.B. & Hassell, C.J.** 2006. Causes of variation in population monitoring surveys: insights from non-breeding counts in north-western Australia, 2004–2005. *Stilt* **50**: 176–193.
- Sandercock, B.K.** 2003. Estimation of survival rates for wader populations: a review of mark-recapture methods. *Wader Study Group Bull.* **100**: 163–174.
- Scheiffarth, G., Wahls, S., Ketzenberg, C. & Exo K.-M.** 2002. Spring migration strategies of two populations of Bar-tailed Godwits, *Limosa lapponica*, in the Wadden Sea: time minimizers or energy minimizers? *Oikos* **96**: 346–354.
- Smit, C.J. & Piersma, T.** 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. In Boyd, H. & Piro, J.-Y. (eds.) *Flyways and Reserve Networks for Water Birds*: 24–63. IWRB, Slimbridge.
- Spaans, B., Brugge, M., Dekinga, A., Horn, H., van Kooten, L. & Piersma, T.** 2009. Space use of Red Knots *Calidris canutus* in the Dutch Wadden Sea. *Limosa* **82**: 113–121.
- Stroud, D.A., Davidson, N.C., West, R., Scott, D.A., Haanstra, L., Thorup, O., Ganter, B. & Delany, S.** (compilers) on behalf of the International Wader Study Group 2004. Status of migratory wader populations in Africa and Western Eurasia in the 1990s. *Intern. Wader Stud.* **15**: 1–259.
- Underhill, L.G. & Prys-Jones, R.P.** 1994. Index numbers for waterbird populations. I. Review and methodology. *J. Appl. Ecol.* **31**: 463–480.
- van Dijk, A.J., de Roder, F.E., Marteiijn, E.C.L. & Spiekman, H.** 1990. Summering waders on the Banc d'Arguin, Mauritania: a census in June 1988. *Ardea* **78**: 145–156.
- van Gils, J.A., Dekinga, A., Spaans, B., Vahl, W.K. & Piersma, T.** 2005. Digestive bottleneck affects foraging decisions in Red Knots (*Calidris canutus*). II. Patch choice and length of working day. *J. Anim. Ecol.* **74**: 120–130.
- van Gils, J.A., Piersma, T., Dekinga, A., Spaans, B. & Kraan, C.** 2006. Shellfish-dredging pushes a flexible avian top predator out of a protected marine ecosystem. *PLoS Biol.* **4**: 2399–2404.
- Warnock, S.E. & Takekawa, J.Y.** 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. *Ibis* **138**: 160–167.
- Wetlands International.** 2002. *Waterbird Population Estimates – Third Edition*. Wetlands International Global Series No. 12, Wageningen.
- Wetlands International.** 2006. *Waterbird Population Estimates – Fourth Edition*. Wetlands International, Wageningen.
- White, G.C.** 1996. NOREMARK: population estimation from mark-resighting surveys. *Wildl. Soc. Bull.* **24**: 50–52.
- White, G. C. & Burnham, K.P.** 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46** (Suppl.): 120–138.
- Wilson, J., Dick, W.J.A., Frivoll, V., Harrison, M., Johnsen, T., Soot, K.M., Stanyard, D., Strann, K.-B., Strugnell, R., Swinfen, B., Swinfen, R. & Wilson, R.** 2007. The migration of Red Knots through Porsangerfjord in spring 2007: a progress report on the Norwegian Knot Project. *Wader Study Group Bull.* **114**: 51–55.

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