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Staging duration and passage population size of Sanderlings in the western Dutch Wadden Sea

A.H. Jelle Loonstra¹, Theunis Piersma^{1,2} & Jeroen Reneerkens^{1,*}

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The population of Sanderlings *Calidris alba* along the East Atlantic flyway has grown considerably during the last decades. Perhaps reflecting this augmented population size, increasing numbers of Sanderling have been reported to stage in the Wadden Sea during spring and autumn migration. Estimates of the numbers of Sanderlings in the Wadden Sea have previously been based on a limited number of counts that were not corrected for the turnover of individuals. In this study, we accounted for turnover using estimates of the probability that individually colour-ringed Sanderlings are still present two days after a sighting. In combination with daily counts during high tide, we estimated the total number of Sanderlings that used the island Griend and surrounding mudflats, in the western Dutch Wadden Sea, during southward passage in 2013 and 2014. We also estimated minimal staging durations of Sanderlings at Griend. Non-moulting birds were significantly heavier upon capture, which suggests that they were refuelling for long non-stop migratory flights. Winter sightings confirmed that the non-moulting Sanderlings winter in sub-Saharan Africa and that the moulting Sanderlings spent the winter in Europe or northern Africa. With an average minimal stay in the western Dutch Wadden Sea of 9 days in 2013 and 12 in 2014, non-moulting Sanderlings stayed for a much shorter time than moulting Sanderlings, which stayed for 32 days in 2013 and 36 days in 2014. Non-moulting individuals were less likely to be resighted between years. Estimates of minimal staging duration are likely underestimates of the true staging duration, and we propose that moulting Sanderlings probably complete their wing moult in the Wadden Sea. We estimated that the total number of Sanderlings using the western Dutch Wadden Sea before migration to European or African wintering areas were 27,546 (95% CI 22,739–41,449) in 2013 and 22,574 (95% CI 16,436–46,114) in 2014. This would amount to 11–14% of a total flyway population of 200,000 individuals, representing an amazing degree of concentration for what is regarded as a rather widely and thinly spread shorebird species.

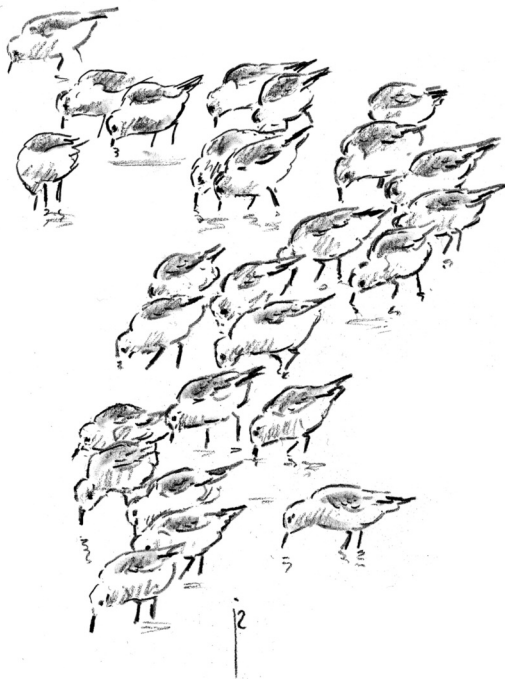
Key words: *Calidris alba*, staging ecology, capture-recapture models, colour-ringing, staging duration, site fidelity, population estimation, Wadden Sea, primary moult, migration

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During their seasonal migrations, birds usually visit a series of distinct areas to rest, moult and/or refuel for subsequent flight episodes. Such staging sites are crucial to successfully complete migration (Piersma 1987, Alerstam & Lindström 1990, Warnock 2010).

The quality of, and environmental conditions experienced at, staging sites is likely to affect subsequent survival and/or breeding success (e.g. Drent *et al.* 2003, Baker *et al.* 2004, Newton 2006, Harrison *et al.* 2011, Piersma *et al.* 2016).



The international Wadden Sea of Denmark, Germany and The Netherlands represents an important staging area for more than 10 million shorebirds during both northward and southward migration (van de Kam *et al.* 2004). The number of Sanderlings *Calidris alba* in the Dutch Wadden Sea has generally been low compared to most other shorebird species (van de Kam *et al.* 2004). With a substantial population increase of Sanderlings along the East Atlantic flyway since the early 1980s (Reneerkens *et al.* 2009, Ntiamoa-Baidu *et al.* 2014), i.e. from an estimated 70,000 in the 1980s (Stroud *et al.* 2004, Delany *et al.* 2009) to 123,000 in the 1990s, and recently 200,000 individuals (van Roomen *et al.* 2015), the number of Sanderlings staging in the Wadden Sea also increased (van Turnhout & van Roomen 2008).

For conservation purposes, accurate quantifications of the numbers of migratory birds using a staging area are important (Kersten & Smit 1984, Chernetsov 2006, Sheehy *et al.* 2011). For example, under the Ramsar Convention it has been agreed that staging sites should be safeguarded from threats when at least 1% of a waterbird population uses a particular wetland (Ramsar Convention Bureau 1988, Boere & Piersma 2012). Also, assuming that population trends of bird species reflect the state of an ecosystem, population trends at staging sites may indicate the need for better conservation and/or a change in site management (Piersma & Lindström 2004, Gillings *et al.* 2009, Eriksson *et al.* 2010).

Typically, peak counts of bird species are used to indicate the relative importance of staging sites (Ramsar Convention Bureau 1988, Boere & Piersma 2012). In the Wadden Sea, counts during one or two days per migration season are used to determine peak numbers. Besides the difficulties associated with accurate counts of large groups of shorebirds (Rappoldt *et al.* 1985), poor temporal coverage may result in serious underestimation of site usage. Although limited and uneven coverage can to some extent be dealt with by 'imputation' (e.g. Atkinson *et al.* 2006), this will add uncertainty to the estimates because the method relies on a few strong assumptions of statistical independence of the factors year, month and site which are used to impute missing values (Underhill & Prŷs-Jones 2004). With 20–84% of the Sanderling estimates being imputed during the migration period in 1980–2006 (van Turnhout & van Roomen 2008), this uncertainty can potentially be very large. Perhaps most critically, the turnover of individuals has to be accounted for to estimate the true usage of staging sites, especially if individual staging times are short compared to the

overall staging period of a species (Caizergues *et al.* 2011, Lourenço *et al.* 2010). Therefore, it has been recommended to correct bird counts at staging sites for turnover by including the probabilities that birds emigrate and immigrate between counts (Frederiksen *et al.* 2001). Given the marked increase of the flyway population during the last decades (Reneerkens *et al.* 2009, Ntiamoa-Baidu *et al.* 2014, van Roomen *et al.* 2015), a re-evaluation of the importance of the Wadden Sea as a staging site for Sanderlings is warranted.

Shorebirds either moult their primary feathers in the Wadden Sea, or fuel up and postpone moult until arrival in southerly non-breeding areas (Boere 1976). Primary moult is a time- and energy-consuming process which limits aerodynamic capacity (Swaddle & Witter 1997, Dietz *et al.* 2013). Therefore, if conditions allow (Dietz *et al.* 2013), this may be an important reason why primary moult usually does not temporally overlap with other demanding events such as migration flights (Buehler & Piersma 2008). Primary moult may thus result in substantially prolonged staging periods. In this study, we compared stopover persistence and minimal staging times of Sanderlings with or without primary moult in the Wadden Sea and used overall daily emigration rates to obtain reliable estimates of the total passage population size during southward migration in two successive seasons of southward migration.

