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An age-dependent fitness cost of migration? Old trans-Saharan migrating spoonbills breed later than those staying in Europe, and late breeders have lower recruitment

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Abstract

1. Migration is a widespread phenomenon in the animal kingdom. On the basis of the considerable variation that exists between and within species, and even within populations, we may be able to infer the (age- and sex-specific) ecological trade-offs and constraints moulding migration systems from assessments of fitness associated with migration and wintering in different areas.
2. During three consecutive breeding seasons, we compared the reproductive performance (timing of breeding, breeding success, chick body condition and post-fledging survival) of Eurasian spoonbills *Platalea leucorodia* that breed at a single breeding site in The Netherlands, but migrate different distances (*c*. 4,500 vs. 2,000 km, either or not crossing the Sahara) to and from wintering areas in southern Europe and West Africa. Using mark–recapture analysis, we further investigated whether survival until adulthood (recruitment probability) of chicks hatched between 2006 and 2010 was related to their hatch date and body condition.
3. Long-distance migrants bred later, particularly the males, and raised chicks of poorer body condition than short-distance migrants. Hatch dates strongly advanced with increasing age in short-distance migrants, but hardly advanced in long-distance migrants, causing the difference in timing of breeding between long- and short-distance migrants to be more pronounced among older birds.
4. Breeding success and chick body condition decreased over the season, and chicks that fledged late in the season or in poor condition were less likely to survive until adulthood. As a result, long-distance migrants—particularly the males and older birds—likely recruit fewer offspring into the breeding population than short-distance migrants. This inference is important for predicting the population-level consequences of changes in winter habitat suitability throughout the wintering range.
5. Assuming that the long-distance migrants—being the birds that occupy the traditional wintering areas—are not the poorer quality birds, and that the observed age-dependent patterns in timing of breeding are driven by within-individual effects and not by selective disappearance, our results suggest that the strategy of long-distance

migration, involving the crossing of the Sahara to winter in West Africa, incurred a cost by reducing reproductive output, albeit a cost paid only later in life.

KEYWORDS
breeding success, carry-over effect, evolution, life history, migration, post-fledging survival, recruitment, timing of breeding, wintering site

1 | INTRODUCTION

Migration is a widespread phenomenon in the animal kingdom (Chapman, Brönmark, Nilsson, & Hansson, 2011; Dingle, 1980) that allows animals to exploit seasonal peaks of resource abundance and avoid seasonal resource depression (Alerstam, Hedenström, & Åkesson, 2003). Rather than being a unitary character, there is considerable variation in migration patterns, even between individuals of the same breeding population (Alerstam, 1990; Newton, 2008). To explain this variation, it is commonly assumed that the suitability of wintering areas increases towards the south (for animals breeding in the northern hemisphere), but that there are also costs involved in getting there (Alerstam et al., 2003; Bell, 2005; Gauthreaux, 1982; Greenberg, 1980; Ketterson & Nolan, 1976). In addition, the trade-off between the benefits of wintering in good quality areas and the costs of migrating long distances may depend on an individual's age and sex, due to differences in competitive ability, body size and in the benefits of arriving early at the breeding grounds (Drent, Both, Green, Madsen, & Piersma, 2003; Ketterson & Nolan, 1976; Kokko, 1999; Myers, 1981).

How far an individual migrates, and where it spends the winter, may have short-term effects on its body condition and survival (Flack et al., 2016; Gill et al., 2001; Lok, Overdijk, & Piersma, 2015; Marra, Hobson, & Holmes, 1998), but may also carry over to the breeding season to affect reproductive output via effects on spring arrival time and body condition (Harrison, Blount, Inger, Norris, & Bearhop, 2011; Senner, Conklin, & Piersma, 2015). Later arrival at the breeding grounds may result in the occupation of poorer quality breeding sites (Ketterson & Nolan, 1976; Kokko, 1999; Myers, 1981), and late breeders (as a consequence of late arrival or arrival in poor body condition) may experience reduced food availability, two mechanisms that will likely result in reduced breeding success (Both, Bouwhuis, Lessells, & Visser, 2006; Daan, Dijkstra, Drent, & Meijer, 1989; Drent et al., 2003).

So far, few studies (all on birds) have investigated breeding performance in relation to migration distance and wintering area. This is probably due to the difficulty in following individuals during both the breeding season (to collect data on breeding parameters) and non-breeding season (to determine an individual's wintering area). Several studies showed that birds wintering in good quality habitats arrive at the breeding grounds earlier (Gunnarsson et al., 2006; Marra et al., 1998; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004; Saino et al., 2004) and in better body condition (Marra et al., 1998). On the other hand, birds migrating longer distances (required to reach presumably better quality wintering areas) generally arrive later at the breeding grounds (Bearhop et al., 2005; Bregnballe, Frederiksen, & Gregersen, 2006; Hötker, 2002; but see Gunnarsson et al., 2006). In both the Icelandic black-tailed godwits *Limosa limosa islandica* (Alves et al., 2012) and the continental black-tailed godwits *L. l. limosa* (Kentie et al., 2017), the benefits of wintering in good quality areas may outweigh the costs of migrating a longer distance, at least in terms of timing of arrival at the breeding grounds, as the longest-distance migrating individuals arrived first. Long-distance migrating females of the *limosa* subspecies, the part of the population that crosses the Sahara, laid smaller eggs though (Kentie et al., 2017). Breeding success was not correlated with individual migration distances in short-distance migrating great cormorants *Phalacrocorax carbo* (Bregnballe et al., 2006) and partially migrating white storks *Ciconia ciconia* (Massemin-Challet et al., 2006).

While some of these studies accounted for age effects on breeding parameters, and some studies found sex-specific effects of migration distance and wintering area (Dale & Leonard, 2011; Gunnarsson et al., 2006; Woodworth et al., 2016; but see Bregnballe et al., 2006), none of these studies considered age-specific effects of migration distance and wintering area on breeding performance. Many birds have been shown to advance timing of breeding with increasing age (Balbontín et al., 2007; McCleery, Perrins, Sheldon, & Charmantier, 2008; van de Pol & Verhulst, 2006; Zhang, Vedder, Becker, & Bouwhuis, 2015), potentially driven by an increase in competitive ability and experience. On the other hand, some bird species delayed their timing of breeding again at older ages, an indication of senescence (Balbontín et al., 2007; McCleery et al., 2008). In migratory birds, age-specific patterns in timing of breeding were shown to be (partly) driven by age-specific migratory performance (e.g. timing of departure, (re)fuelling rates and migration speed), affecting timing of arrival at the breeding grounds (Balbontín et al., 2007; Sergio et al., 2014).

