RESEARCH ARTICLE

Low fitness at low latitudes: Wintering in the tropics increases migratory delays and mortality rates in an Arctic breeding shorebird

Jeroen Reneerkens[1] | Tom S. L. Versluijs[1] | Theunis Piersma[1,2] |
José A. Alves[3,4] | Mark Boorman[5] | Colin Corse[6] | Olivier Gilg[7,8] |
Gunnar Thor Hallgrimsson[9] | Johannes Lang[8,10] | Bob Loos[11] |
Yaa Ntiamoa-Baidu[12,13] | Alfred A. Nuoh[12] | Peter M. Potts[14] | Job ten Horn[2] |
Tamar Lok[2]

[1]Rudi Drent Chair in Global Flyway Ecology, Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands; [2]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Utrecht University, Texel, The Netherlands; [3]DBIO & CESAM – Centre for Environmental and Marine Studies, University of Aveiro, Aveiro, Portugal; [4]South Iceland Research Centre, University of Iceland, Laugarvatn, Iceland; [5]Global Flyway Network, Swakopmund, Namibia; [6]Orkney Ringing Group, Kirkwall, UK; [7]UMR 6249 Chrono-Environnement, Université de Bourgogne Franche-Comté, Besançon, France; [8]Groupe de Recherche en Ecologie Arctique, Francheville, France; [9]Institute of Biology, University of Iceland, Reykjavik, Iceland; [10]Clinic for Birds, Reptiles, Amphibians and Fish, Working Group for Wildlife Biology, Justus Liebig University Giessen, Giessen, Germany; [11]Global Flyway Network, Texel, The Netherlands; [12]Centre for African Wetlands, University of Ghana, Legon, Accra, Ghana; [13]Department of Animal Biology and Conservation Science, University of Ghana, Legon, Accra, Ghana and [14]Farlington Ringing Group, Warsash, Southampton, UK

Correspondence
Jeroen Reneerkens
Email: jeroen.reneerkens@nioz.nl

Abstract

1. Evolutionary theories of seasonal migration generally assume that the costs of longer migrations are balanced by benefits at the non-breeding destinations.

2. We tested, and rejected, the null hypothesis of equal survival and timing of spring migration for High Arctic breeding sanderling *Calidris alba* using six and eight winter destinations between 55°N and 25°S, respectively.

3. Annual apparent survival was considerably lower for adult birds wintering in tropical West Africa (Mauritania: 0.74 and Ghana: 0.75) than in three European sites (0.84, 0.84 and 0.87) and in subtropical Namibia (0.85). Moreover, compared with adults, second calendar-year sanderlings in the tropics, but not in Europe, often refrained from migrating north during the first possible breeding season. During northward migration, tropical-wintering sanderlings occurred at their final staging site in Iceland 5–15 days later than birds wintering further north or south. Namibia-wintering sanderlings tracked with solar geolocators only staged in West Africa during southward migration.

4. The low annual survival, the later age of first northward migration and the later passage through Iceland during northward migration of tropical-wintering sanderlings, in addition to the skipping of this area during northward but not southward

Jeroen Reneerkens and Tom S. L. Versluijs contributed equally.

migration by Namibia-wintering sanderlings, all suggest they face issues during the late non-breeding season in West Africa.

5. Migrating sanderlings defy long distances but may end up in winter areas with poor fitness prospects. We suggest that ecological conditions in tropical West Africa make the fuelling prior to northward departure problematic.

KEYWORDS
demography, fitness, migration, nutrient storage strategies, site fidelity, solar geolocation, survival, timing

1 | INTRODUCTION

Seasonal movements between areas of reproduction and non-breeding are suggested to maximize the fitness of migrating animals through benefits from favourable ecological conditions encountered year-round (Lack, 1968; Newton, 2008). The overall balance between costs and benefits of migration will depend on the distance, route and timing of such movements and on the ecological conditions both *en route* and at the 'winter' destinations (hereafter 'variation in migration') (Alerstam & Lindström, 1990). Variation in migration-related traits that underlie fitness is the basis of natural selection (Pulido, 2007), but the relationships between fitness correlates and intraspecific variation in migration routines of long-distance migrants, for obvious logistic reasons, have remained understudied.

Migratory flights entail substantial energy expenditure (Drent & Piersma, 1990; Flack et al., 2016), which will increase with the distance covered (Weber & Houston, 1997). The season of migration has been shown to be associated with increased mortality in some species (Lok, Overdijk, & Piersma, 2015; Rushing et al., 2017), but not in others (Leyrer et al., 2013; Rakhimberdiev, Hout, Brugge, Spaans, & Piersma, 2015). A survival cost of migration would selectively favour shorter migration distances, unless counterbalanced by advantages in survival in the rest of the year, age at maturity or reproduction. Indeed, such costs have been suggested to be traded-off against reduced metabolic expenditure (Castro, Myers, & Ricklefs, 1992; Kersten, Bruinzeel, Wiersma, & Piersma, 1998), reduced competition (Lundberg & Alerstam, 1986; Myers, Maron, & Sallaberry, 1985) and/or higher densities of harvestable prey (Grond, Ntiamoa-Baidu, Piersma, & Reneerkens, 2015; Mathot, Smith, & Elner, 2007; Piersma, de Goeij, & Tulp, 1993) at the non-breeding destinations. Different balances between costs and benefits across the non-breeding range may maintain migration variation within breeding populations (Gilroy, 2017). Such a balance can be the result of increased survival but lower reproductive success (fewer breeding attempts or fewer offspring per attempt) with increasing migration distance (Fernández, O'Hara, & Lank, 2004) or, if there is no such trade-off, of survival (Conklin, Senner, Battley, & Piersma, 2017) and reproduction (Kentie et al., 2017) not being correlated with migration distance. Alternatively, costs and benefits of migration are not in balance and both survival and reproduction increase

(Alves et al., 2013), or decrease, with migration distance. The former might occur when the benefits of high habitat quality in the farthest destinations exceed the costs of longer migration distances. The latter could occur when subordinate individuals (juveniles, small individuals, one of the sexes) are forced by competition to settle in presumed suboptimal sites furthest away from the breeding grounds (Gauthreaux, 1982).