METHODS

Study area

We conducted our research in the western Dutch Wadden Sea, on and near the island of Griend (53° 14'N, 5° 15'E; Figure 1). The island is surrounded by extensive intertidal mudflats with a semidiurnal tide and tidal amplitudes between 1.5–2.5 m (Piersma *et al.* 1993). During high tide the majority of Sanderlings used a communal roost at Griend, but the sand bank Richel was also used for roosting. A study by Van den Hout & Piersma (2013) showed that within the Dutch Wadden Sea, Sanderlings almost exclusively forage on the mudflats around Griend and near Richel (7 km from Griend, 53° 17'N, 5° 7'E; Figure 1). We searched for colour-ringed Sanderlings on Griend and surrounding mudflats and counted their number at the roost(s) on the island Griend during high tide daily.

Study species

Based on sightings of individually colour-ringed birds, Sanderlings passing through the Wadden Sea during southward migration are known to belong to the

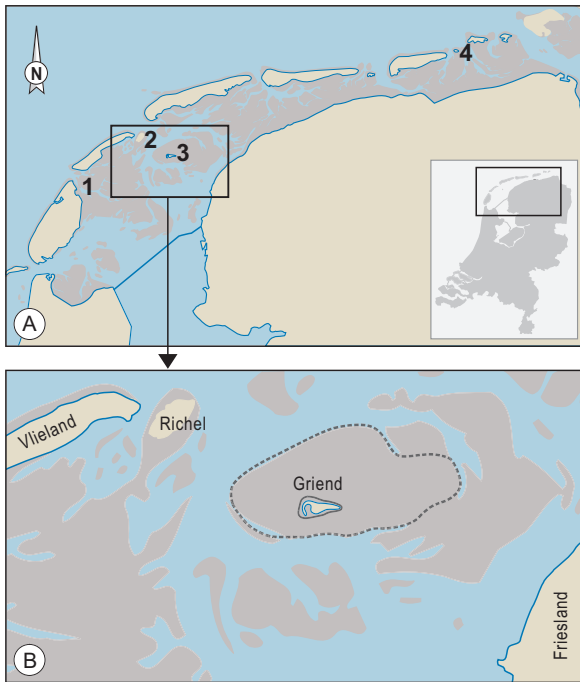


Figure 1. (A) An overview of the different capture sites: (1) De Hengst, (2) Richel, (3) Griend and (4) Simonszand, in the Wadden Sea. (B) The study site in the western Wadden Sea; the area within the dotted line was checked for colour-ringed Sanderlings on a daily basis and high-tide counts were performed within the area with the black line.

Greenlandic breeding population. It remains uncertain whether Siberian breeding individuals also pass through (Reneerkens *et al.* 2009, Conklin *et al.* 2016). Resightings of Sanderlings that were previously colour-ringed in the Wadden Sea indicate onward migration to a nonbreeding area ranging across 90 degrees of latitude, between the coasts of the United Kingdom and Namibia (Reneerkens *et al.* 2012). During southward migration, Sanderlings typically arrive in the Wadden Sea from mid-July onwards, with the majority having left the Wadden Sea by the end of September. Only a small number of Sanderlings use the intertidal area of the Wadden Sea in winter (van Turnhout & van Roomen 2008).

Fieldwork procedures

At the start of our field seasons in 2013 and 2014, respectively 5701 and 5999 Sanderlings had been individually colour-marked in a large collaborative effort along the East Atlantic flyway since 2002 (Reneerkens *et al.* 2009). In the Dutch Wadden Sea, Sanderlings were colour-ringed during southward migration in 2007–2013. Sanderlings were also ringed in wintering

areas in Ghana (2007–2014), Mauritania (2002–2013), Portugal (2009–2014), The Netherlands (2007–2009) and the United Kingdom (2011–2013), during northward migration on SW Iceland (2007–2014), southward migration in Poland (2009–2012) and The Netherlands (Wadden Sea: 2007–2014) and in their breeding area in northeast Greenland (2007–2014). Each individual was ringed with a unique combination of four colour-rings (two on each tarsus) and a flag (elongated colour-ring) of five possible colours (white, yellow, red, blue and green). The position and colour of the flag indicated the country of ringing. After capture, all individual birds were scored for primary moult and aged using plumage criteria (Prater *et al.* 1977).

On a daily basis, between 22 July and 25 September 2013 and 2014, the study area was checked for the presence of colour-ringed Sanderlings. Checks were performed using a spotting telescope with a 20–60 zoom eyepiece. Colour-ring observations were performed by AHJL with the help of several other experienced observers. The daily counts were performed by AHJL alone. A large group of observers in Europe and Africa reported observations of colour-marked individuals, which indicated the wintering area if birds were observed between 15 October and 15 March.

Primary moult classification

Consistent with the findings of Boere (1976), we found evidence that two groups of Sanderlings are present in the Wadden Sea during late summer: one group consisting of individuals with low body mass and active primary and body moult, and another group of non-moulting individuals with larger body mass. We assumed that if individuals had been encountered in the Wadden Sea in primary moult, they would consistently do so in the following years. Individuals that were caught in the Wadden Sea in July–September ($n = 235$), were thus categorised based on the presence ($n = 145$) or absence ($n = 90$) of primary moult. Individual Sanderlings that were ringed or observed in Sub-Saharan Africa in winter ($n = 105$) were assumed to moult their primary feathers at their southern wintering grounds (following Summers *et al.* 1987, Remisiewicz 2011). Shorebirds that winter north of the Sahara, as a rule, moult their primary feathers at European moulting sites including the Wadden Sea (Summers *et al.* 1987, Remisiewicz 2011). We assumed here that Sanderlings that were reported north of the Sahara in winter moulted their primary feathers in the Wadden Sea. Sanderlings that could not be categorized according to these criteria, because they were not caught in the Wadden Sea and their wintering areas



A flock of several thousand Sanderlings roosting at the west shore of Griend, in front of the warden's house (photo Jeroen Reneerkens, 14 August 2014).

remained unknown ($n = 98$), were left out of our analyses. We considered the Banc d'Arguin in Mauritania, where we have been colour-ringing and observing colour-ringed Sanderlings since 2002, to be at the northern border of, what we refer to as 'Sub-Saharan Africa'.

We tested our assumptions regarding the relationship between the moult location and the winter location, by comparing winter locations (locations of observed colour-ringed individuals between 15 October and 15 March) of Sanderlings with or without primary moult when they were caught in the Wadden Sea. This included 464 individuals that were caught in July–September in the Dutch Wadden Sea near high tide roosts at Simonszand, Griend, Richel and De Hengst (Figure 1) and also involved individuals that were not observed near Griend in 2013 or 2014.