As a result of their longer migration that involves more or longer refuelling periods, age-specific improvement and deterioration of fuelling rates and migration speed may have more pronounced effects on spring arrival dates of long-distance migrants than of short-distance migrants. On the other hand, if arrival time at the breeding grounds is mainly driven by departure time from the wintering grounds, as in black kites *Milvus migrans* (Sergio et al., 2014), and if long-distance migrants are less flexible in adjusting their timing of migration to the advancing onset of spring at the breeding grounds (Both & Visser, 2001; Kullberg et al., 2015), a capacity that birds may develop and improve with age, the advancement of spring migration with increasing age may be less pronounced in long-distance migrants than in short-distance migrants. As a result, the relationship between age and spring arrival date, and thus timing of breeding, may be different for long- and short-distance migrating individuals, and result in an age-specific cost of long-distance migration.

Here, we compare breeding performance in relation to wintering area, and hence migration distance, of Eurasian spoonbills *Platalea leucorodia leucorodia* of 3–19 years old. Our study population breeds in The Netherlands and winters along the Atlantic coast between France and Senegal (Lok, Overdijk, Tinbergen, & Piersma, 2011). This range in wintering latitudes leads to a difference of 4,000 km one-way migration distance between the southernmost and northernmost winterers, a distance that includes the crossing of the westernmost Sahara (Lok et al., 2015). We investigate whether reproductive performance differs between long-distance migrants that travel 4,500–5,000 km each way and cross the Sahara to spend the winter in West Africa, and short-distance migrants that winter in Europe and commute over only 1,000–2,000 km. Importantly, we examine whether this difference varies with age and sex. We investigate several mechanisms that could reduce the reproductive output of long-distance migrants by testing whether they (i) breed later, (ii) have lower breeding success, and (iii) whether their chicks fledge in poorer condition. In addition, using a much larger dataset that also includes the many birds of which age and/or wintering area was unknown, we assessed whether breeding success and chick body condition decreased over the season and whether a chick's hatch date and body condition correlated with its probability to recruit into the breeding population. This allowed us to infer the likely consequences of the observed relationships between migration strategy, hatch date, breeding success and chick condition for short-distance and long-distance migrants' probability of recruiting offspring into the breeding population.

2 | MATERIALS AND METHODS

2.1 | Study population

We studied the breeding population of Eurasian spoonbills on the island of Schiermonnikoog, The Netherlands (53°29′N, 6°15′E), during the breeding seasons of 2006–2010. The first year (2006) was a pilot-year to develop and fine-tune the methods to estimate timing of breeding and breeding success and to verify that our activities did not have observable disturbing effects on the breeding spoonbills; in 2010 only a selection of colonies were followed. During 2007–2009, timing of breeding and breeding success were assessed for all nests on the Schiermonnikoog saltmarsh, an area covering *c*. 4 km^2. A total of 232, 217 and 223 nests were counted during these years. Apart from some occasional solitary nests, nests were aggregated in 11–12 colonies that varied in size from 2 to 60 nests. Distance between colonies varied from 100 m to 3 km (for a typical colony in the study area, see Figure S1).

Spoonbills are long-lived birds that show delayed maturity (Cramp & Simmons, 1977) and most start breeding in their 3rd or 4th calendar year (pers. obs.). Spoonbills have a long breeding season, with egg-laying occurring between late March and early July. They usually lay an egg every 2nd day and clutch sizes vary between 1 and 5 eggs. In our study population 91% of the nests ($N = 632$) that were checked after clutch completion and before hatching (i.e. checked within 15 days before hatching) contained 3 or 4 eggs (43% vs. 48%). Egg depredation was never observed during the 900 hr of colony observations (see Appendix S1). Incubation takes 25–26 days and begins with the laying of the first or second egg, causing asynchronous hatching (Lok, Overdijk, & Piersma, 2014). Spoonbill chicks are altricial and fledge when *c*. 35 days old, after which they are still fed by their parents for at least another month (Cramp & Simmons, 1977).

2.2 | Age, sex, wintering area and nest of colour-ringed parents

Since 1982, spoonbills have been individually colour-ringed as prefledged chicks in several colonies in The Netherlands, including Schiermonnikoog. As a result, 40% of the spoonbills breeding on Schiermonnikoog are colour-ringed and their exact age is known. Their nests were determined through visual observations from a hide during the incubation and early chick-rearing phase (see Appendix S1 for further details). While these birds have not been molecularly sexed, males are on average 12% larger than females (Lok et al., 2014), which enabled us to confidently distinguish the sexes of 80% of the colour-ringed parents when observed as a pair.

Observations of these colour-ringed birds at their wintering grounds were used to determine an individual's wintering area (see Appendix S1 for further details). As spoonbills are highly faithful to their wintering area from their 2nd winter onward (Lok et al., 2011), a bird's wintering area was defined as the most southern area where a bird was observed within a winter as 2nd winter or older bird. To select resightings of birds at their terminal wintering sites, we used resightings between October and February in West Africa, but only the months December and January in Europe to exclude stopover resightings of birds wintering further south (Lok et al., 2011). We defined two migration strategies: short-distance migrants (with a one-way migration distance of <2,400 km, wintering in Europe) and long-distance migrants (>4,000 km, i.e. the trans-Sahara migrants, wintering in West Africa), in addition to a category of unknown migration strategy.

Although the majority of birds remained faithful to their wintering areas (Lok et al., 2011), 18 of the 152 colour-ringed birds in our study population were short-distance migrant in one winter, and long-distance migrant in another. As these cases may have been due to ring reading errors, or a very late (autumn) or early (spring) stopover observation, we selected the migration strategy that was observed in the majority of winters. For birds that were observed an equal number of winters in Europe and West Africa, migration strategy was set as unknown ($N = 7$). Of the 152 different colour-ringed breeding birds during 2007–2009, 57 were short-distance migrant (22 females, 29 males and 6 individuals of which sex could not be reliably determined), 32 long-distance migrant (14 females, 10 males and 8 individuals with unknown sex) and 65 with unknown migration strategy (Figure 1). Migration strategies of males and females were not statistically different ($\chi^2 = 0.96$, $df = 1$, $p = .33$).