The trade-offs shaping migration variation are difficult to study experimentally; instead, we have to rely on observational studies (Flack et al., 2016; Lok, Overdijk, Tinbergen, & Piersma, 2011). So far, such studies have been limited to species whose entire geographical range is north of the equator, where daily energy expenditures decrease with increasing migration distances (Castro et al., 1992) and/or studies that addressed a single demographic parameter only (Ely & Meixell, 2016).

Sanderlings *Calidris alba* offer a remarkably tractable system to examine whether and how survival and/or (indicators of) reproduction are correlated with migration distance. The species breeds in the High Arctic and migrates annually to temperate and tropical coasts along a range of latitudes spanning 100° (Conklin et al., 2016; Loonstra, Piersma, & Reneerkens, 2016; Myers et al., 1985). During the non-breeding season, sanderlings from a single breeding site in northeast Greenland have been shown by individual colour-ringing to distribute themselves along the length of the entire East Atlantic Flyway (Figure 1), with annual migration distances varying sixfold between 3,700 and 22,200 km. Within their first 3–6 months of life, sanderlings, like other migratory shorebirds, settle at a shoreline winter area to which they return throughout their life (Lourenço et al., 2016; Townshend, 1985). Their large, near-continuous variation in migration distances offers the possibility to explore the factors underlying the maintenance of intra-population variation in avian migration (e.g., Castro et al., 1992).

We estimated adult apparent survival, age at first northward migration and the timing of northward passage through a final staging area for sanderlings from non-breeding sites across a huge non-breeding range between Scotland (60°N) and Namibia (25°S). Throughout the rest of the paper, we refer to these measures as fitness correlates, as they are likely to affect fitness (i.e., lifetime reproductive success): (a) adult survival determines life span and

consequently the number of breeding seasons available within a lifetime (Ricklefs, 2000), (b) the age (first year or older) at which birds embark on their first northward migration likely affects whether the first opportunity for reproduction is used (Stearns, 1992) and has multiplicative effects on fitness because young produced by yearling parents can also enter the population earlier and start producing young themselves (Oli & Zinner, 2001), and (c) timing of staging at a final spring passage site is expected to affect timing of arrival at the breeding grounds, with earlier arrival often being correlated with enhanced reproductive success (Drent, Both, Green, Madsen, & Piersma, 2003). In the High Arctic where the window of opportunities for reproduction is short (Reneerkens et al., 2016), early arrival matters as it will affect the mating and re-nesting opportunities (Morrison, Alves, Gunnarsson, Þórisson, & Gill, 2019) in facultative polygamous sanderlings (Reneerkens, Veelen, Velde, Luttikhuizen, & Piersma, 2014). As a null hypothesis, we expected no variation in the above described fitness correlates with migration distance. To help the interpretation of the patterns, we explore whether individuals of different sizes, ages and sexes are differently distributed along the flyway.

2 | MATERIALS AND METHODS

2.1 | Individual marking

Sanderlings were captured at three High Arctic breeding sites in northeast Greenland (Zackenberg, Karupelv Valley and Hochstetter Forland), at staging areas during migration (SW Iceland, N Scotland and the Dutch Wadden Sea) and in winter areas (Scotland, England, France, north Iberia, Portugal, Mauritania, Ghana and Namibia; Table 1). In total, information on 5,863 individual sanderlings captured between 1 January 1977 and 15 October 2013 (Table 1) was used for the analyses of morphology and age and sex composition. Of all 5,863 captured individuals, 5,220 (89%) were individually colour-ringed from 1 October 2006–31 March 2013 with unique combinations of two colour-rings on each tarsus and an additional flag (i.e., an extended colour-ring) on either tarsus or tibia. During the 7-year period 2007–2013, we checked the presence of colour-ringed sanderlings at all winter areas (except for Scotland and north Iberia), and in Iceland during northward staging, to estimate the three fitness correlates simultaneously (see below). The winter destination was known for 3,397 colour-ringed individuals, of which 3,148 wintered in one of the eight studied winter areas (see below). Different subsets of these 3,148 birds were used to analyse adult survival, age-dependent probability of migration to breeding areas and the timing of northward migration (see below). To analyse the timing of northward migration, we included birds from winter destinations as long as these destinations generated a minimum of ten observations of at least five birds during northward migration in Iceland. Birds caught between 1 October and 31 March across the entire winter range, whether colour-ringed or not, were used to analyse variation in morphometrics, sex and age ratio with latitude.
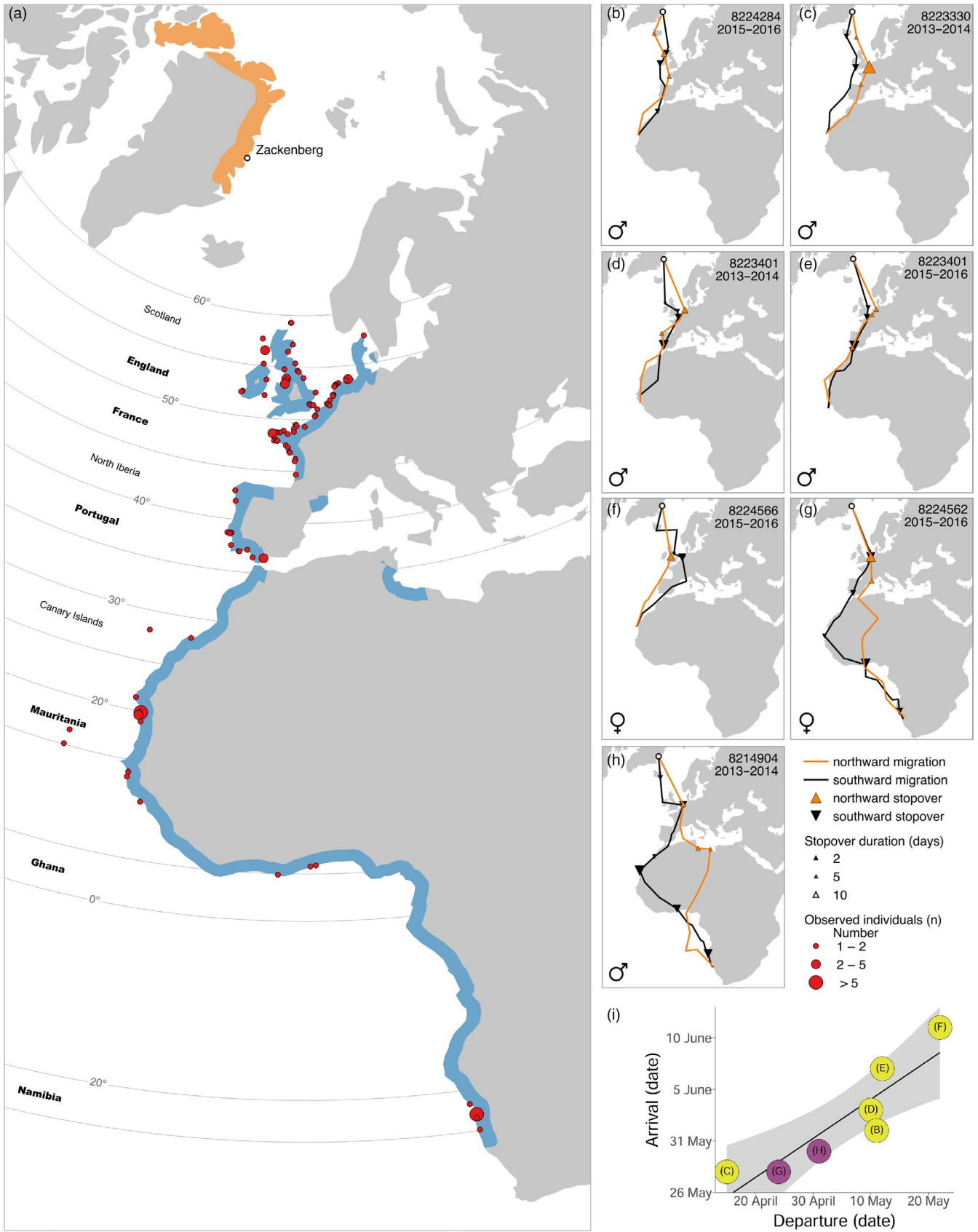
2.2 | Assignment of winter destinations and migration period