We caught ten birds without wing moult that nevertheless were later seen in Europe in winter. These individuals had a significantly lower body mass than the other non-moulting individuals (Kruskal-Wallis test, $H_1 = 4.25$, $P = 0.034$). Also, these ten birds had average minimal staging durations of 43.8 days in 2013

(± 4.8 SE, $n = 4$) and 34.4 days in 2014 (± 8.6 SE, $n = 5$). Both the winter area and the lengths of stay in the Wadden Sea being typical for moulting birds (see Results), suggested that these individuals were wrongly assigned to the non-moulting category. They probably represented birds that were caught immediately after arrival in the Wadden Sea before they even started to moult. For this reason these ten birds were categorised as moulting individuals. Including these birds as moulting, instead of non-moulting individuals, in our analyses, did not change the relative importance of the models. With only marginally different estimates for stopover persistence (φ) and relative densities of either moult categories, estimates of passage population size differed only less than one percent by classifying these birds as moulting.

Resighting histories and stopover persistence

Because it is impossible to determine how long newly ringed individuals would already have been present in the study area at the date of marking (Verkuil *et al.* 2010), in our analyses we only included resightings of birds that were caught and ringed before arrival in the

Wadden Sea in the particular year of study. The birds included in the analyses were caught and ringed either in the study area in a previous year or in other countries before they were observed in the Wadden Sea. As the daily number of sightings of ringed individuals was low at the start and end of each study season, we used two-daily resighting occasions for each individual. Spanning 22 July – 25 September, our resighting matrices included 33 occasions of two-day observation periods in both 2013 and 2014.

Based on these 33 sampling occasions per year, local survival during southward migration in our study area was calculated using Cormack-Jolly-Seber mark-recapture models in program MARK v. 5.1 (White & Burnham 1999). Justified by our short study periods, we assumed that no mortality occurred during the study period (i.e. true survival was assumed to be 1). Local ‘survival’ thus equalled the probability that individuals stayed in the study area, and is referred to as ‘stopover persistence’ (φ) hereafter. In our models we included a group effect (g), with two groups of Sanderlings that either moulted their primaries in the Wadden Sea or not, a year effect (γ), date (t), and their interactions, as well as the resighting probability (p). If one of the parameters was held constant in our models this was indicated with a dot (.). We only compared models with a time dependent effect on φ , because in staging areas the stopover persistence will by definition decrease in the course of the season. Sanderlings cannot be aged based on their plumage once they have reached an age of one year old (Prater *et al.* 1977). Because we only observed a single juvenile Sanderling with colour-rings (ringed as a chick in Greenland in 2013), we excluded age as a factor from the analysis.

Our candidate model set consisted of 32 different models. Model selection was based on Akaike’s Information Criterion for small samples (AICc) and Akaike weights (w_i) were used to infer support for models in the candidate model set. Models differing by <2 AICc

units from the most parsimonious model were considered equally parsimonious (Burnham & Anderson 2002).

Testing goodness-of-fit

To test whether our resighting data adequately fitted the global capture-recapture model, we performed a goodness-of-fit (GOF) test using U-CARE v. 2.3 (Choquet *et al.* 2009) and checked for the occurrence of heterogeneity of survival and capture probabilities between animals. A lack of fit can be the result of different resighting probability between individuals that were observed and those that were not observed at the previous occasion (trap-dependence). Transients, individuals that stayed in the study area for only one occasion, can be another source of heterogeneity. The overall test for GOF for the most general model revealed a significant effect ($\chi^2_{299} = 534$, $P < 0.001$). Therefore, we implemented a variance inflation factor in our model selection ($\hat{c} = 1.79$; Table 1).

Population estimation and phenology of migration

The total number of Sanderlings that staged in our study area, and the 95%-confidence intervals for the estimates, were estimated using the formulas by Frederiksen *et al.* (2001) for passage population size

$$N_{\text{tot}} = N_1 + \sum_{i=2}^k (N_1 - N_{i-1}) \varphi_{i-1}$$

in which N_{tot} is the passage population size, N_i the number of counted individuals on occasion i and φ_i the stopover persistence from occasion i to the next occasion. Frederiksen *et al.* (2001) assumed stopover sites to be closed, but in our study system birds sometimes temporarily roosted on Richel (where they were not counted). These birds could return to Griend in the following days, for example during spring tide (as is described for Red Knots *Calidris canutus*; Piersma *et al.* 1993), which could lead to an overestimate of the total

Table 1. Goodness of fit test results for the global model, which included a time dependent stopover persistence $\varphi(t)$ and resighting probability $p(t)$, for two datasets with encounter histories of Sanderlings staging at Griend in the western Dutch Wadden Sea.

Dataset/year	$\chi^2_{\text{transient}}$	df	P	$\chi^2_{\text{trap-dependence}}$	df	P
2013						
Primary moult	48.4	18	<0.001	150.1	30	<0.001
No primary moult	16.9	20	0.66	108.5	25	<0.001
2014						
Primary moult	11.1	10	0.35	12.4	26	0.98
No primary moult	33.9	16	0.006	2.4	14	0.99

passage population size if these birds were considered new arrivals at Griend. To correct the 66 daily counts for emigration and immigration, we converted the two-day φ to a daily φ by taking the square root. In the few (8 in 2013 and 13 in 2014) occasions with negative numbers of arriving individuals, we instead used the counts of the preceding days corrected for emigration using the estimate of stopover persistence.

It was impossible to determine the daily number of individuals belonging to either moult category at the roost. Therefore, we assumed the relative abundance of moulting and non-moulting birds on the roost to be the same as the proportion of moulting and non-moulting colour-ringed birds that should have been present in the study area based on the first and last observation of an individual. Using the estimated daily numbers and the estimates of stopover persistence for each moult category, we calculated the passage population size for both moult categories, which were summed for each year separately to represent the total passage population size within each year.

Minimal staging duration and site fidelity

Minimal staging duration (hereafter MSD) was calculated as the time interval between the first and the last resighting of an individual in the study area. We calculated average MSD for both groups of Sanderlings in two separate years. Because individuals may already be present in the study area before the first observation and could be still present after the last, MSD is an underestimation of the true stopover duration (Schaub *et al.* 2001, Choquet *et al.* 2014). We compared MSD between the two different categories of Sanderlings, assuming an equal resighting probability of birds in both classes. Differences in MSD between categories and the first (arrival date) and last date (departure date) at which an individual was observed per group per year were tested using a Kruskal-Wallis (hereafter K-W) test because the data were not normally distributed. We compared the return rates of both categories between 2013 and 2014 as a measure of site fidelity to our study area, using a Pearson's χ^2 -test.

RESULTS

In total, we collected resighting histories for 340 individuals that were assigned to a moult strategy. In 2013 and 2014, respectively 152 (50%) and 89 (55%) of the marked individuals were moulting their primary wing feathers. At least 134 (43%) individuals that were observed in 2013 were also present in 2014. The return

rate to the study area differed significantly between the categories, with 54% of the moulting and 29% of the non-moulting individuals returning ($\chi^2 = 19.29$, $df = 1$, $P < 0.001$).

Wing moult and winter location

With an average of 64.0 ± 2.5 g (means are shown with SE), non-moulting Sanderlings were significantly heavier than the moulting individuals (52.0 ± 1.8 g) at the moment of catch (K-W test, $H_1 = 410.9$, $P < 0.001$; Figure 2).

Of the 464 Sanderlings that were caught and colour-ringed in the Dutch Wadden Sea in 2007–2014, 263 (56%) were in wing moult and 201 were not. Resightings in winter of 142 moulting individuals (54% of the 263 moulting individuals) confirmed that they all wintered north of the Sahara (Figure 3A). In contrast, the 19 non-moulting Sanderlings (9% of this category) that were observed in winter were all along the African coastline south of the Sahara (Figure 3B).