2.3 | Breeding success and chick body condition

Breeding success was defined as the number of chicks per nest that survived until the age at which they were colour-ringed (at 2–5 weeks old, see below). At this age, spoonbill chicks are no longer attached to their own nest but gather in crèches (Cramp & Simmons, 1977).

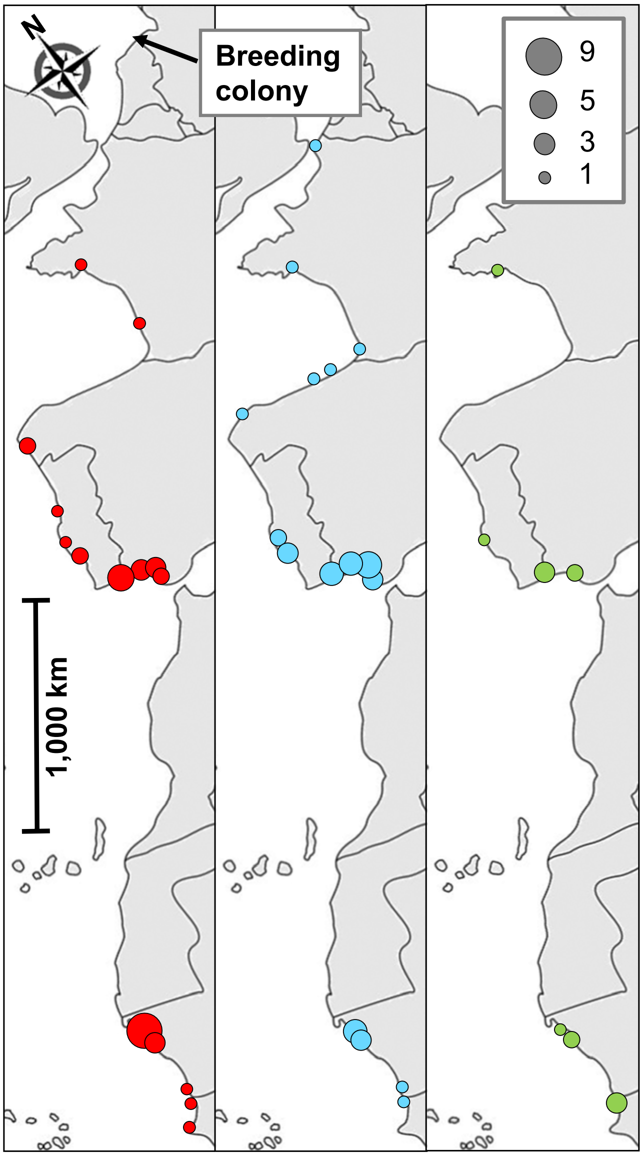

FIGURE 1 Distribution of wintering sites of female (red), male (blue) and unsexed (green) Eurasian spoonbills breeding on the island of Schiermonnikoog, The Netherlands

To be able to determine from which nests these surviving chicks had hatched, they received a temporary band (an individually numbered cotton band attached around the tibia with a clamp) when still attached to their own nest (within 2 weeks after hatching).

To avoid repeated disturbances, colour-ringing events were timed such that the oldest chicks in the colony were close to fledging, which allowed a maximum number of chicks to be colour-ringed during a single visit to the colony, but caused the age of the chicks at colour-ringing to vary from 16 to 39 days (with 75% ringed between 21 and 32 days). All chicks in the colony were colour-ringed. For small and synchronized colonies this could be achieved within a single visit, whereas for large, usually somewhat less synchronized, colonies two or sometimes three visits were required to colour-ring all chicks. To minimize disturbance, ringing activities were timed during periods of favourable weather conditions and preferably around low tide, when many breeding birds are off foraging.

TABLE 1 Parameter estimates and 95% confidence intervals of the most parsimonious model for timing of breeding (Table S2)

		95% CI	
Hatch date	**Estimate**	**Lower**	**Upper**
Intercept	46.29	34.35	58.24
Age	−0.88	−2.17	0.40
Migration strategy[a]	12.43	−0.16	24.87
Sex[b]	−4.73	−17.74	8.27
Migration strategy[a]:Age	−1.60	−2.95	−0.24
Age:Sex[b]	1.44	0.23	2.64
Migration strategy[a]:Sex[b]	−10.51	−19.57	−1.42
Random effects			
$\sigma_{\text{individual}}$	7.59	5.33	9.04
σ_{residual}	6.59	5.63	7.80

[a] Reference migration strategy: long-distance migrants.

[b] Reference sex: females.

Of the 827 chicks that were colour-ringed during 2007–2009, 79 chicks had lost their temporary band, hence their nest of origin could not be traced back. In some cases, it was still possible to determine its nest when the chick was fed by a colour-ringed parent. The loss of temporary bands will have led to an underestimation of breeding success. This probability of band loss may increase with chick age at ringing, as the older chicks had been wearing the bands for a longer period. In addition, as some chick mortality still occurs between the 2nd and 5th week, breeding success will be somewhat overestimated for broods ringed at a young age. However, as there was no relationship between hatch date and chick age at ringing ($\beta = 0.014$, SE = 0.016, $p = .39$), these biases can be assumed to be randomly distributed with respect to the explanatory variables of interest.

During colour-ringing, the chick's temporary band was replaced by a unique colour-ring combination, and head-bill length, 8th primary length and body mass were measured to estimate age and derive an index of body condition (Lok et al., 2014). For molecular sex determination, a blood sample of 10–80 µl was collected from the brachial vein and stored in 96% ethanol. DNA was extracted from the blood and sex-specific DNA fragments were replicated using primers 2550F/2718R (Fridolfsson & Ellegren, 1999).

Chick body condition was calculated as the deviation in body mass from the predicted body mass, divided by the predicted body mass, using the sex-specific Gompertz growth curves for body mass estimated by Lok et al. (2014) (females: $y_\infty = 1467$, $k = 0.148$ and $T_i = 8.0$ and males: $y_\infty = 1729$, $k = 0.130$ and $T_i = 9.4$). To calculate the predicted body mass, age was estimated from head-bill length at temporary banding, or, when not available, from the 8th primary length at colour-ringing.

Body condition may be affected by the relative age of a chick in the nest, which was determined from head-bill length during temporary banding relative to that of its siblings that survived to ringing, or otherwise, from 8th primary length at ringing relative to that of its siblings.