Observations from 1 October–31 March of sanderlings colour-ringed in Zackenberg were used to assess the extent of intra-population variation in migration (Figure 1a). We divided the winter distribution of Greenlandic sanderlings into sectors of 5 degrees latitude (Figure 1), which we considered separate winter areas (hereafter 'winter area') and which we named after the country or region within this winter area with most observations of colour-ringed individuals. Within most, but not all, winter areas, we caught ringed and/or observed colour-ringed sanderlings at a single main study site. We had sufficient data to compare fitness correlates of sanderlings from eight winter areas between 25°S and 60°N (named after the country or region with most resightings within these 5 degree latitude sectors: Namibia, Ghana, Mauritania, Portugal, North Iberia, France, England and Scotland; Figure 1) with distances of 1,500 to 13,000 km between breeding and winter areas (Figure S1). Individual sanderlings have been shown to be highly site faithful to their winter area, both within and between years (Lourenço et al., 2016). Therefore, we assumed that for their entire life birds used the winter area in which they were observed at least once between 1 October and 31 March. However, 99 of 3,148 individuals were observed in two different winter areas. Sixty-four of these individuals were observed in adjacent winter areas (i.e., in both England and France, or in different 5 degree latitude sectors within Ghana) and assigned to the winter area in which they were most often observed. The remaining 35 individuals were removed from all analyses as it remained uncertain whether this concerned observational errors or true movements between winter areas. Only 0.6% of all observations occurred more than 1 degree latitude north or south of an individual's average winter latitude (Figure S2).

In all our analyses below, we considered individuals to have embarked on northward migration if they were observed outside the wintering period 1 October–31 March and if they were observed at least 2 degrees latitude further north of their average winter latitude.

2.3 | Variation in sex, age and size with winter latitude

Birds were molecularly sexed based on DNA extracted from blood samples (Table 1), using primer set 2602F/2669R (van der Velde, Haddrath, Verkuil, Baker, & Piersma, 2017). The eight sanderlings deployed with a geolocator at Karupelv Valley were molecularly sexed using the 2550F/2718R primer pair (Fridolfsson & Ellegren, 1999). We determined the age ('juvenile' [first-year] or 'adult' [older than first-year]) based on plumage characteristics (Prater, Marchant, & Vuorien, 1977). We examined whether the probability of catching a female (excluding winter areas with <20 birds of known sex) or a juvenile differed between winter areas using a generalized linear mixed effect model with a binomial error structure. We included year as a random effect and compared models

with and without winter area as a fixed effect on the basis of AIC (Burnham & Anderson, 2002) using R-package lme4 (Bates, Maechler, Bolker, & Walker, 2015).

Bill lengths (*n* = 2,674) of birds captured in the winter area were measured with callipers to the nearest 0.1 mm and wing lengths (stretched with completed moult of 10th primary; *n* = 2,603) with

FIGURE 1 (a) Locations where sanderlings, individually colour-ringed at Zackenberg, a breeding site in northeast Greenland (white dot), were observed in winter (between 1 October and 31 March; red dots). The size of the red dots is indicative of the number of individuals. The dark yellow and light blue areas indicate the breeding location and the winter range of Greenlandic sanderlings (based on van de Kam, Ens, Piersma, & Zwarts, 2004, modified after Reneerkens et al., 2009). The grey horizontal lines indicate the zones of 5 degrees latitude which separate winter areas as used in our analyses. Winter areas in bold were analysed for both timing of northward migration and adult survival. (b–h) Seven tracks of six individual sanderlings equipped with a solar geolocator in northeast Greenland. Numbers in the right top of each panel are ring numbers, below which the years of southward (autumn) migration and northward (spring) migration are given. Two tracks in 2013–2014 and 2015–2016 of the same individual with ring number 8,223,401 are shown in separate, adjacent panels. Southward movements are indicated with black lines in which staging sites (stationary periods as indicated by FLightR) are downward triangles. Northward migration tracks are in orange, with upward triangles indicating staging sites. The size of the triangles indicates the length of the staging period. The sex of each tracked bird is shown in the lower left corner of each panel. Small white dots indicate the location of solar geolocator deployment and retrieval (i.e., Zackenberg, except for 8,214,904 which was ringed and recaptured at Karupelv Valley). (i) Dates at which individuals arrived in the Arctic (i.e., permanent daylight was recorded) in relation to the date of departure from the winter area for the six tracked sanderlings. Colour of the dots refers to winter areas in West Africa (yellow) or Namibia (purple) and letters in the dots to the corresponding tracks in panels b–h