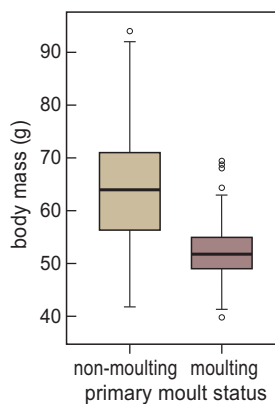


Figure 2. Body mass of 346 moulting and 321 non-moulting Sanderlings caught during southward migration (20 July – 27 September) in the Dutch Wadden Sea (Simonszand, Griend, Richel and De Hengst; see Figure 1) from 2004–2014. Box plots show median values (solid horizontal line), 50th percentile values (box outline), 90th percentile values (whiskers) and outliers (open circles).

Stopover persistence

The model selection resulted in a single most parsimonious model with an interaction effect of moult category and time on daily stopover persistence and an interaction effect of year and time on two-daily resighting probability (Table 2). There was not much support for models that contained an effect of year on stopover persistence. In both years, moulting Sanderlings showed decreasing stopover persistence over

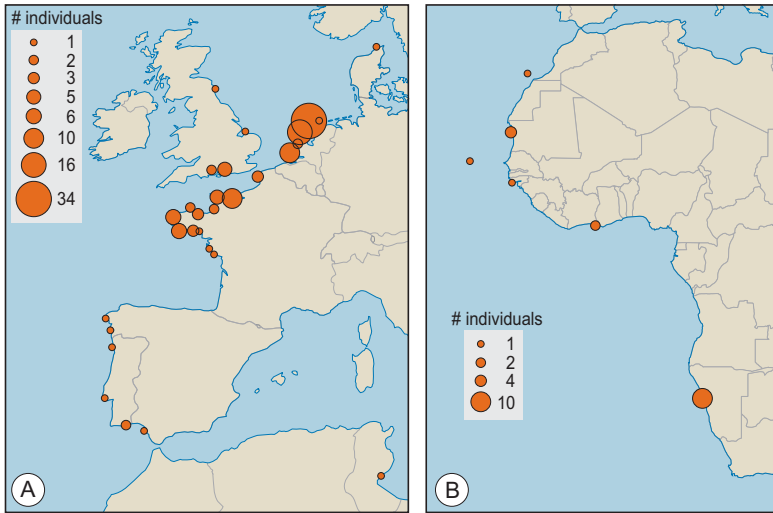


Figure 3. Winter locations of Sanderlings classified as (A) mouling in the Wadden Sea ($n = 142$) and (B) not mouling in the Wadden Sea ($n = 19$).

time, especially toward the end of the season (Figure 4A). This indicates that most mouling Sanderlings had left the study area towards the end of the study period (Table 3). In contrast to the mouling individuals, the stopover persistence of non-mouling Sanderlings

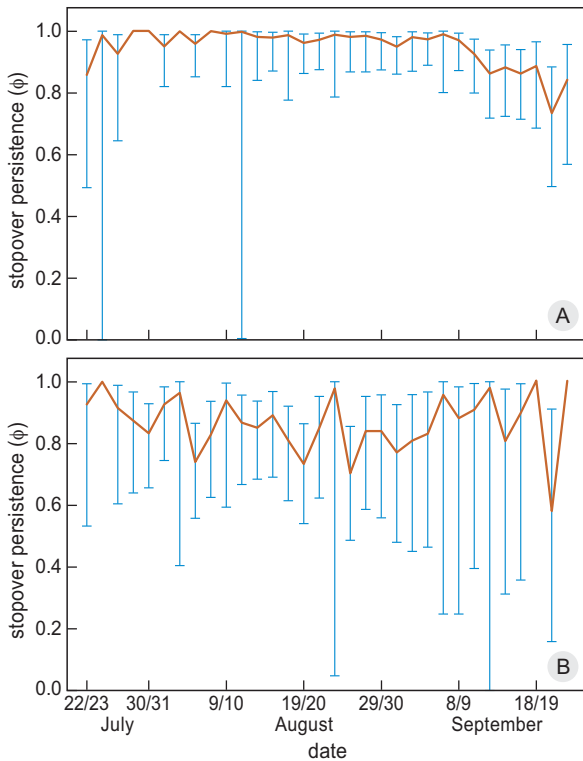


Figure 4. Estimated stopover persistence of (A) mouling and (B) non-mouling Sanderlings staging in the western Dutch Wadden Sea during southward migration. Error bars indicate 95%-confidence intervals.

Table 2. Model selection for stopover persistence of colour-ringed Sanderlings staging at Griend in the western Dutch Wadden Sea in 2013 and 2014, with respect to date. Indicated are the number of parameters in the model (NP) deviance, (Q)AICc, $\Delta(Q)AICc$ and (Q)AICc weight. Only the 20 most parsimonious models are shown. Symbols in the listed models indicate moult class – or group (g) –, time (t), year (y) or constant (.) effects (between brackets) on stopover persistence φ and two-daily resighting probability p .

Model	NP	Deviance	QAICc	$\Delta QAICc$	QAICc weight
$\varphi(g \times t) p(y \times t)$	116	3112.1	4272.4	0.0	0.99
$\varphi(g \times y \times t) p(y \times t)$	147	3056.1	4282.3	10.0	0.01
$\varphi(g \times t) p(g \times y \times t)$	158	3051.6	4301.5	29.1	0.00
$\varphi(g \times y \times t) p(g \times y)$	90	3197.7	4303.4	31.0	0.00
$\varphi(g \times t) p(g \times y \times t)$	61	3263.8	4309.4	37.0	0.00
$\varphi(g \times y) p(g \times y \times t)$	114	3159.0	4315.1	42.7	0.00
$\varphi(g \times y \times t) p(g \times y \times t)$	191	3001.1	4322.7	50.3	0.00
$\varphi(g \times t) p(t)$	88	3232.2	4333.7	61.4	0.00
$\varphi(g \times t) p(g)$	59	3292.5	4334.0	61.6	0.00
$\varphi(g \times y \times t) p(t)$	119	3168.7	4335.3	63.0	0.00
$\varphi(g \times y \times t) p(g)$	91	3229.2	4337.0	64.6	0.00
$\varphi(g \times t) p(y)$	59	3295.8	4337.3	64.9	0.00
$\varphi(g \times y \times t) p(y)$	91	3231.5	4339.3	66.9	0.00
$\varphi(g \times y) p(t)$	36	3350.1	4344.5	72.2	0.00
$\varphi(g \times y) p(g \times y)$	8	3406.7	4344.6	72.2	0.00
$\varphi(g \times y) p(.)$	58	3313.3	4352.8	80.4	0.00
$\varphi(g \times y) p(g \times y)$	114	3205.1	4361.2	88.8	0.00
$\varphi(g \times y \times t) p(.)$	89	3258.3	4361.9	89.5	0.00
$\varphi(g \times y \times t) p(g \times t)$	148	3142.5	4370.9	98.6	0.00
$\varphi(t) p(y \times t)$	91	3454.2	4386.1	113.7	0.00

Table 3. Median dates and interquartile range of arrival and departure dates of Sanderlings for different moult categories based on observed minimal staging durations.