2.4 | Timing of breeding

Because spoonbills appear sensitive to disturbance during the egg-laying period (pers. obs., Appendix S1), for the sake of security, timing of breeding was determined on the basis of the hatch date of the chicks. This restricted the data on timing of breeding to nests that successfully hatched. Fortunately, nest failure prior to hatching was very rare in our study population, as we seldom found abandoned (empty) nests in the colonies and rarely observed nests during the (late) egg incubation phase that were abandoned prior to hatching (pers. obs.). The only exception was a storm flood in late June 2007, which led to the failure of eight nests that still contained eggs or small chicks that were not yet measured. It resulted in an underestimation of the number of failed nests with (expected) hatch dates in late June and early July 2007.

The hatch date of a nest was determined on the basis of the visual observations from a hide (see Appendix S1 for details), or back-calculated from the estimated age of the largest chick in the nest. Chick age (t) was estimated from head-bill length during temporary banding or 8th primary length during colour-ringing (y_t), using the Gompertz growth curves estimated by Lok et al. (2014) (head-bill: $y_\infty = 184$, $k = 0.052$ and $T_i = 7.9$; 8th primary: $y_\infty = 247$, $k = 0.095$ and $T_i = 19.3$).

For those nests that had been observed on a daily basis from a hide, the observed hatch date was 0.81 (± 0.16 *SE*) days and 1.34 (± 0.23 *SE*) days later than the hatch date estimated from head-bill length at temporary banding or from 8th primary length at colour-ringing. This difference is probably due to the fact that the small altricial chicks (*c*. 55 g at hatch) need some time after hatching before they are able to reach with their bill above the nest edge, hence to become observable from the hide. Nonetheless, there were also cases where the hatch date estimated from the head-bill length (but not from the 8th primary) was later than the observed hatch date. This was likely due to early mortality of the first hatched chick(s) prior to the temporary banding (and measurement of head-bill lengths). We were able to accurately determine the hatch date for 565 nests, preferably from the head-bill length of the largest chick during temporary banding ($N = 438$ nests) or, when not available, from its 8th primary length at colour-ringing ($N = 17$). In absence of any morphometric measurements (mostly due to failure of the nest shortly after hatching, $N = 38$) or when the estimated hatch date from morphometric measurements was later than the observed hatch date ($N = 71$), we used the observed hatch date.

2.5 | Statistical analysis of breeding performance

Analyses of breeding performance (timing of breeding, breeding success and chick body condition) were performed on several selections of the data. The first analysis included all nests for which timing of breeding could be accurately determined during the years of intensive monitoring (2007–2009)—whether the parents were colour-ringed or not—to test for annual variation in breeding parameters. In this first analysis, we tested whether timing of breeding, breeding success and chick body condition varied between years, and whether breeding success and chick body condition depended on hatch date of the chicks. We further tested whether chick body condition was associated with the number of siblings in the nest that survived until colour-ringing and with age relative to that of its siblings.

In a second analysis, only nests with at least one colour-ringed parent were included to test the effect of age, sex and migration strategy of the parent(s) on timing of breeding, breeding success and chick body condition. Because age-related changes in breeding performance have now been established in a variety of birds (McCleery et al., 2008; Reed et al., 2008; Reid, Bignal, Bignal, McCracken, & Monaghan, 2003), with an initial increase in breeding performance often followed by a decrease at old ages, we considered both linear and quadratic effects of age. We also explored, but found no statistical support for, more flexible nonparametric modelling of age effects using general additive models. In addition, we investigated age- and sex-specific effects of migration strategy, as well as sex-specific age effects on reproductive parameters by considering all two- and three-way interactions between migration strategy, age (linear or quadratic) and sex. Furthermore, an individual's breeding performance may depend on the conditions experienced during migration, which are variable between years, and may differ between long- and short-distance migrants. Consequently, we may expect an interaction between year and migration strategy on breeding performance. For this second analysis, we initially included only the birds with known sex and migration strategy. When our data did not support an effect of either sex or migration strategy on breeding performance, to improve the estimation of potential age effects we also included the birds of unknown sex and unknown migration strategy into the analysis.

When testing an effect of timing of breeding on breeding output (as measured by breeding success and chick body condition), we considered both linear and quadratic effects of hatch date. Under stabilizing selection, conditions to raise chicks are expected to be optimal, hence breeding output to be highest, in the middle of the breeding season. In contrast, under directional selection for early breeding, a decrease in breeding output over the season is predicted. In addition, the optimal timing of breeding may vary between years, due to variation in spring phenology. We therefore also considered an interactive effect of year and hatch date (squared) on breeding success and chick body condition.

The analyses involved data of the same individuals in different breeding seasons. However, because unringed individuals cannot be individually identified, we could not account for such pseudoreplication in the first analysis. In the second analysis, based on individually colour-ringed breeders, we included random individual effects in the models explaining variation in timing of breeding, breeding success and body condition of their chicks. In 49 of the 261 monitored nests of which one parent was colour-ringed, the partner was also colour-ringed. Using both partners in the analyses would result in serious pseudoreplication, as the collected data only provides information at the level of the nest, not at the level of the individual bird. To avoid this, we selected one colour-ringed parent per nest. Where possible, an adult with a known wintering area was selected. When the migration strategy of both partners was either known or unknown, one adult was chosen randomly. This selection procedure reduced the dataset of adults with known sex and migration strategy by 10% for timing of breeding (from 161 to 145 observations) and breeding success (from 158 to 138 observations) and by 7% (from 201 to 186 observations) for the chick body condition analysis. For the analyses of chick body condition, to account for the dependency of chick body condition of chicks within the same nest, we additionally modelled random nest effects.

Breeding success was modelled with a log-link function and Poisson errors. We checked for, but did not find, trends or heteroscedasticity in residuals or overdispersion. Statistical analysis of timing of breeding, breeding success and chick body condition were performed using (generalized) linear (mixed) models using program R (R Core Team, 2015) and the R package lme4 (Bates, Maechler, Bolker, & Walker, 2015). Model selection is based on Akaike information criterion adjusted for small sample size (AIC_c) (Burnham & Anderson, 2002). Parameter estimates and profile likelihood confidence intervals of the most parsimonious models are reported, with the most parsimonious model being the model with the fewest parameters within 2 ΔAIC_c of the top model. Where applicable, least square means and 95% confidence intervals are reported.