rulers to the nearest mm, and their body mass was measured to the nearest gram ($n = 2,525$). Because sanderlings in Namibia start fuelling for northward migration around 1 March (Summers & Waltner, 1979), we selected body mass data collected between 1 October and 28 February only. For Namibia, we used archived data from 1971 to 1979, whereas data from other sites were collected in recent years (Table 1). We assumed that no change in size occurred over time (but see (Lank et al., 2017)). As sanderlings of different age classes are of similar size and show only a small degree of sexual dimorphism with a great overlap in size between sexes (Lourenço et al., 2016), we pooled the ages and sexes. We explored whether bill and wing length and body mass varied linearly or quadratically with winter latitude based on AIC (Burnham & Anderson, 2002). All statistical tests were performed using software R version 3.5.1 (R Core Team, 2018).

2.4 | Seasonal adult survival

We estimated seasonal apparent survival using encounter histories based on live observations of individually colour-ringed individuals that spent the non-breeding period at six of the eight winter areas along the non-breeding range of Greenlandic sanderlings (Figure 1a). Even though we did not capture and mark sanderlings in France and Namibia, we could use individuals ringed elsewhere along the flyway during migration or breeding that were later on observed in France or Namibia in winter. To avoid any bias, we started such encounter histories in the year of observation after the year of capture (where the next year starts after the summer, on 1 July). Consequently, only adult (i.e., >1 year old) birds were included in this analysis. To have sufficient number of observations of birds from all winter areas in most of the years, we selected the years 2007 to 2013 for this analysis (Table S1), which is the same period during which we observed sanderlings in Iceland to document the timing of northward migration (see below). This resulted in a dataset of 1,358 colour-ringed individuals with known winter areas (sample sizes: England 94, France 166, Portugal 158, Mauritania 415, Ghana 484 and Namibia 41). Note that the number of seasons between colour-ringing and the start of the encounter histories did not differ between individuals from the six different winter areas (Poisson GLM: an intercept-only

model was not outperformed by the model containing a main effect of winter area (ΔAIC = 0.5; Figure S3).

We estimated adult apparent survival (Φ) and resighting probability (p) using Cormack–Jolly–Seber (CJS) models (Lebreton & Burnham, 1992). To estimate survival from winter to summer (1 January to 1 July) and from summer to winter (1 July to 1 January), we used a 6-month resighting period (1 October–31 March) in an individual's winter area ('winter') and a 6-month resighting period (1 April–30 September) at sites at least 2° north of an individual's winter area ('summer'). While the resighting periods are long relative to the intervals over which survival is estimated, a simulation study showed that this does not bias, yet actually increases the precision of survival estimates (O'Brien, Robert, & Tiandry, 2005). Furthermore, the average date of observation during winter and summer (relative to the start of each season) was similar among birds from different winter areas (Figure S4). Assuming that all alive individuals from the sampled (discrete) winter areas are available for detection during the summer season (i.e., are not permanently or temporary absent), estimates of apparent survival will closely resemble true survival (hereafter referred to as 'survival'). We believe this to be a reasonable assumption, as summer resightings are made at all key spring and autumn staging sites, supplemented by many auxiliary resightings along the entire migratory range.

In the full model, both Φ and p were modelled as a function of group (i.e., winter area; g), year and season as well as their interactive effects ($\Phi_{site*year*season}$ $p_{site*year*season}$). We compared reduced parameterizations of Φ and p (see Table S2 for a complete list of parametrizations).

Models were run with program MARK (White & Burnham, 1999) using the RMark package (Laake, 2013) in program R version 3.5.1 (R Core Team, 2018). We used the Akaike's information criterion corrected for low sample size and overdispersion (QAIC$_c$, Burnham & Anderson, 2002) to select the best approximating model among the 40 candidate models. Models with ΔQAIC$_c$ <2 without uninformative parameters (Arnold, 2010) were considered as supported by the data. We assessed the goodness of fit of our data to the full model using program U-Care version 2.3.2 (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009). There was only moderate lack

TABLE 1 Number of full-grown individuals (i.e., excluding non-fledged birds in Greenland) ringed and/or molecularly sexed per study site within the range of Greenlandic sanderlings. Season during which animals were caught refers to the breeding period (B; June–10 August in Greenland), the migration period (M;1 April - 30 September outside Greenland) and in winter (W; 1 October–31 March). 'n' refers to the number of birds captured, 'n marked' refers to the number of birds that were individually colour-ringed, and 'n sexed' refers to the number of individuals that were molecularly sexed. The winter area of individuals that were caught during the breeding period or during migration may or may not be known; see the different analyses within the Materials and Methods for sample sizes per winter area. Notice that in some studied winter areas, there was no main study site where birds were caught. Hence, no study sites in France and north Iberia are mentioned in this table