	Arrival date		Departure date	
	Median date	Interquartile range	Median date	Interquartile range
Moulting individuals 2013	8 Aug	30 Jul – 18 Aug	9 Sep	3 Sept – 20 Sept
Non-moulting individuals 2013	5 Aug	26 Jul – 14 Aug	14 Aug	5 Aug – 22 Aug
Moulting individuals 2014	6 Aug	30 Jul – 15 Aug	12 Sep	8 Sept – 24 Sept
Non-moulting individuals 2014	6 Aug	30 Jul – 12 Aug	15 Aug	5 Aug – 21 Aug

varied strongly between two-day intervals (Figure 4B). Almost all non-moulting Sanderlings left the study area by mid-September, resulting in unreliable estimates with large confidence intervals from the second week of September onwards (Figure 4B; Table 3).

Minimal staging duration, migration phenology

In both years, the MSD of moulting Sanderlings (on average in 2013: 32.3 ± 1.6 d, in 2014: 37 ± 2.0 d) was significantly longer than that of non-moulting Sanderlings (on average in 2013: 9 ± 0.6 d, in 2014: 10 ± 1.2 d; K-W test $H_1 = 161.63$, $P < 0.001$; Figure 5). The MSD did not differ between years within the two different moult groups ($H_1 = 3.39$, $P = 0.21$ for moulting birds, $H_{27} = 1.41$, $P = 0.24$ for non-moulting birds; Figure 5). Arrival dates did not differ between birds using either moult strategy in either 2013 ($H_1 = 43.77$, $P = 0.18$) or 2014 ($H_1 = 40.14$, $P = 0.73$; Table 3). Departure dates, however, significantly differed between the two categories. Non-moulting individuals

departed about one month earlier than the moulting individuals, both in 2013 ($H_1 = 143.93$, $P < 0.001$) and in 2014 ($H_1 = 75.43$, $P < 0.001$; Table 3).

Passage population size

The numbers of Sanderlings counted at high tide peaked on 2 August 2013 with 9500 individuals and on 16 August 2014 with 8900 individuals (Figure 6). The estimated passage population size was nearly three times as large as the peak counts, with 27,546 (95%-CI: 22,739–41,448) individuals using the site in 2013 and 22,574 (95%-CI: 16,436–46,114) in 2014.

DISCUSSION

Moulting and non-moulting Sanderlings did not differ in their date of arrival in the Wadden Sea, but moulting individuals stayed longer than those that postponed primary moult until their arrival in wintering areas south of the Sahara. Moulting individuals emigrated significantly later than non-moulting individuals. Non-moulting Sanderlings used the area primarily in the first half of August and, with a minimal staging duration (MSD) of on average 9–12 days, stayed for a much shorter period than individuals that moulted their wing feathers in the Wadden Sea and stayed for on average at least 32–36 days.

Shorebirds with extensive wintering ranges, from northern temperate areas to the southern limits of continents in the Southern Hemisphere, show considerable intra-specific variation in both the onset and the duration of primary moult (e.g. Underhill 2003, Summers *et al.* 2004, Summers *et al.* 2010, Dietz *et al.* 2015). Individuals wintering in northern temperate regions typically complete their wing moult in autumn, whereas individuals wintering in the southern hemisphere moult later and the completion of moult takes considerably longer (Remisiewicz *et al.* 2011, Dietz *et al.* 2015). In southern Africa, complete wing moult in

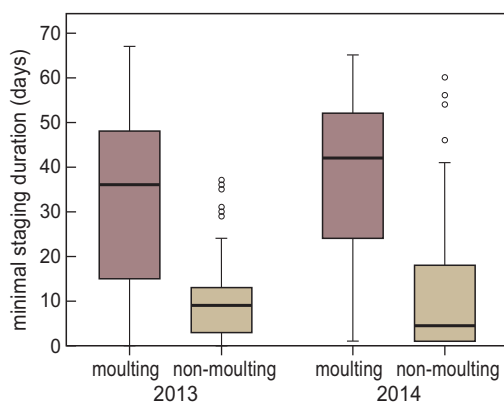


Figure 5. Minimal staging duration of Sanderlings during southward migration in the western Dutch Wadden Sea. Box plots show median values (solid horizontal line), 50th percentile values (box outline), 90th percentile values (whiskers) and outliers (open circles).

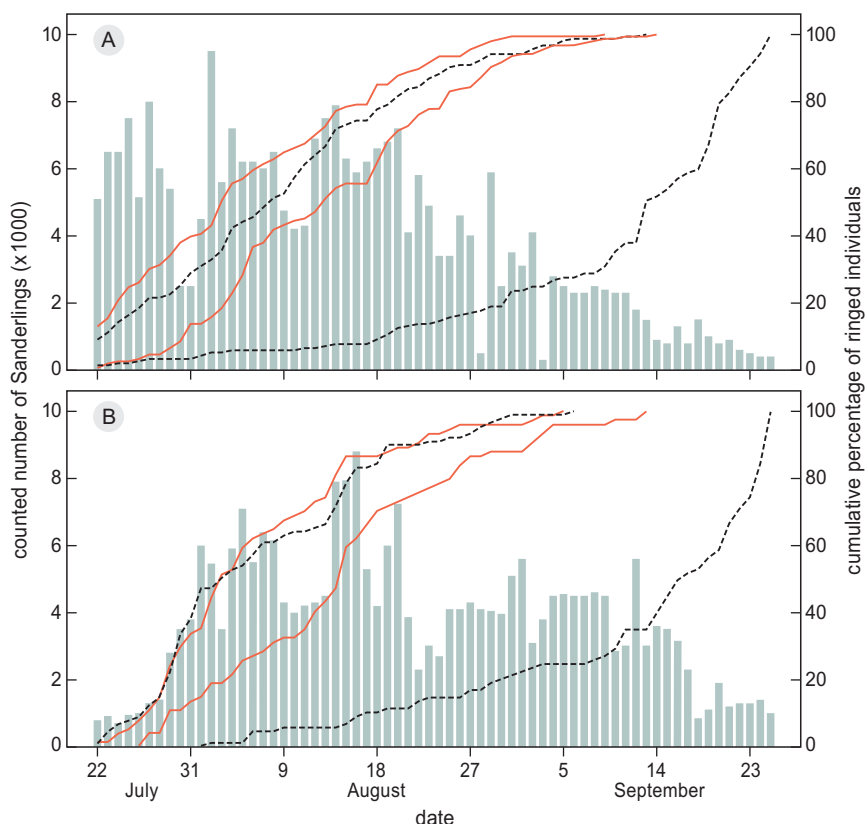


Figure 6. Migration phenology of Sanderlings during southward migration in the western Dutch Wadden Sea in 2013 (A) and 2014 (B). Bars represent the daily Sanderlings counts on the high tide roosts of Griend. Solid red lines represent the cumulative percentage of first (left line) and last (right line) sightings from non-moulting individuals, and dashed black lines represent these cumulative percentages for moulting individuals.