2.6 | Post-fledging survival

To investigate the performance of the young after they had been colour-ringed, we estimated their survival probability after fledging in relation to hatch date and body condition using mark-recapture modelling (Lebreton, Burnham, Clobert, & Anderson, 1992). We applied Cormack-Jolly-Seber models (Lebreton et al., 1992) which allow the separation of apparent survival and resighting probabilities. Apparent survival estimates are the product of true survival and fidelity to the area of resighting. Since this area encompasses both breeding and wintering grounds (see Appendix S1), fidelity is expected to approach unity. As a result, our estimates of apparent survival will approach true survival.

The analysis was based on all chicks colour-ringed in 2006–2010 on Schiermonnikoog (220, 244, 350, 222 and 42 chicks, respectively), and resighted during late summer (August–September) in The Netherlands, anywhere in winter (November–February) or anywhere in summer (April–September) in the years until the winter of 2012–2013. This allowed us to estimate survival until adulthood (when 3 years old) for all yearly cohorts, separating survival during post-fledging (*c*. during the 3 month period after colour-ringing), first autumn migration (September–January), first “winter” (January–July, as first-year bird) and subsequent survival. Due to limited data, we did not distinguish between survival of subadult (age 1–2) and adult birds (age 3–4) and did not model annual variation in survival.

In all models, we accounted for a potential effect of age at ringing (estimated from head-bill length at temporary banding, or 8th primary length at ringing, see formulas above) on post-fledging survival. On the basis of previous results (Lok, Overdijk, Tinbergen, & Piersma, 2013b), we also accounted for annual variation in resighting probabilities during the post-fledging, winter and summer periods, and modelled resighting probability in summer separately for subadult and adult birds.

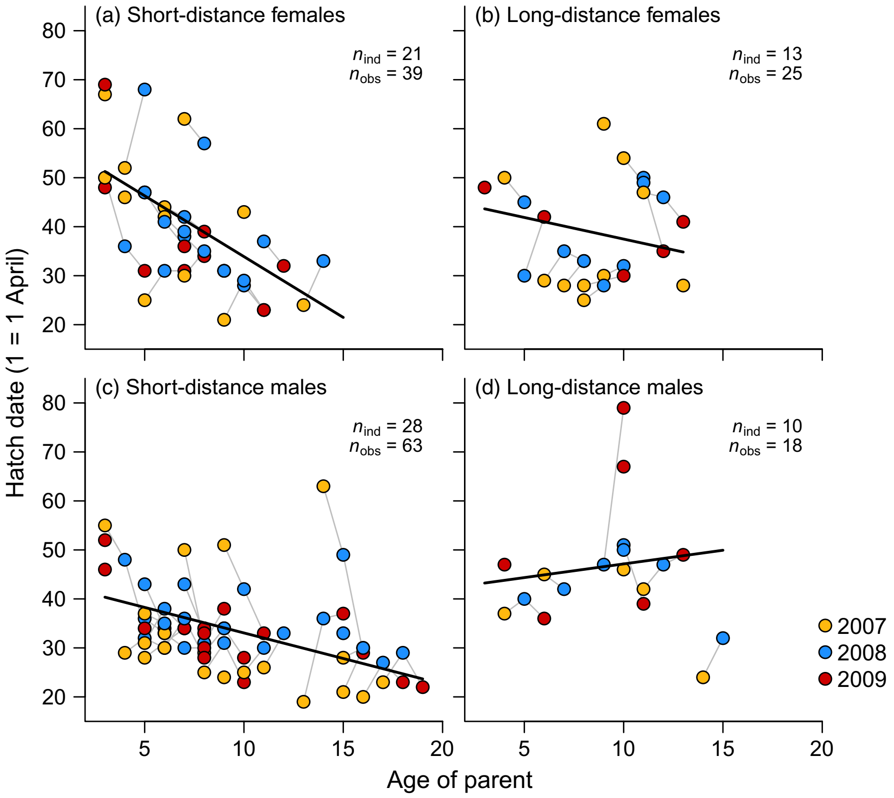

FIGURE 2 Hatch date as a function of age, sex and migration strategy of parent Eurasian spoonbills. Black lines represent the estimated relationships from the most parsimonious model (Table S2). Grey lines connect points of the same individuals

We first separately tested a linear relationship between hatch date and chick body condition, as well as a quadratic effect of hatch date, on survival during post-fledging (Φ_{pf}), first autumn migration (Φ_{m1}), first winter (Φ_{w1}) and of older birds (Φ_{older}). We then tested combinations of covariates that found substantial support in the separate tests.

Goodness-of-fit of the full model, Φ_{pf} Φ_{m1} Φ_{w1} Φ_{older} $p_{pf}(t)$ $p_w(t)$ $p_{s,sub}(t)$ $p_{s,ad}(t)$, was assessed using the median-$\hat{c}$ test in program MARK (White & Burnham, 1999). The level of overdispersion was estimated at $\hat{c} = 1.17 \pm 0.01$ *SE*.

Post-fledging survival was analysed using the package RMark (Laake, 2013) in program R (R Core Team, 2015) and program MARK (White & Burnham, 1999). Model selection is based on the Akaike Information Criterion adjusted for small sample sizes and overdispersion ($QAIC_c$) (Burnham & Anderson, 2002).

3 | RESULTS

3.1 | Timing of breeding

In 2007–2009, 95% of the 565 nests hatched between 22 April and 24 June, with 11 May as the average and no support for year-to-year variation ($\Delta AIC_c = 3.62$). We found strong support for the two-way interactions between migration strategy and (linear) age and sex, but not for the three-way interaction (Table S2). Hatch dates advanced more strongly with increasing age in short-distance migrants than in long-distance migrants (Table 1, Figure 2). Moreover, the difference in hatch date between short- and long-distance migrants was much larger in males (4 [1–8] May vs. 16 [11–23] May) (mean [95% CI]) than in females (7 [3–11] May vs. 9 [4–14] May) (Table 1, Figure 2). We also found some support for the two-way interaction between age and sex (Table S2), with hatch dates of females advancing more strongly with increasing age than of males, although the age-specific pattern of long-distance migrating females was poorly described by a linear age effect (Table 1, Figure 2). We found no statistical support for quadratic age effects (to describe delayed hatch dates at very old ages), whether or not in interaction with sex and/or migration strategy (Table S2).