Location (country)	Coordinates (decimal degrees)	Season	Period (years)	n	n marked (%)	n sexed (%)
Hochstetter Forland (Greenland)	75.16666, –19.75000	B	2010–2013	108	107 (99%)	86 (80%)
Zackenberg (Greenland)	74.46665, –20.56684	B	2007–2013	268	267 (100%)	263 (98%)
Karupelv Valley (Greenland)	72.49994, –23.99954	B	2011–2013	52	52 (100%)	27 (52%)
Sandgerði (Iceland)	64.04261, –22.71404	M	2007–2013	1,218	1,205 (99%)	560 (46%)
Sanday (Scotland)	59.24081, –2.51783	M,W	1987–2013	378	163 (43%)	167 (44%)
Wadden Sea (Netherlands)	53.24967, 5.24271	M, W	2007–2013	750	505 (67%)	285 (38%)
Hayling Island (England)	50.78336, –0.93620	M,W	2001–2013	103	103 (100%)	0 (0%)
Tagus estuary (Portugal)	38.74658, –8.97778	M,W	2008–2013	382	381 (100%)	13 (3%)
Iwik, Banc d'Arguin (Mauritania)	19.87754, –16.30356	W	2002–2013	1,483	1,302 (88%)	922 (62%)
Esiama (Ghana)	4.92577, –2.33373	M,W	2007–2013	1,136	1,135 (100%)	194 (21%)
Swakopmund (Namibia)	–22.71218, 14.52589	W	1971–1979	34	0 (0%)	0 (0%)

of fit (χ^2 = 238.83, df = 165, p < .001), which we corrected for by implementing a variance inflation factor ($\hat{c}$ = 1.45).

2.5 | Age of first northward migration

For this analysis, we used individuals that were caught and individually colour-marked during the winter season in the winter areas England (38 juveniles, 221 adults), Portugal (88 juveniles, 196 adults), Mauritania (489 juveniles, 365 adults) or Ghana (318 juveniles, 500 adults; Table S3).

Multi-event mark–recapture models (Pradel, 2005) were used to estimate the probability of migration of first-year birds relative to adult birds, while accounting for potential differences in Φ and p in relation to winter area and season. We used the same winter and summer resighting seasons as in the adult survival analysis and defined three states: (a) alive and observable, (b) alive and unobservable and (c) dead; and two events: (a) observed and (b) not observed. All individuals started in the observable state when caught during winter in their winter area. The probability to stay in the observable state between the winter in which the birds were ringed and the subsequent summer (migration and breeding) season can be interpreted as migration probability (only when birds embark

on northward migration, they can be observed during the summer season). We set this probability to one for adults, but allowed this probability to vary between sites for first-year birds (i.e., only in the first season after they were captured as juvenile). The transition probability from the unobservable to the observable state was also set to one, so that first-year individuals can only be in the unobservable (non-migratory) state in the first summer after capture, but not later on. To avoid identifiability problems, we assumed the same survival for observable and unobservable individuals and the same resighting probabilities for first-year and adult birds from the same winter area. We modelled Φ and p using the parametrization from the best supported model from the adult survival analysis described above and compared the two models in which the migration probability of first-year birds is either constant or winter area-dependent.

These models were constructed and run in program E-Surge (Choquet, Rouan, & Pradel, 2009). Since no formal goodness-of-fit tests exist for multi-event models, we assessed the goodness of fit for the CJS model Φ_{site} $p_{site*year*season}$ (ignoring the unobservable state) in U-Care (Choquet, Lebreton, et al., 2009). There was only moderate lack of fit (χ^2 = 305, df = 167, p < .001) that we corrected for ($\hat{c}$ = 1.87).

2.6 | Timing of northward migration

Iceland is the last possible staging site on northward migration before birds migrate to their Arctic breeding area. Observations in Iceland were thus considered the best possible indicator of arrival time in the Arctic breeding grounds. During northward staging in Iceland, between 1 April and 15 June, we collected 1,870 observations of 289 individuals with known winter area (Scotland: 45, England: 55, France: 114, Spain: 10, Portugal: 23, Mauritania: 19, Ghana: 14, Namibia: 7; Table S4). Observations of individuals in the year of first capture in Iceland were excluded. Multiple observations of the same individual at the same date and location were considered single observations.

Following the methods in Zuur, Ieno, Walker, Saveliev, and Smith (2009), we applied a linear mixed effect model using the nlme package in R (Pinheiro, Bates, DebRoy, & Sarkar, 2015) with date (day of year, centred around the mean) of observation in Iceland as a response variable and sex and winter area as additive fixed effects. Only 67% of the sanderlings were molecularly sexed, so we included 'unknown' as a third category next to male and female. The model with the main effects and the interaction between sex and winter area was our full model.

We first visually explored the residuals of the full model for normality and homoscedasticity. Normality and homoscedasticity assumptions for linear models were violated. However, linear regression is relatively robust against violations of normality assumptions, especially when sample sizes are large (Fitzmaurice, Laird, & Ware, 2004). Violations of homoscedasticity in the linear mixed model were dealt with by fitting different variance structures to our models (Table S5). We compared 32 full models with different combinations of variance structures and random effects. The considered random effects in our models included a random intercept for year, individual, individual nested within year and models without random effects. The variance structures used included separate variances for each winter area, sex or year (the VarIdent function in the nlme package) and model variance as an exponential function of the fitted values in general and separately for each non-breeding area, sex or year (VarExp). Last, we used a combination of model variance structures (VarComb) by combining model variance as an exponential function of the fitted values with a separate variance for each winter area (Table S5). The models were fitted using restricted maximum likelihood estimation and compared based on AIC. Models within 2 ΔAIC of the best model were considered equally parsimonious, but models with additional parameters to other strongly supported models were not considered fitting the data well because model deviance is not reduced sufficiently to overcome the penalty of 2 AIC for the additional parameters (Arnold, 2010). Four fixed effects models were considered: sex, winter area and additive and interaction effects of sex and winter area.

2.7 | Itineraries assessed by solar geolocation

We deployed solar geolocators (Intigeo-W65A9, Migrate Technology Ltd) on 44 sanderlings in June–July 2013 and 2015 at Zackenberg (26 males and 18 females) and on eight sanderlings in June–July 2013 in Karupelv Valley (2 males, 3 females and 3 of unknown sex). The geolocators were attached to a leg flag, which did not affect annual return rates (Brlík et al., 2019; Weiser et al., 2016). We retrieved eight of the 52 geolocators (15%), seven of which we were able to download data from. Six geolocators from five individuals (three males and two females) were from Zackenberg and one from Karupelv Valley (a female). Light intensity data collected by the geolocators were analysed using the FlightR package (Rakhimberdiev, Saveliev, Piersma, & Karagicheva, 2017) in R. For details about the data selection and analysis, see Appendix S1.