Sanderlings takes 98 days between early November and mid-February (Underhill 2003). Primary moult is thus completed considerably later in southern Africa compared with the Wadden Sea. Unlike individuals moulting in the tropics, Sanderlings moulting in the Wadden Sea might find it difficult to complete moult without compromising feather quality before the ambient temperature decreases and food resources become limited, a selection pressure that was earlier invoked to explain the relatively fast and compressed wing moult of Red Knots *Calidris canutus islandica* in the Wadden Sea (cf. Dietz *et al.* 2013). To our knowledge, no precise estimates of wing moult duration of Sanderlings in the Wadden Sea or other temperate regions are available, although Boere (1976), based on three individuals that were captured twice within an autumn, estimated it to take at least 50 days. Based on the relationship between latitude and mass on primary moult duration in shorebirds, Sanderlings are expected to complete primary moult in c. 65 days in the Northern Hemisphere (Dietz *et al.* 2015).

Moulting Sanderlings stayed in our study area for a minimum of 32–36 days, which is only half the time needed to complete wing moult. However, given that MSD is by definition an underestimation of true staging duration (see Schaub *et al.* 2001), we remain uninformed about how long Sanderlings actually stayed in our study area near Griend, or on the Wadden Sea mudflats in general. Individuals that moved away from Griend to other areas within the Wadden Sea without returning, or that stayed in the study area after the end of our observations, will have caused differences between minimal and true staging durations. Sanderlings classified as moulting in the Wadden Sea are typically reported outside the Wadden Sea from mid-October onwards (JR unpubl. data). Given the median arrival date in the first week of August, the moulting birds would have stayed for c. 70 days in the Wadden Sea, which is twice as long as the average MSDs. The actual length of stay, and thus whether Sanderlings complete primary moult in the Wadden Sea, remains uncertain.

None of the Sanderlings showing primary wing moult weighed more than 70 g. This is consistent with the assumption that non-moulting individuals are the longer-distance migrants that winter along the coast of western Africa from Mauritania to Namibia (Boere 1976). Their high body masses upon capture compared to moulting individuals suggests fuelling for long non-stop migratory flights. Sanderlings weighing 80 g or more are maximally fuelled for migration and have the potential to fly non-stop for more than 2000 km (Gudmundsson *et al.* 1991). Sandpipers may migrate southward relatively early to stay ahead of migrating Peregrines *Falco peregrinus*; Lank *et al.* 2003, Ydenberg *et al.* 2007). Perhaps, non-moulting Sanderlings postpone wing moult and stay shortly in the Wadden Sea to avoid being heavy and thus vulnerable (Dietz *et al.* 2007) to predation from Peregrines that arrive in September (van den Hout 2009).

The number of Sanderlings that spend the winter on the mudflats near Griend, or indeed anywhere on the Dutch Wadden Sea mudflats, is small (van Turnhout & van Roomen 2008). Some of the moulting individuals in our study spent the winter on the North Sea beaches of Dutch Wadden Sea islands only a few kilometres away from Griend, but other individuals wintered on beaches elsewhere in Europe or even northern Africa. We can only speculate why Sanderlings wintering in Europe leave the Wadden Sea after the completion of their wing moult. It may be related to their prey. We observed Sanderlings to predominantly forage on juvenile Brown Shrimp *Crangon crangon*. Shrimps grow rapidly and move to the deep gullies from October–November onwards (Kuipers & Dapper 1981), where they are inaccessible to foraging Sanderlings. Also, the several small polychaetes which are eaten by Sanderlings (Reneerkens *et al.* 2009, Grond *et al.* 2015) bury deeper in the colder winter and become much less accessible to Sanderling (Zwarts & Wanink 1993). The time that Brown Shrimps leave the mudflats for the deeper gullies (October–November; Kuipers & Dapper 1981) coincides with the period of migration of Sanderling from the Wadden Sea, as indicated by the increasing number of Sanderlings along the Dutch North Sea beaches (van Turnhout & van Roomen 2008), and by the observations of colour-ringed Sanderlings elsewhere along European coasts after primary moult in the Wadden Sea from mid-October onwards (JR unpubl. data).

Long distance migrants have been shown to have a high philopatry to stopover areas (Catry *et al.* 2004). We demonstrate that the inter-annual return rates differ between moulting and non-moulting individuals.

Sanderlings that moult their primary feathers in the Wadden Sea had an inter-annual return rate similar to individuals on a spring stop-over site in Iceland (Gudmundsson & Lindström 1992). The different return rates between moult categories may hint at biological causes for differences in philopatry depending on moult and/or migration strategies, inviting further scrutiny. However, we cannot rule out that the differences are (also) caused by different sighting probabilities (non-moulting birds may have had a lower probability to be re-sighted due to their shorter stays in the study area) and/or annual survival between Sanderlings with different moult strategies.

Based on the peak counts in 2013 (9500/200,000) and 2014 (8900/200,000), 4–5% of the estimated flyway population in 2014/2015 (van Roomen *et al.* 2015) used Griend and the surrounding mudflats. However, corrected for the turnover of individuals, almost three times as many individuals made use of the western Dutch Wadden Sea. The accuracy of these estimates depends on the length of the study period, and the accuracy of the counts. We are confident that the counts on Griend were accurate and precise because the roost could be observed from an elevated dune at a short distance (<20 m) from the roost. However, because Sanderlings did not exclusively use Griend to roost but also used Richel to an unknown extent, we will have missed an unknown proportion of birds using the area.

Furthermore, our survey would ideally have taken place throughout the complete migration period of Sanderling. In 2013, we counted 5100 Sanderlings on the first day of our survey (22 July), indicating that the passage had already started. Also, Sanderlings were still present near Griend when we finished our observations and counts in early October. It should also be noted, that the percentage of the total flyway population that used Griend (11–14% in either year) depends on the accuracy of the flyway population estimates. Those are likely conservative because they are based on estuarine sites, while Sanderlings are known to also use non-estuarine habitats (Burton *et al.* 2008).

A comparison of our counts with historical peak count data from Griend in August–September indicates that the occurrence of Sanderlings on Griend and the surrounding mudflats is a recent phenomenon (Piersma 2006). The largest number reported near Griend between 1974 and 1987 was 450 individuals only in early October 1986 (Veen & van de Kam 1988). Monthly peak counts in August–September between 1995 and 2006 resulted in a maximum estimate of c. 6000 Sanderlings in the entire Dutch Wadden Sea (van

Turnhout & van Roomen 2008). Our peak counts of 8900–9500 on Griend, suggest that the increase in the Wadden Sea is large and still ongoing.

The Sanderling population of the East Atlantic flyway has increased rapidly during the last decades (van Roomen *et al.* 2015) and this will be reflected in the numbers at staging sites, such as the Wadden Sea, if the carrying capacity has not been reached (cf. Ntiamao-Baidu *et al.* 2014). That the total flyway population increased three-fold since the early 1980s, whereas peak numbers on Griend increased approximately 18-fold, suggests that local conditions near Griend may also have become (relatively) more favourable for Sanderlings. Future studies should examine why Griend has become increasingly attractive for staging Sanderlings.

