

Population fitness has a concave relationship with migration distance in Sanderlings

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Abstract

In Focus: Reneerkens, J., Versluijs, T. S. L., Piersma, T., Alves, J. A., Boorman, M., Corse, C., ... Lok, T. (2020). Low fitness at low latitudes: wintering in the tropics increases migratory delays and mortality rates in an Arctic breeding shorebird. *Journal of Animal Ecology*, 89, 691–703. A central question in migratory ecology has been to understand the fitness consequences of individual variation in migration distance among different species and populations. Reneerkens et al. (2020) investigated the demographic consequences of long-distance migration for Sanderlings *Calidris alba*, an Arctic-breeding species of sandpiper. Their study population has a remarkable geographic distribution with a breeding range that is concentrated in north-east Greenland and Ellesmere Island, Canada but a nonbreeding range that extends across 85° of latitude from Scotland to Namibia. The authors report on unexpected patterns of latitudinal variation in three demographic parameters: timing of passage on northward migration, probability of juvenile migration and apparent survival of adults. Sanderlings travelling 1,800–2,800 km to settle at north temperate sites during the nonbreeding season had earlier passage dates, and also higher probabilities of migration and apparent survival. In contrast, birds travelling 6,000–7,800 km to equatorial sites experienced later passage dates, delayed maturity and lower apparent survival. However, if Sanderlings migrated even farther and flew over 11,000 km to nonbreeding sites in Namibia, then their performance was restored to early passage dates and higher survival. Movement tracks from birds tagged with geolocators showed that birds wintering in Namibia make nonstop flights of 7,500 km that bypass West Africa during northward migration. Thus, all lines of evidence suggest that Sanderlings face adversity when spending the nonbreeding season at equatorial latitudes. Moreover, the central finding that components of fitness can have nonlinear relationships with migration distance is a novel discovery that leads to many additional questions. The new findings have broader implications for theoretical models of migration, and for understanding how different patterns of movements may arise or be maintained in migratory species.

KEYWORDS

age at maturity, apparent survival, citizen science, demography, mark-recapture, shorebird, timing of migration

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Long-distance migration has evolved multiple times in different groups of animals and is one of the most amazing features of the natural world. Patterns of migration vary widely with numerous examples of partial migration where populations include both resident and migratory individuals, and differential migration where migration distances vary among different demographic groups (Cristol, Baker, & Carbone, 1999). Investigations of migratory behaviour from a cost-benefit perspective often consider migration to be a costly stage of the life cycle due to high energetic costs and elevated mortality rates, with the expectation that exposure to risk should increase over longer migration distances (Alerstam, Hedenström, & Åkesson, 2003). Arctic-breeding waders are an interesting group for field studies of the costs of migration due to their global distribution and use of different habitats, an ability to cross ecological barriers with extreme nonstop flights and a remarkable diversity of mating systems and parental care (Conklin, Senner, Battley, & Piersma, 2017; García-Pena, Thomas, Reynolds, & Székely, 2009). Now, new results from a research project led by Jeroen Reneerkens and Tom Versluijs demonstrate that costs of migration might need to be reconsidered because different components of fitness can have nonlinear relationships with migration distance.

Sanderlings *C. alba* have been the focus of rangewide studies in the eastern Atlantic flyway (Grond, Ntiamoa-Baidu, Piersma, & Reneerkens, 2015) and the Western Hemisphere (Myers et al., 1990). Sanderlings are intriguing because they exhibit a diverse range of behaviours at all stages of their annual cycle. During the breeding season, the mating system includes social monogamy with biparental incubation, but also social and genetic polygamy with uniparental incubation (Reneerkens, Veelen, Velde, Luttkhuizen, & Piersma, 2014). During the nonbreeding season, Sanderlings can adjust their social behaviour to alternate between territorial defence or flocking depending on resource dispersion and the cost of defending feeding territories against intruders (Myers, Connors, & Pitelka, 1979). Here, Reneerkens et al. (2020) present new data that show that Sanderlings also vary greatly in their migration behaviour with a fivefold difference in migration distance for birds that travelled to different nonbreeding sites across 85° of latitude between Scotland and Namibia. Tracking small-bodied birds across such vast distances presents great logistical challenges. Reneerkens and Versluijs successfully led an international coalition of investigators with coauthors from eight different countries in Europe and West Africa. Together, the research team captured a total of 5,863 birds, of which 89% were individually colour-ringed and available for resighting in a 7-year period from 2007 to 2013. Resighting data were collected by the authors with additional help from over 2,000 citizen science observers who helped to track colour-ringed birds across the entire eastern Atlantic flyway.