3 | RESULTS

3.1 | Sizes, body mass, age and sexes of sanderlings along the flyway

Bill length did not vary with latitude. Our best supported model was an intercept-only model that was not outperformed by a model with a linear effect of latitude (dAIC = 1.0) nor a quadratic effect of latitude (ΔAIC = 0.8) (Figure S5a). Wing length varied quadratically with latitude with shortest wings at lowest latitudes (ΔAIC = 4.3 compared to a model with a linear effect of latitude and ΔAIC = 4.8 compared to an intercept-only model), but with a maximum mean difference in wing length of only 1.5 mm on a mean of 126.4 mm (1.2%) between the winter areas at the highest latitudes (Scotland and Namibia). Body mass also varied quadratically with latitude (ΔAIC = 349.5 compared to a model with a linear effect of latitude and ΔAIC = 552.6 to an intercept-only model) and was lowest close to the equator (Figure S5c). The maximum mean difference in body mass between Scotland and Mauritania was 7.9 g on an overall mean of 49.7 g (16%). Thus, in contrast to wing length, the variation in body mass with latitude appears to be of biological relevance. The proportion of juveniles caught was 0.32 on average but varied across winter areas (ΔAIC = 337 compared with the intercept-only model) due to the high proportion of juveniles (0.54, 95% confidence interval: 0.42–0.68) in Mauritania (Figure S5d). The proportion of females ranged between 0.42 and 0.63 and varied between winter areas (ΔAIC = 19.9 with the intercept-only model), with the lowest proportion of females in Mauritania (0.41, 0.32–0.51), and a majority of females in Ghana (0.62, 0.54–0.70) and Scotland (0.55, 0.41–0.69) (Figure S5e).

3.2 | Lower adult survival in West Africa compared with Europe and Namibia

Adult survival probabilities differed considerably between sanderlings from the different winter areas. In the best supported model, survival probabilities differed between winter areas but not between seasons (Table 2, Figure 2a). Resighting probability was most parsimoniously explained by an interaction between winter area and time (Table 2, Figure S6). In the three European winter areas, adult sanderlings showed annual survival ranging from 0.84 in France (95% confidence interval: 0.78–0.89) and Portugal (0.74–0.91) to 0.87

Model	QAIC$_c$	ΔQAIC$_c$	w_i	K	QDeviance
Φ(winter area) p(winter area*year*season)	5,800	0	0.53	84	1,480
Φ(winter area + season) p(winter area*year*season)	5,801	1.05	0.31	85	1,479
Φ(winter area*season) p(winter area*year*season)	5,803	3.51	0.09	90	1,471
Φ(constant) p(winter area*year*season)	5,805	5.34	0.04	79	1,496
Φ(season) p(winter area*year*season)	5,806	5.84	0.03	80	1,495

TABLE 2 Models for seasonal survival of adult sanderlings at six winter areas along the East Atlantic Flyway in 2007–2013. Of 40 candidate models, only those with ΔQAIC$_c$ <65 are shown. Model parameterization is explained in Table S2. Models are ranked by ascending ΔQAICc, w_i is the model weight, and K is the number of parameters
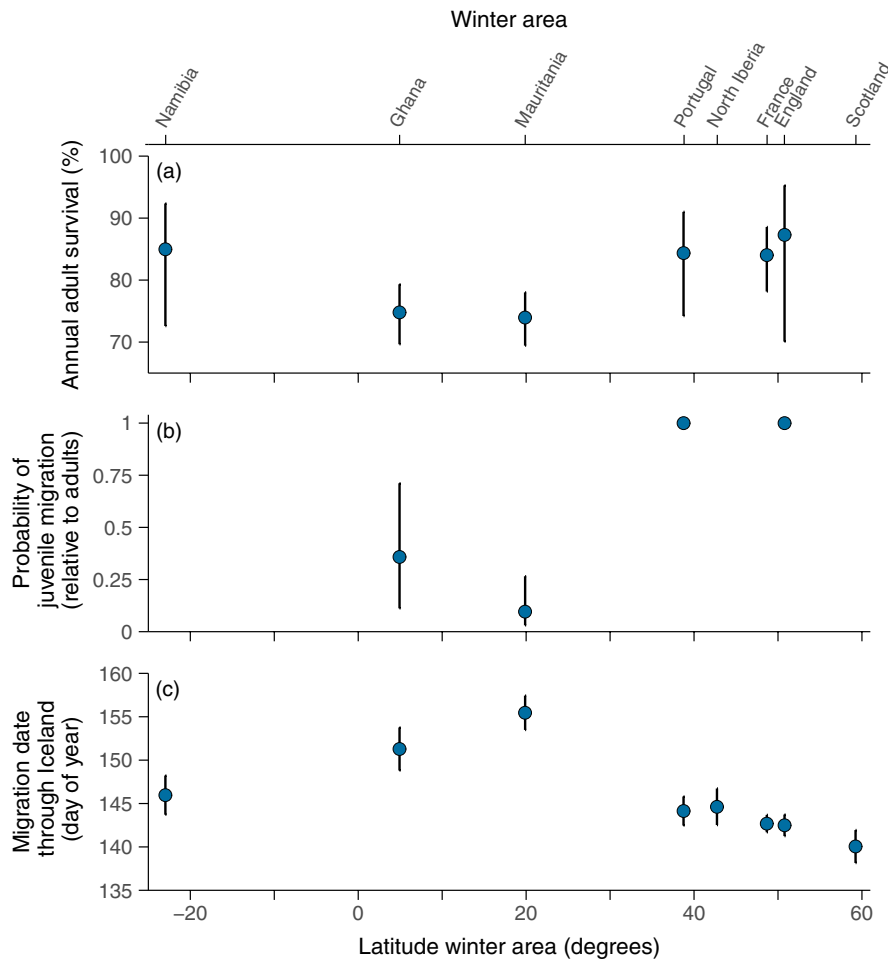