3.2 | Breeding success and chick body condition

Breeding success, i.e. the number of chicks colour-ringed per nest, differed between years and decreased over the season; it was best described by a quadratic relationship with hatch date (Figure 3a, Table 2). Across the restricted dataset, breeding success did not depend on migration strategy ($\beta_{short} = -0.081$ [−0.388 to 0.227], Table S4, model 3), but increased with increasing age of the parents ($\beta = 0.030$ [0.003 – 0.057]) (Tables S5 and S6). The effect of hatch date on breeding success was no longer supported in these smaller datasets (Tables S4 and S5).

Chick body condition also differed between years and decreased over the season (Figure 3b, Tables S7 and S8). Relative age within a nest was more important in explaining variation in body condition than the number of siblings: third chicks in the nest had a lower body condition than their older siblings (Tables S3 and S8). Across the restricted dataset, short-distance migrants fledged chicks of significantly better body condition than long-distance migrants, but the effect of hatch date on chick body condition was no longer supported in this smaller dataset (Tables S3 and S9).

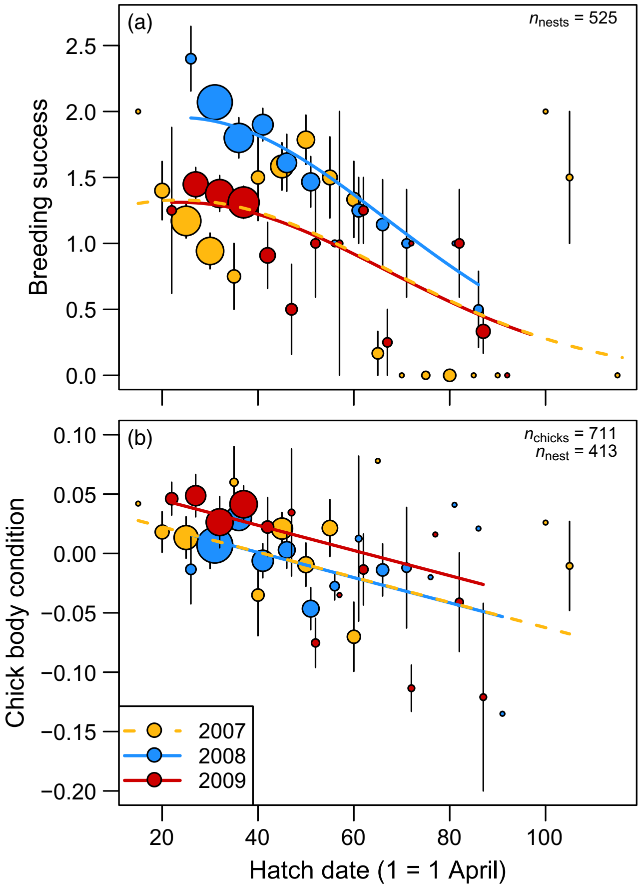

FIGURE 3 (a) Breeding success and (b) chick body condition (of the oldest chick in the nest) as a function of hatch date and year. Points and error bars represent the mean and standard errors of the raw data pooled over 5 day-periods, with point size proportional to sample size. Lines represent estimates from the most parsimonious models of Tables S3 and S7, respectively

TABLE 2 Parameter estimates (on a log-scale) and 95% confidence intervals of the most parsimonious model for breeding success (Table S3). Results are based on 525 nests

		95% CI	
Breeding success	**Estimate**	**Lower**	**Upper**
Intercept	0.134	−0.494	0.735
Hatch date	0.013	−0.015	0.041
Hatch date squared	−0.0003	−0.0006	0.0000
Year[a]			
2008	0.385	0.209	0.564
2009	−0.013	−0.210	0.183

[a] Reference year: 2007.

TABLE 3 Parameter estimates and 95% confidence intervals of the most parsimonious model for chick body condition (Table S9). Results are based on 186 chicks from 105 nests and 59 parents (20 long-distance and 39 short-distance migrants, see Table S1)

Chick body condition	Estimate	95% CI Lower	95% CI Upper
Intercept	−0.023	−0.051	0.005
Migration strategy[a]	0.041	0.008	0.074
Order[b]			
Second	−0.004	−0.028	0.020
Third	−0.143	−0.191	−0.096
Random effects			
$\sigma_{\text{nest:colony}}$	0.035	0.000	0.060
$\sigma_{\text{individual}}$	0.028	0.000	0.049
σ_{colony}	0.006	0.000	0.031
σ_{residual}	0.076	0.066	0.088

[a] Reference migration strategy: long-distance migrants.

[b] Reference order: first chick.

We found no support for quadratic age effects, nor for the two- and three-way interactions between age, sex and/or migration strategy, in explaining variation in breeding success (Tables S4 and S5) and chick body condition (Table S9).

3.3 | Post-fledging survival

Post-fledging survival was positively correlated with age at ringing and negatively correlated with chick body condition (Figure 4 and Table S13). Post-fledging survival decreased with hatch date for chicks hatched in April and May (92% of the chicks), but appeared to increase again for chicks hatched very late in the season (Figure 4). The increased survival of late hatched chicks may be an artefact, because those chicks had a much shorter post-fledging period (and hence, less time to die) than the early hatched chicks. Chick body condition was not correlated with survival during the first autumn migration and first winter, but tended to be positively correlated with survival after the first year (slope: 2.01 [−0.02 to 4.04], Table S13, model 1). Parameter estimates of the most parsimonious model are shown in Table 4.

4 | DISCUSSION

We showed that long-distance migrating spoonbills, and in particular the males, breed later than short-distance migrants and produced chicks of poorer body condition. Combined with the seasonal decrease in breeding success and the lower recruitment probability of chicks hatched late in the season or fledged in poor condition, long-distance migrants likely recruit fewer offspring into the breeding population than short-distance migrants (Figure 5).