One immediate question that arises from the new results is: what factors determine the incredible variation in migration distance for Sanderlings, which are presumably due to settlement decisions taken during their natal year? Differential migration is common among Arctic-breeding sandpipers (*Calidris* spp.) with the general patterns that males and juveniles tend to winter at more northerly sites, whereas females and adults often migrate longer distances (Nebel et al., 2002; Tavera, Lank, & Gonzalez, 2016). In an early paper, Myers (1983) suggested that 'Sanderlings have no friends' and argued that intraspecific competition

is important for structuring populations during the nonbreeding season. In the case of Western Sandpipers *Calidris mauri*, the sexes exhibit strong dimorphism in bill length, and differential migration is related to latitudinal clines in intertidal food resources (Mathot, Smith, & Elnor, 2007). Reneerkens et al. (2020) were able to reject similar explanations for Sanderling in the eastern Atlantic flyway because they found little evidence of biologically relevant variation in morphology, body condition or demographic classes across their latitudinal gradient of nonbreeding sites. The factors that determine initial settlement at a nonbreeding site remain unknown but the authors suggest that equatorial sites in West Africa could be an ecological trap if strong site fidelity limits the options for surviving birds to explore or disperse to a better nonbreeding site.

Reneerkens et al. (2020) confirmed that migration distance entails fitness costs, but quite unexpectedly, they found that the relationships with fitness were nonlinear. One of the great features of their study system was that Sanderlings from different nonbreeding sites stage together at coastal estuaries in Iceland before migrating to Greenland and northern Canada. Their first finding was that passage dates on northward migration (D_m) had a convex relationship with migration distance for birds from different nonbreeding sites. Timing of migration was estimated for birds resighted at the staging site and actual passage dates might be different if some proportion of the population did not stop in Iceland. Nevertheless, timing of northward migration was early for Sanderling from Europe, intermediate for Namibia, and with later passage dates for birds from West Africa. Supplementary tracks from birds tagged with geolocators showed that birds wintering in Namibia were able to bypass West Africa on northward migration and catch up with more northerly populations. Timing of migration is likely to be correlated with arrival at the breeding grounds, particularly since Iceland is the last stop for northbound birds. Fitness could be affected by seasonal declines in reproductive performance (Weiser et al., 2018), but daily nest survival actually increases during the breeding season for Sanderlings at the authors' long-term study site in eastern Greenland (Reneerkens et al., 2016). Early breeding might still be advantageous if it allows females to find mates or lay replacement clutches (Morrison, Alves, Gunnarsson, Þórisson, & Gill, 2019). Another component of fitness that remains poorly known for arctic-breeding waders is the effect of seasonal timing on juvenile survival on southbound migration. Early breeding and early departure might also help juveniles avoid seasonal increases in predation risk from falcons at stopover sites (Niehaus & Ydenberg, 2006).

A second key finding was that migration distance had an effect on the subsequent probability that a juvenile Sanderling would migrate north as a yearling (M_j). Reneerkens et al. (2020) found that the probability of juvenile migration followed a threshold model where it was <0.3 for birds at nonbreeding sites in West Africa but increased to one for birds at nonbreeding sites in Europe. The authors had no information on probability of migration for Namibia, but juvenile Sanderlings that winter further south in South Africa have a high probability of migration ($M_j = 0.95$, Summers, Underhill, & Prŷs-Jones, 1995). Other species of arctic-breeding sandpipers also overwinter as yearlings with delayed maturity (O'Hara, Fernandez, Becerril, de la Cueva, & Lank, 2005;

Summers et al., 1995; Tavera et al., 2016), and sometimes as adults with intermittent breeding (Martínez-Curci et al., 2015). Migratory divides where yearlings migrate north to breed from northern nonbreeding sites but overwinter at equatorial sites are now known to occur in Sanderlings and also Western Sandpipers (Fernández, O'Hara, & Lank, 2004). Proximate explanations for delayed maturity might include effects of migration distance on feather wear and the timing or costs of moult, or access to the food resources needed for migratory fueling. Counterintuitively, Sanderlings spend less time foraging and have higher rates of food intake at nonbreeding sites at equatorial latitudes, but food quality was lower because the diet was mainly bivalves in Ghana but soft-bodied polychaetes in the Netherlands (Grond et al., 2015). Overwintering as yearlings likely reduces fitness due to delayed entry of their offspring into the breeding population. Delayed age at maturity could be adaptive if life-history trade-offs with productivity or adult survival were present, but that does not seem to be the case in Sanderlings. If Sanderlings do not overwinter as yearlings in Namibia, then the life-history strategy of long-distance migrants may have a comparable fitness to birds that winter at north temperate latitudes.