FIGURE 2 Fitness correlates for sanderlings wintering in different areas. Latitudes are those from the main study sites within winter areas. Dots are averages, and error bars indicate 95% confidence intervals. (a) Annual adult survival probabilities of six winter areas within Greenlandic sanderlings' flyway. Survival estimates are those from the most parsimonious model from a set of 40 used to explain year-round observation histories at and outside the study sites (See Materials and Methods and Table 2, Table S2). (b) Probability that juvenile relative to adult sanderlings migrated northwards in the summer following the winter during which individuals were caught and individually colour-ringed in four winter areas. Estimates are based on a multi-event mark–recapture model (see Materials and Methods). (c) Timing of northward migration through Iceland of sanderlings wintering in eight winter areas. The average timing of migration through Iceland is estimated from the most parsimonious linear mixed effects model with individual nested within year as random effects (see Materials and Methods). Day of year 140 represents 20 May. The 95% confidence intervals are based on a normal distribution for the survival probabilities and on a *t*-distribution for the migration dates

(0.70–0.95) in England, all very similar to the estimate of 0.85 (0.73–0.92) for sanderlings wintering in Namibia (Figure 2a). Annual survival probabilities of adult sanderlings at tropical latitudes in Mauritania (0.74; 0.69–0.78) and Ghana (0.75; 0.70–0.79) were considerably lower (Figure 2a).

3.3 | Sanderlings from West Africa are more likely to forego their first northward migration

The model in which migration probability of first-year birds was site-dependent was much better supported than the model with

constant migration probability ($\Delta QAIC_c = 11.38$). While juvenile and adult sanderlings from England and Portugal were estimated to be equally likely to migrate northward in the season after capture, juveniles from Ghana and especially Mauritania were much less likely to do so than adults from the same winter areas (Figure 2b). Our estimate of probability of northward migration by first-year birds is relative to adults within the same winter area. Thus, the absolute estimates may differ if the probability to embark on northward migration is not 1 for adults and differs between sites. In recent years, the resighting probabilities during summer of birds wintering in Ghana were lower than of birds from the other three winter areas (Figure S7), suggesting that also adults wintering in Ghana may have a lower probability to embark on northward migration, implying an even lower fitness of birds wintering in Ghana.

3.4 | In spring, sanderlings from West Africa migrate later through Iceland

Timing of spring migration through Iceland depended on the winter area; the most parsimonious model only included a main effect of winter area (Table 3). Time of passage did not linearly increase with migration distance, as sanderlings from Namibia were present at the same time as birds wintering in Europe (around 25 May; Figure 2c). Birds from Ghana were observed in Iceland 5–11 days later and those from Mauritania 9–15 days later than birds from European winter destinations and Namibia.

3.5 | Sanderlings skip West Africa during northward migration

Of the seven geolocator tracks from six individuals, four individuals wintered in West Africa (three in Mauritania and one in Guinea-Bissau) and two in Namibia (Figure 1b–h, Table S6). In contrast to their southward migration, birds wintering in Namibia did not stage in West Africa during northward migration (Figure 1g,h). Instead, they made non-stop flights of ca. 7,500 km (assuming great circle distances) across the African continent including the Sahara desert (Figure 1g,h). All West-African wintering individuals migrated non-stop from Africa to Europe (Figure 1b–h), but one of the two Namibian wintering individuals briefly stopped at the Mediterranean coast in Libya and Tunisia (Figure 1h, Table S6).

During northward migration, individuals staged longest in NW Europe between 51–57°N (Figure 1b–h, Table S6), although one individual had a marginally longer refuelling stage in Spain than in the Wadden Sea in one of the 2 years (Table S6). Four of the six individuals staged in the Wadden Sea during northward migration (Figure 1b–h, Table S6). The other two individuals staged at the north-west coast of the United Kingdom before a direct flight to the Arctic (Figure 1a; Table S6). At least two individuals had a final stopover in Iceland before continuing to Greenland (Figure 1b,c, Table S6). Date of departure from the wintering destination was tightly correlated with the date of arrival in the Arctic ($F_{1,5} = 20.3$, $p = .006$, $R^2_{adj} = 0.76$; Figure 1i).

4 | DISCUSSION

In contrast to our prediction of equal survival and timing of migration across their large non-breeding range, we found that sanderlings from winter areas in West Africa had (a) lower adult survival, (b) delayed first northward migration and (c) later passage through their last spring staging site in Iceland than birds wintering either further north or south. Individual fitness correlates of sanderlings thus varied across their large non-breeding range, but did not increase with migration distance. Sanderlings from low-latitude winter areas in West Africa seem to perform poorly. In contrast to the situation in other sandpipers (Fernández et al., 2004; O'Hara, Fernández, Becerril, Cueva, & Lank, 2005), the delayed age of first northward migration by sanderlings wintering in West Africa was not compensated for by higher adult survival, although potential trade-offs with other demographic parameters (e.g., enhanced juvenile survival and/or reproductive success at older ages) cannot be excluded and warrant further study. How can these patterns be explained? Do sanderlings of relatively poor overall condition end up in West Africa? Or do differences in non-breeding habitat quality explain this pattern? Interestingly, while they used West-African staging sites during southward migration (Figure 1b–h), during northward migration the two tracked individuals from Namibia flew 7,500 km non-stop across the African continent during northward migration.

Unlike other shorebirds (Nebel et al., 2002; O'Hara, Fernández, Haase, Cueva, & Lank, 2006), we found no convincing evidence for larger sanderlings to winter farther south or in a pattern matching their fitness correlates (Figure S5). Although sanderlings had a lower body mass in tropical winter areas compared with areas further away

TABLE 3 Models for timing of northward migration through Iceland with different fixed effects. We fitted a random structure with individual nested within year (~1|Year/Individual) and varExp(form=~fitted(.)) as variance structure (Table S5) for all models. See Materials and Methods for explanation. The following parameters are shown: residual degrees of freedom (df), log-likelihood (logLik), Akaike's information criterion (AIC), the difference in AIC with the top-supported model (ΔAIC), model weights (w_i) and residual deviance (deviance)