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REFERENCES

- Alerstam T. & Lindström Å. 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E. (eds) *Bird migration: the physiology and ecophysiology*. Springer, Berlin, p. 331–351.
- Atkinson P.W., Austin G.E., Rehfisch M.M., Baker H., Cranswick R., 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.
- Baker A.J., González P.M., Piersma T., Niles L.J., Nascimento I.L.S., Atkinson P.W., Clark N.A., Minton C.D.T., Peck M.K. & Aarts G. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proc. R. Soc. Lond. B* 271: 875–882.
- Boere G.C. 1976. The significance of the Dutch Wadden Sea in the annual life-cycle of arctic, subarctic and boreal waders. Part 1. The function as a moulting area. *Ardea* 64: 210–291.
- Boere G.C. & Piersma T. 2012. Flyway protection and the predicament of our migrant birds: A critical look at international conservation policies and the Dutch Wadden Sea. *Ocean Coast. Manage.* 68: 157–168.
- Buehler D.M. & Piersma T. 2008. Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Phil. Trans. R. Soc. Lond. B* 363: 247–266.
- Burnham K. & Anderson D. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. 2nd ed. Springer, New York.
- Burton N.H.K., Rehfisch M.M., Stroud D.A. & Spray C.J. 2008. The European non-estuarine coastal waterbird survey. *Int. Wader Stud.* 18. International Wader Study Group, Thetford, United Kingdom.
- Caizergues A., Guillemain M., Arzel C., Devineau O., Leray G., Pilvin D., Lepley M., Massez G. & Schricke V. 2011. Emigration rates and population turnover of teal *Anas crecca* in two major wetlands of western Europe. *Wildl. Biol.* 17: 373–382.
- Catry P., Encarnação V., Araújo A., Fearon A., Armelin M. & Delaloye P. 2004. Are long-distance migrant passerines faithful to their stopover sites? *J. Avian Biol.* 35: 170–181.
- Chernetsov N. 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. *J. Ornithol.* 147: 185–191.
- Choquet R., Lebreton J.D., Gimenez O., Reboulet A.M. & Pradel R. 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating CAPTURE-RECAPTURE data. *Ecography* 32: 1071–1074.
- Choquet R., Béchet A. & Guédon Y. 2014. Applications of hidden hybrid Markov/semi-Markov models: from stopover duration to breeding success dynamics. *Ecol. Evol.* 4: 817–826.
- Conklin J.R., Reneerkens J., Verkuil Y.I., Tomkovich P., Palsbøll P.J. & Piersma T. 2016. Low genetic differentiation between Greenlandic and Siberian Sanderling populations implies a different phylogeographic history than found in Red Knots. *J. Ornithol.* 157: 325–332.
- Delany S., Dodman T., Stroud D. & Scott D. 2009. *An atlas of wader populations in Africa and Western Eurasia*, 1st ed. Wetlands International, Wageningen.
- Dietz M.W., Piersma T., Hedenström A. & Brugge M. 2013. Intraspecific variation in avian pectoral muscle mass: constraints on maintaining manoeuvrability with increasing body mass. *Funct. Ecol.* 21: 317–326.
- Dietz M.W., Rogers K.G. & Piersma T. 2013. When the seasons don't fit: Speedy molt as a routine carry-over cost of reproduction. *PLoS ONE* 8, e53890.
- Dietz M.W., Rogers K.G., Gutiérrez J.S. & Piersma T. 2015. Body mass and latitude both correlate with primary moult duration in shorebirds. *Ibis* 157: 147–153.
- Drent R., Both C., Green M., Madsen J. & Piersma T. 2003. Pay-offs and penalties of competing migratory schedules. *Oikos* 103: 274–292.
- Eriksson B.K., van der Heide T., van de Koppel J., Piersma T., van der Veer H.W. & Olff H. 2010. Major changes in the ecology of the Wadden Sea: human impacts, ecosystem engineering and sediment dynamics. *Ecosystems* 13: 752–764.

- Frederiksen M., Anthony D.F., Madsen J. & Colhoun K. 2001. Estimating the total number of birds using a staging site. *J. Wildl. Manage.* 65: 282–289.
- Gillings S., Atkinson P.W., Baker A.J., Bennett K.A., Clark N.A., Cole K.B., González P.M., Kalasz K.S., Minton C.D.T., Niles L.J., Porter R.C., de Lima Serrano I., Sitters H.P. & Woods J.L. 2009. Staging behavior in Red Knot (*Calidris canutus*) in Delaware Bay: implications for monitoring mass and population size. *Auk* 126: 54–63.
- Grond K., Ntiamao-Baidu Y., Piersma T. & Reneerkens J. 2015. Prey type and foraging ecology of Sanderlings *Calidris alba* in different climate zones: are tropical areas more favourable than temperate sites? *PeerJ* 3: e1125.
- Gudmundsson G.A. & Lindström Å. 1992. Spring migration of Sanderlings *Calidris alba* through SW Iceland: wherefrom and whereto? *Ardea* 80: 315–326.
- Gudmundsson G.A., Lindström Å. & Alerstam A. 1991. Optimal fat loads and long-distance flights by migrating Knots *Calidris canutus*, Sanderlings *C. alba* and Turnstones *Arenaria interpres*. *Ibis* 133: 140–152.
- Harrison X.A., Blount J.D., Inger R., Norris D.R. & Bearhop S. 2011. Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.* 80: 4–18.
- Kersten M. & Smit C.J. 1984. The Atlantic coast of Morocco. In: Evans P.R., Goss-Custard J.D. & Hale W.G. (eds) *Coastal waders and wildfowl in winter*. Cambridge University Press, Cambridge, pp. 276–292.
- Kuipers B.R. & Dapper R. 1981. Production of *Crangon crangon* in the tidal zone of the Dutch Wadden Sea. *Neth. J. Sea Res.* 15: 33–53.
- Lank D.B., Butler R.W., Ireland J. & Ydenberg R.C. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 2: 303–319.
- 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.
- Newton I. 2006. Can conditions experienced during migration limit the population levels of birds? *J. Ornithol.* 147: 146–166.
- Ntiamao-Baidu Y., Nuoh A.A., Reneerkens J. & Piersma T. 2014. Population increases in non-breeding Sanderlings in Ghana indicate site preference. *Ardea* 102: 131–137.
- Piersma T. 1987. Hop, skip or jump? Constraints on migration of arctic waders by feeding, fattening, and flight speed. *Limosa* 60: 185–194. (in Dutch with English summary)
- Piersma T. 2006. Waarom nonnetjes samen klaarkomen en andere wonderen van het wad. Utrecht: KNNV Uitgeverij.
- Piersma T. & Lindström Å. 2004. Migrating shorebirds as integrative sentinels of global environmental change. *Ibis* 146: S61–S69.
- Piersma T., Hoekstra R., Dekinga A., Koolhaas A., Wolf P., Battley P. & 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.
- Piersma T., Lok T., Chen Y., Hassell C.J., Yang H.-Y., Boyle A., Slaymaker M., Chan Y.-C., Melville D.S., Zhang Z.-W. & Ma Z. 2016. Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. *J. Appl. Ecol.* 53: 479–490.
- Prater A.J., Marchant J.H. & Vuorinen J. 1977. Guide to the identification and ageing of Holarctic waders. British Trust for Ornithology, Tring.
- Ramsar Convention Bureau. 1988. Convention on wetlands of international importance especially as waterfowl habitat. Proc. 3rd meeting of the conference on contracting parties, Regina, Canada, 1987. Ramsar Convention Bureau, Gland, Switzerland.
- Rappoldt C., Kersten M. & Smit C. 1985. Errors in large-scale shorebird counts. *Ardea* 73: 13–24.
- Remisiewicz M. 2011. The flexibility of primary moult in relation to migration in Palearctic waders – an overview. *Wader Study Group Bull.* 118: 141–152.
- Reneerkens J., Benhoussa A., Boland H., Collier M., Grond K., Günther K., Hallgrimsson G.T., Hansen J., Meissner W., de Meulenaer B., Ntiamao-Baidu Y., Piersma T., Poot M., van Roomen R.W., Summers P.S., Tomkovich P.S. & Underhill L.G. 2009. Sanderlings using African-Eurasian flyways: a review of current knowledge. *Wader Study Group Bull.* 116: 2–20.
- Reneerkens J., Loonstra J., Spaans B. & Piersma T. 2012. Large numbers of Sanderling *Calidris alba* from all directions near Griend in the Dutch Wadden Sea in late summer of 2011. *Limosa* 85: 73–79. (in Dutch with English summary)
- Schaub M., Pradel R., Jenni L. & Lebreton J.D. 2001. Migrating birds stop over longer than usually thought: An improved capture-recapture analysis. *Ecology* 82: 852–859.
- Sheehy J., Taylor C.M. & Norris D.R. 2011. The importance of stopover habitat for developing effective conservation strategies for migratory animals. *J. Ornithol.* 152: 161–168.
- Stroud D.A., Davidson N.C., West R., Scott D.A., Haanstra L., Thorup O., Ganter B. & Delany S. 2004. Status of migratory wader populations in Africa and Western Eurasia in the 1990s. *Int. Wader Studies* 15.
- Summers R.W., Underhill L.G., Waltner M. & Whitelaw D.A. 1987. Population, biometrics and movements of the Sanderling *Calidris alba* in southern Africa. *Ostrich* 58: 24–39.
- Summers R.W., Underhill L.G., Nicoll M., Strann K.-B. & Nilsen S.Ø. 2004. Timing and duration of moult in three populations of Purple Sandpipers *Calidris maritima* with different moult/migration patterns. *Ibis* 146: 394–403.
- Summers R.W., Underhill L.G., Waltner M. & Swann R.L. 2010. Differences in biometrics and moult of non-breeding Red Knots *Calidris canutus* in southern Africa and Scotland reflect contrasting climatic conditions. *Ibis* 152: 127–135.
- Swaddle J.P. & Witter M.S. 1997. The effects of molt on the flight performance, body mass and behaviour of European starlings (*Sturnus vulgaris*): an experimental approach. *Can. J. Zool.* 75: 1135–1146.
- Underhill L.G. 2003. Within ten feathers: primary moult strategies of migratory waders (Charadrii). In: Berthold P., Gwinner E. & Sonnenschein E. (eds) *Avian migration*. Springer, Berlin, pp. 187–197.
- Underhill L.G. & Prýs-Jones R.P. 1994. Index numbers for waterbird populations. I. Review and methodology. *J. Appl. Ecol.* 31: 463–480.
- van den Hout P.J. 2009. Mortality is the tip of an iceberg of fear: Peregrines *Falco peregrinus* and shorebirds in the Wadden Sea. *Limosa* 82: 122–133. (in Dutch with English summary)
- van den Hout P.J. & Piersma T. 2013. Low-tide distribution of shorebirds in the Wadden Sea. *Limosa* 86: 25–30. (in Dutch with English summary)