Rather than being uniform throughout the population, the difference in timing of breeding between short- and long-distance migrants depended on age. In contrast with long-distance migrants, hatch date strongly advanced with increasing age in short-distance migrants, in both males and females. While many studies found age-specific timing of breeding (Forslund & Part, 1995; McCleery et al., 2008; van de Pol & Verhulst, 2006), our study is the first to show that this pattern interacted with migration strategy. Because our study period spanned only 3 years, statistical power was too low to distinguish within-individual (indicative of individual improvement and senescence) and between-individual effects (selective appearance or disappearance of early vs. late breeders) (van de Pol & Verhulst, 2006). At this point, we can

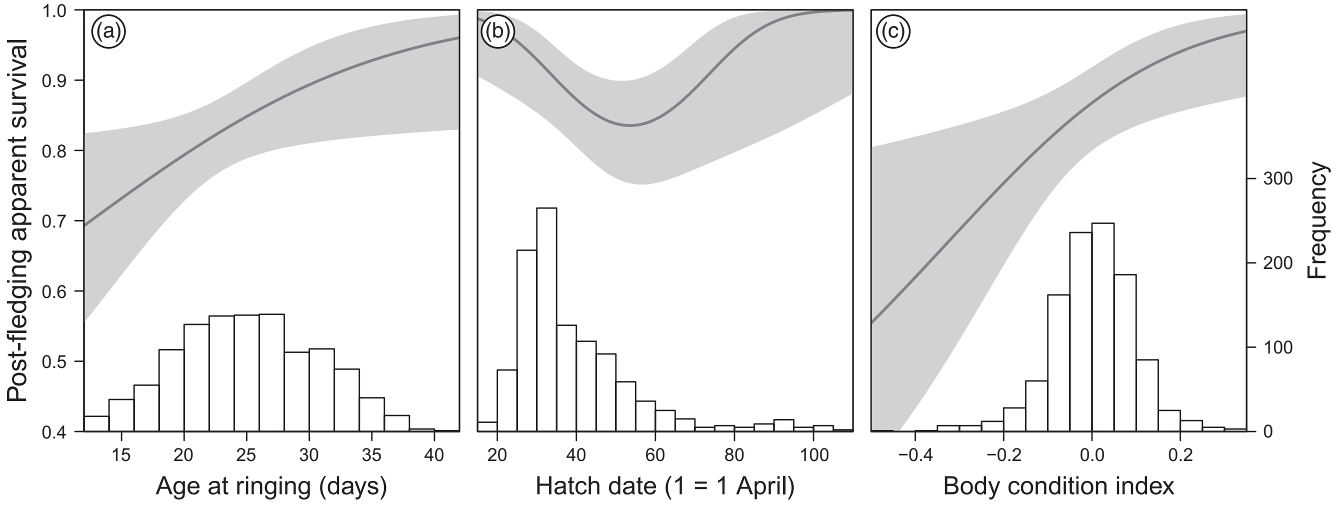

FIGURE 4 Post-fledging apparent survival (over 3 months, from colour-ringing (June) until the onset of autumn migration (September)) as a function of (a) age at ringing, (b) hatch date and (c) body condition index. For the estimates in each panel, the mean covariate values for the other two explanatory individual covariates are used, i.e. mean ringing day is 27 days, mean hatch date 41 (11 May) and mean body condition index is 0. Means (solid lines) and 95% confidence intervals (grey area) are estimated by the most parsimonious model in Table S13 and adjusted for overdispersion ($\hat{c}$ = 1.17). Histograms represent the frequency-distribution of the individual covariates of the chicks in the dataset

TABLE 4 Parameter estimates and 95% confidence intervals of the most parsimonious model of post-fledging apparent survival (Table S13). Apparent survival estimates are reported for mean ring age (27 days), hatch date (day 41) and chick body condition (BCI = 0). For comparison, both monthly and seasonal (proportion surviving the entire season) apparent survival estimates are provided. 95% confidence intervals have been adjusted for overdispersion ($\hat{c}$ = 1.17)

	Estimate (95% CI)	
(a) Apparent survival (Φ)	**Monthly**	**Seasonal**
Post-fledging (Jun–Aug)	0.95 (0.93–0.97)	0.87 (0.80–0.92)
First autumn migration (Sep–Dec)	0.96 (0.93–0.98)	0.84 (0.73–0.91)
First winter (Jan–Jun)	0.97 (0.95–0.98)	0.82 (0.72–0.90)
Subadult/Adult (Jul–Jun)	0.99 (0.98–0.99)	0.86 (0.82–0.88)
(b) Resighting probability (*p*)		
Post-fledging (Aug–Sep)		
2006	0.81 (0.73–0.87)	
2007	0.73 (0.65–0.80)	
2008	0.54 (0.47–0.61)	
2009	0.77 (0.69–0.83)	
2010	0.79 (0.59–0.91)	
Winter (Nov–Feb)		
2006/2007	0.22 (0.16–0.31)	
2007/2008	0.20 (0.16–0.26)	
2008/2009	0.23 (0.19–0.28)	
2009/2010	0.11 (0.08–0.14)	
2010/2011	0.14 (0.11–0.18)	
2011/2012	0.17 (0.13–0.21)	
2012/2013	0.14 (0.10–0.19)	
Subadult summer (Apr–Sep)		
2007	0.46 (0.37–0.56)	
2008	0.30 (0.25–0.37)	
2009	0.29 (0.24–0.35)	
2010	0.36 (0.30–0.42)	
2011	0.50 (0.39–0.60)	
2012	0.52 (0.27–0.76)	
Adult summer (Apr–Sep)		
2009	0.64 (0.53–0.73)	
2010	0.66 (0.59–0.73)	
2011	0.70 (0.63–0.77)	
2012	0.53 (0.46–0.60)	

therefore only speculate about the possible mechanisms underlying the observed age-specific patterns in timing of breeding. Similarly, we cannot confidently distinguish age from cohort effects. However, the fact that old birds hatched in the same year breed at very different times depending on their migration strategy (Figure 2), makes it unlikely that cohort effects drive the observed age-specific patterns in timing of breeding.

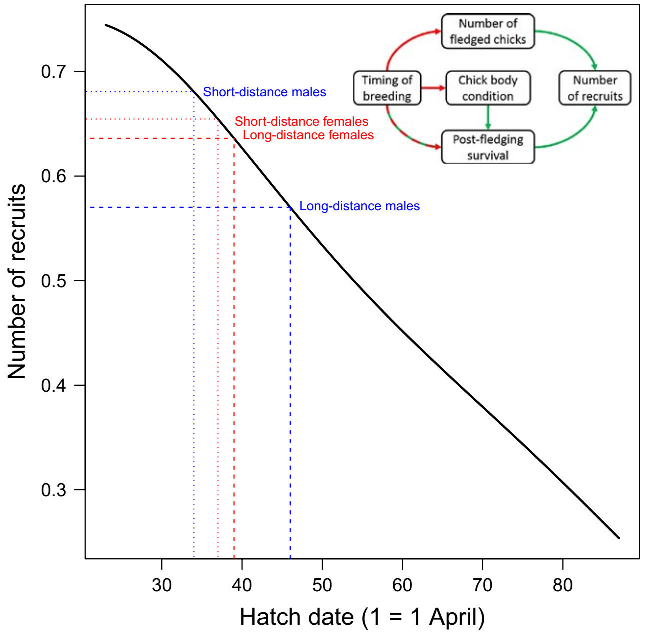

FIGURE 5 The expected number of recruits of male and female long- and short-distance migrants based on their average timing of breeding after correcting for age effects (using the least square means from model 7, Table S2). The number of recruits (number of chicks becoming at least 3 years old) per breeding pair is plotted as a function of hatch date, calculated from the estimated relationships (where applicable averaged over the three study years) between hatch date, breeding success (Table 2, Figure 3), chick body condition (Figure 3) and post-fledging and subadult survival (Table 4). Mean age of ringing (27 days) was used to calculate post-fledging survival. The diagram shows the relationships between the different parameters measured, being either positive (green), negative (red) or quadratic (dashed red-green)