Model	df	logLik	AIC	ΔAIC	w_i	Deviance
Winter area	18	−5,420.84	10,877.7	0	0.67	10,841.7
Winter area + Sex	20	−5,419.54	10,879.1	1.4	0.33	10,839.1
Winter area * Sex	34	−5,412.31	10,892.62	15.0	0	10,824.6
Sex	13	−5,535.13	11,096.3	218.6	0	11,070.3

from the equator, this may be explained by adaptive fuel storage in colder and more unpredictable temperate areas (Kelly & Weathers, 2002; Lima, 1986) instead of being interpreted as poorer individual conditions of birds in tropical winter areas. The proportion of juveniles was considerably larger in Mauritania (Figure S5d) compared with the other winter areas. However, we believe that this is to a large extent caused by catching method (Robinson et al., 2005), as birds in Mauritania were caught with bait during high tide, when juveniles are more prone to continue foraging compared with adults (J. Reneerkens personal observations). In Ghana, where sanderlings performed equally poor as in Mauritania, juvenile proportions were much lower. Based on an examination of the annual cycles of shorebirds, it was concluded earlier that there is little support for the idea that subordinate individuals are forced south by competition (Meltofte, 1996). Thus, we consider it unlikely that sanderlings of relatively poor overall condition end up in West Africa.

Many different ecological aspects combine to determine the quality of non-breeding habitats (Piersma, 2012), with food availability being of key importance. For shorebirds, it has been shown that prey quality and prey biomass are lowest close to the equator (Aharon-Rotman, Gosbell, Minton, & Klaassen, 2016; Piersma et al., 1993, 2005). In these tropical areas, the relatively low harvestable prey biomass (Aharon-Rotman et al., 2016; Catry et al., 2016; Piersma et al., 1993) would result in low fuelling rates and low body masses at northward departure in a closely related High Arctic sandpiper, the Red Knot *Calidris canutus* (Piersma et al., 2005). Indeed, food availability during migratory fuelling has been shown to positively influence timing of migration and survival of Red Knots and Bar-tailed Godwits *Limosa lapponica* (e.g., Atkinson et al., 2007; Rakhimberdiev et al., 2018) and explained why less proficiently foraging juvenile shorebirds may skip northward migration (Hockey, Turpie, & Velásquez, 1998). On the basis of (a) the lower survival and later passage through Iceland of sanderlings wintering in West Africa, (b) the correlation between date of departure from the winter area and date of arrival in the Arctic and (c) the fact that sanderlings skipped West Africa during northward migration, we suggest that the conditions in West Africa were somehow ecologically compromised, especially during the season of northward migration. Outside the period of northward fuelling, sanderlings have a higher food intake in Ghana compared with the Netherlands. However, food quality in Ghana is much poorer and sanderlings in Ghana spent considerable more time processing indigestible shell fragments (Grond et al., 2015). When fuelling for northward migration, this could result in lower fuelling rates in Ghana compared with the Netherlands.

Sanderlings show strong within- and between-year winter site fidelity (Lourenço et al., 2016). In large long-lived birds, winter site fidelity has been shown to increase with age (e.g., Lok et al., 2011; Marchi et al., 2010), but we have no evidence that sanderlings move to different winter areas after their first year of life. Why would individuals return to areas where conditions are such that survival is low and departure difficult or late? Here we are reminded that function is not a cause (Hogan, 2017): sanderlings will not be able to build up the knowledge on what is coming with respect to ecological conditions at the end of the wintering period. Even though returning to West Africa is not the best option at the population level, individuals surviving their first year of life would have experienced that it 'worked' for them. Assuming an absence of exploratory migrations along the West-African coast, only the southernmost wintering birds would have had the opportunity to collect information on habitat quality along the length of the flyway. Furthermore, habitat quality will vary within and between years. If conditions in West Africa deteriorate throughout most wintering periods, for example through depletion of food stocks (Ahmedou Salem, Geest, Piersma, Saoud, & Gils, 2013), individuals staging at these sites during southward migration (Figure 1) may initially encounter profitable conditions and decide to stay, but get 'trapped' when conditions get worse.

The population of sanderlings along the East Atlantic Flyway has been growing for decades (van Roomen et al., 2015), which may lead to disproportionally large densities of individuals relative to the resources. For both Great Britain (Méndez, Gill, Alves, Burton, & Davies, 2018) and Ghana (Ntiamoa-Baidu, Nuoh, Reneerkens, & Piersma, 2014), there is evidence that the growing sanderling population reached 'carrying capacity' at preferred sites, buffering the use of some sites by forcing individuals to settle in alternative sites of (presumed) lower quality (Gill et al., 2001; Moser, 1988). At a local scale, high densities of birds competing for resources may limit their performance and eventually limit flyway scale population growth (Gunnarsson, Gill, Petersen, Appleton, & Sutherland, 2005).

Over half of the flyway population of sanderlings winters in West Africa (van Roomen et al., 2015), where we show that adult survival and presumably also (lifetime) reproductive success are lowest. Clearly, the settling decisions of juveniles will determine their fitness (Senner, Conklin, & Piersma, 2015) and it is of interest whether and to what extent social learning and/or the early environment—at the Arctic tundra, during the first southward migration or at the chosen winter area—impact such decisions.

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AUTHORS' CONTRIBUTIONS

J.R., Y.N.-B. and T.P. conceived the ideas. J.R., T.S.L.V., T.P., J.A.A., M.B., C.C., G.T.H., O.G., J.L., B.L., Y.N.-B., A.A.N., P.M.P. and J.t.H. collected data; J.R., T.S.L.V. and T.L. analysed the data. J.R. led the writing, and T.S.L.V., T.P., J.A.A., C.C., O.G., J.L., Y.N.-B., P.M.P. and T.L. contributed to drafts. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m73n280 Reneerkens et al. (2019).

ORCID

Jeroen Reneerkens https://orcid.org/0000-0003-0674-8143

Theunis Piersma https://orcid.org/0000-0001-9668-466X

José A. Alves https://orcid.org/0000-0001-7182-0936

Olivier Gilg https://orcid.org/0000-0002-9083-4492

Johannes Lang https://orcid.org/0000-0002-7387-795X

Yaa Ntiamoa-Baidu http://orcid.org/0000-0002-3915-3341

Tamar Lok https://orcid.org/0000-0003-3753-8501

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.