- van de Kam J., Ens B.J., Piersma T. & Zwarts L. (eds) 2004. Shorebirds: an illustrated behavioural ecology. KNNV Publishers, Utrecht.
- van Turnhout C. & van Roomen M. 2008. Trends and phenology of Sanderling *Calidris alba* in the Netherlands. *Limosa* 81: 1–10. (in Dutch with English summary)
- van Roomen M., Nagy S., Foppen R., Dodman T., Citegetse G. & Ndiaye A. 2015. Status of coastal waterbird populations in the East Atlantic Flyway. With special attention to flyway populations making use of the Wadden Sea. Programma Rijke Waddenzee, Leeuwarden.
- Veen J. & van de Kam J. 1988. Griend, vogeileiland in de Waddenzee. Natuurmonumenten, 's- Graveland, The Netherlands.
- Verkuil Y.I., Wijmenga J.J., Hooijmeijer J.C.E.W. & Piersma T. 2010. Spring migration of Ruffs *Philomachus pugnax* in Fryslân: estimates of staging duration using resighting data. *Ardea* 98: 21–33.
- White G.C. & Burnham K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120–139.
- Warnock N. 2010. Stopping vs. staging: The difference between a hop and a jump. *J. Avian Biol.* 41: 621–626.
- Ydenberg R.C., Butler R.W. & Lank D.B. 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing and molt of long-distance migrants. *J. Avian Biol.* 38: 523–529.
- Zwarts L. & Wanink J.H. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Neth. J. Sea Res.* 31: 441–476.

SAMENVATTING

De Waddenzee is voor veel steltlopers een belangrijk gebied om te ruïen en om op te vetten tijdens de trek. In de eerste jaren van de georganiseerde tellingen in de Waddenzee werden nog niet veel Drieteenstrandlopers *Calidris alba* geteld. Sinds het begin van deze eeuw lijkt de Waddenzee echter voor deze soort een belangrijke functie te vervullen tijdens de voor- en najaarstrek, een ontwikkeling die wellicht samenhangt met de toename van de populatie Drieteenstrandlopers die de Oost-Atlantische trekroute gebruikt. Aan de hand van waarnemingen van gekleurde Drieteenstrandlopers bij Griend in de westelijke Waddenzee hebben we in 2013 en 2014 vogels die tijdens de najaarstrek hun vleugels in de Waddenzee ruiden, vergeleken met vogels die hier niet ruiden. Waarnemingen uit de winter en hun zwaardere gewicht bevestigden dat de niet ruiende vogels slechts opvetten in de Waddenzee voor verdere trek naar de Afrikaanse kust ten zuiden van de Sahara. We waren vooral benieuwd naar eventuele verschillen tussen beide groepen vogels in de verblijfsduur in de Waddenzee, de dagelijkse kans dat vogels uit het onderzoeksgebied vertrokken en de jaarlijkse trouw aan het westelijk deel van de Nederlandse Waddenzee. Corrigerende voor het verloop, maakten we tenslotte een schatting van het totaal aantal Drieteenstrandlopers dat in beide jaren gebruikt maakte van het gebied. Drieteenstrandlopers die in de Waddenzee hun vleugelpennen ruiden alvorens verder te trekken, verbleven daar in 2013 gemiddeld 32 dagen en in 2014 gemiddeld 36 dagen tegenover 9 respectievelijk 12 dagen voor de niet-ruiende vogels, die half september al weer waren vertrokken. Het aandeel ruiende Drieteenstrandlopers dat in het tweede onderzoeksjaar werd teruggezien in ons onderzoeksgebied, was groter dan het aandeel niet-ruiende vogels. We berekenden dat in 2013 27.546 (95% betrouwbaarheidsinterval CI: 22.739 - 41.449) en in 2014 22.574 (95% CI: 16.436- 46.114) Drieteenstrandlopers gebruik hebben gemaakt van dit deel van de Waddenzee. Dat is 11–14% van de totale populatie Drieteenstrandlopers die gebruik maakt van de Oost-Atlantische trekroute. Het westelijk deel van de Nederlandse Waddenzee, en met name het eiland Griend en omliggende wadplaten, is dus van groot belang voor Drieteenstrandlopers die langs deze trekroute overwinteren.

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