The last major finding was a concave relationship between the annual probability of adult survival (S_a) and nonbreeding latitude where apparent survival rates were c. 0.74 in West Africa but 0.84–0.87 in Namibia and Europe. Interpretation of apparent survival as a measure of fitness can be challenging because population losses

can be due to mortality, permanent emigration or some combination of the two processes (Sandercock, 2020). If all losses were due to mortality, low apparent survival at equatorial nonbreeding sites would indicate fitness costs are due to low true survival. Reneerkens et al. (2020) argued that their estimate was close to true survival because Sanderlings were highly site faithful to nonbreeding areas, observers resighted birds at all key staging sites and auxiliary resightings were collected rangewide. However, site fidelity of waders to nonbreeding sites can be variable (Myers, 1984; Rehfish, Insley, & Swann, 2003), and short movements might have led to emigration to sites without observers. The geolocator tracks also demonstrate that Sanderlings can skip staging sites during migration and might not always be available for resighting. Even with remarkable effort from a network of citizen scientists, it is unlikely that sampling coverage could be complete for the entire migratory range. Thus, an alternative explanation for low apparent survival at equatorial latitudes could be that poor quality feeding conditions led to emigration from tropical nonbreeding sites or to migratory movements where birds were harder to detect.

The three demographic parameters can be combined with components of fecundity and seasonal estimates of daily nest survival to calculate fitness (McGraw & Caswell, 1996). Population fitness of Sanderlings has a concave relationship with migration distance and is also sensitive to annual variation in nest survival (Figure 1). The new

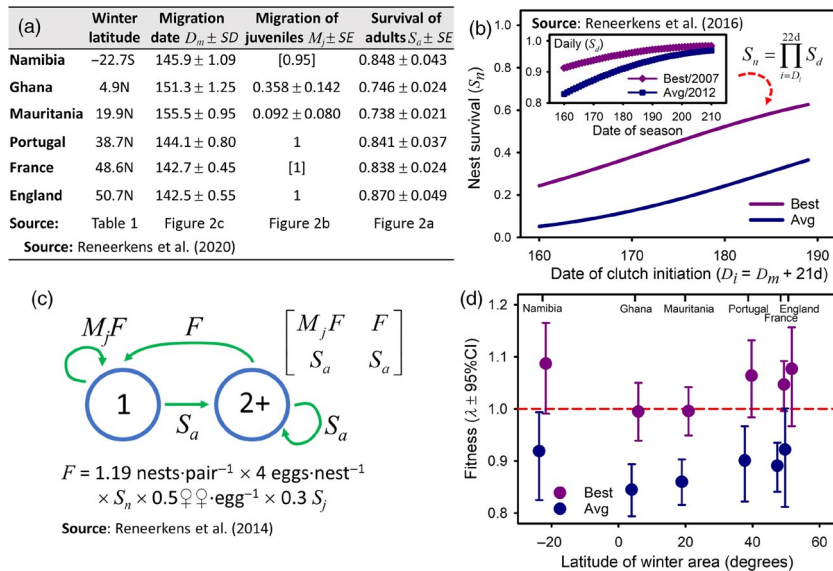


FIGURE 1 Sanderlings *Calidris alba* breed at arctic sites in Greenland and Canada but have a fivefold variation in migration distance to nonbreeding sites that extend across 85° of latitude from Scotland to Namibia. (a) Reneerkens et al. (2020) report that three demographic parameters varied among nonbreeding populations at different latitudes: a convex relationship for passage dates on northward migration through Iceland (D_m , day 145 = 25 May), a threshold relationship for the probability of migration among juveniles (M_j), and a concave relationship for the apparent survival of adults (S_a). What are the combined effects of such variation on population fitness? (b) Migration dates can be extrapolated to expected nest survival based on a 3-week delay before clutch initiation, with nest survival (S_n) calculated as the product of consecutive daily survival rates for a 22-day exposure period (day 175 = 24 June, Reneerkens et al., 2016). (c) Other components of fecundity were calculated from nests attended by 1–2 parents (135 nests for 113 pairs) and a modal clutch size of four eggs (Reneerkens et al., 2014), with a sex ratio set at 1:1 and juvenile survival set to be $S_j = 0.3$. (d) Population fitness (λ) for the different nonbreeding sites was then estimated from a pre-breeding matrix model where the confidence intervals were calculated with parametric bootstrapping. Population fitness of Sanderlings has a concave relationship with migration distance and is affected by annual variation in nest survival: fitness is lower for birds that winter in Ghana or Mauritania, and higher for birds at the edges of the nonbreeding range in Namibia and Europe

finding that the costs of migration have a nonlinear relationship with migration distance has interesting implications for understanding the evolution and maintenance of migratory systems. If nonbreeding sites at equatorial latitudes are ecological sinks with low fitness, they might be maintained by immigration from other areas or eventually be abandoned. Spatial variation in fitness among different sites in a flyway could also be a stepping stone towards development of more complex distribution patterns resulting from chain or leap-frog migration. In the future, comparative data are needed to determine whether the lower fitness of Sanderlings at equatorial sites is a general pattern that also occurs in other populations of migratory birds in the same or different flyways.

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SUPPORTING INFORMATION

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