The migration strategy-specific age patterns may be driven by (a lack of) within-individual advancement of breeding. In migratory birds, a within-individual advancement of breeding can result from an advancement in arrival time, or a reduction in the period between arrival and breeding. Young birds may breed later because they arrive later at the breeding grounds due to later departure from the wintering grounds (Sergio et al., 2014) or slower migration, and/or because they require more time upon arrival to find a partner and start breeding due to higher susceptibility to social interference in the colony (McCleery et al., 2008).

However, these mechanisms do not explain why long-distance migrants did not advance breeding. A potential explanation lies in the fact that weather conditions in early spring in Europe are more comparable to those at the breeding grounds than those in West Africa (Figure S3). As a result, birds wintering in Europe may be better able to adjust their timing of migration to variation in the onset of spring at the breeding grounds (Winkler et al., 2014) than birds from West Africa, that may rely on less flexible cues that are endogenously controlled (Gwinner, 1996) or fixed early in life (Gill et al., 2014). When this ability to predict the onset of spring at the breeding grounds from conditions at the wintering grounds improves with age, with spring advancing over time, this could explain why short-distance migrants more strongly advanced breeding with increasing age than long-distance migrants.

In addition to the age effects, the extent to which long-distance migrants bred later than short-distance migrants depended on sex, being larger in males. A similar result was obtained for savannah sparrows *Passerculus sandwichensis*, where wintering in more distant wintering areas negatively correlated with timing of territory acquisition of males, but positively with timing of breeding of females (Dale & Leonard, 2011; Woodworth et al., 2016). This suggests that the costs and benefits of long-distance migration are sex-specific. A possible explanation is that timing of breeding of males primarily depends on arrival date at the breeding grounds, while timing of breeding of females more strongly depends on body condition upon arrival, as females arriving in good condition may lay eggs earlier (Bêty, Gauthier, & Giroux, 2003). When wintering conditions are more important than migration distance in determining body condition upon arrival, and when wintering conditions are more benign in West Africa than in Europe, females from West Africa may arrive in better condition at the breeding grounds and—despite potentially arriving later due to their longer migration—be able to lay eggs at similar times (at least among the younger birds) as females from Europe. Establishing the link between timing of arrival and breeding in relation to sex and migration strategy would help to better understand the mechanisms underlying the observed patterns.

Despite the facts that long-distance migrants on average bred later and that breeding success decreased over the season, we did not find a direct effect of parental migration strategy on breeding success. The absence of such a direct effect may have been due to the limited sample size of birds with known migration strategy, combined with the large variation in breeding success within and between seasons (Figure 3a). This large variation in breeding success may have been caused by methodological issues (variation in chick age at ringing, see Methods) and by environmental stochasticity. Chicks are very vulnerable to rainfall, especially when they are no longer able to shelter under their parents (after *c*. 10 days) but not yet have a waterproof plumage (Jovani & Tella, 2004). Indeed, 15% of the variation in breeding success turned out to be explained by the amount of rain that fell when the chicks were between 0 and 27 days old (the latter being the mean age at ringing, the moment when breeding success is evaluated) and was an important factor in explaining the annual variation in breeding success (2008 was a very dry year, compared with 2007 and 2009, Figure S4). Breeding success increased with increasing age of the parents, which, in combination with the fact that young birds on average breed later in the season, could result in a decrease in breeding success over the season. However, the estimated age effect was not able to explain the magnitude of the observed seasonal decline in breeding success (Figure S5).

To summarize, long-distance migrants, particularly the males and older birds, breed later and, as a result, are likely to recruit fewer offspring than short-distance migrants (Figure 5). As our study is observational, care should be taken to interpret this finding as an effect of migration distance or winter habitat quality on individual fitness, as it could instead be driven by differences in individual quality between the long- and short-distance migrants (Stearns, 1992). It goes without saying that such a quality difference would be interesting in itself. However, we have indications that long-distance migrating spoonbills are unlikely to be poor quality birds given that these birds occupy the traditional wintering areas (Lok, Overdijk, & Piersma, 2013a) and experience similar survival as short-distance migrants in all seasons except during spring migration (Lok et al., 2015). Our results, therefore, suggest that wintering in West Africa, including the long migration to get there and back, incurs a fitness cost and that this cost is sex- and age-dependent. To confirm that within-individual effects (e.g. (lack of) within-individual advancement and senescence) are indeed more important than selective (dis)appearance of early and late breeders in causing the observed age-specific patterns in timing of breeding of long- and short-distance migrants, longer term longitudinal studies should be carried out.

Historically, most spoonbills wintered in West Africa, but the proportion of the population wintering in Europe has increased over the past 20 years (Lok et al., 2013a). This distributional change may have been driven by improved wintering conditions in Europe or deteriorating conditions in West (and North) Africa, and was associated with higher survival of spoonbills wintering in Europe (Lok et al., 2013a). As the results presented here suggest that these birds also recruit more offspring, spoonbills wintering in Europe contribute more to the Dutch breeding population than spoonbills that cross the Sahara to winter in West Africa. This inference is important for predicting the population-level consequences of changes in winter habitat suitability throughout the wintering range.

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AUTHORS' CONTRIBUTIONS

T.L., T.P. and J.T. conceived the ideas and designed methodology; T.L., L.V. and O.O. collected the data; O.O. coordinated the spoonbill colour-ringing programme; T.L. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.8d7m7 (Lok, Veldhoen, Overdijk, Tinbergen, & Piersma, 2017).

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SUPPORTING INFORMATION

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