The paradox of spoonbill migration: most birds travel to where survival rates are lowest

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Migrant birds face a choice where to spend the winter. Presumably there is a trade-off between migration distance (costs) and the quality of the wintering site (benefits). Wintering site fidelity is often high and increases with age. Hypotheses to explain such a pattern assume that wintering site choice maximizes fitness. We compared wintering site choice and age-dependent site fidelity in Eurasian spoonbills, Platalea leucorodia leucorodia, for the period 1992–2010. During their first southward migration, most spoonbills migrated to the southernmost wintering region (Mauritania and Senegal). Other birds were likely to move there from their first to their second winter, whereas hardly any birds moved to a more northerly wintering area. For the rest of their life, spoonbills remained highly site faithful. This resulted in most birds wintering in Mauritania and Senegal with smaller numbers in France and Iberia. We judged suitability of sites on the basis of annual survival probabilities in these three wintering areas. Surprisingly, survival was lowest in Mauritania and Senegal. None of the existing fitness maximization hypotheses explain this pattern and we discuss potential alternatives. Wintering site choice could still be optimal for individual birds if birds wintering in Mauritania and Senegal are competitively inferior to the European winterers or more susceptible to severe winter weather. Alternatively, wintering site choice of spoonbills is suboptimal and, assuming that spoonbills can assess differences in suitability, limited flexibility may prevent them from switching to more suitable sites.

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Migration is one of the most remarkable behaviours of animals and occurs throughout the animal kingdom (Dingle 1980). There is enormous variation in migration tendencies, both within and between species, and sometimes even within populations of the same species. The latter is most pronounced, or at least best documented, in birds. Birds that breed in one area may have an extended wintering range (Newton 2008). Conditions experienced on the wintering grounds have been correlated with components of fitness such as arrival time on the breeding grounds (Marra et al. 1998; Saino et al. 2004), reproductive output (Sedinger et al. 2006) and survival (Peach et al. 1991; Schaub et al. 2005). These wintering conditions, in combination with the route and distance of migration, determine the suitability of a wintering site. When wintering site suitability varies along the wintering range, the choice of a wintering site affects an individual's fitness prospects.

In many species in which breeding populations have an extended wintering range, individuals show high fidelity to a single site (references in Robertson & Cooke 1999; Lindberg et al. 2007; Williams et al. 2008). None the less, the widespread occurrence of age-differential migration, that is, different geographical wintering distributions of juvenile and adult birds (reviewed in Cristol et al. 1999), suggests that at least during early life individuals may change wintering site. This has recently been confirmed by individual-based studies showing young birds to be less faithful to wintering sites than older birds. Wintering site fidelity of Greenland white-fronted geese, Anser albifrons flavirostris, increased from ca. 82% to ca. 95% between the first and fourth year of life (Marchi et al. 2010). Lesser black-backed gulls, Larus fuscus, made large between-winter displacements in the direction of the breeding grounds during the first 3 years of life, after which between-winter displacement distances strongly decreased (Marques et al. 2010).

Two hypotheses, both proposed to explain age-differential migration, predict the optimal wintering site of an individual to change with age. Assuming that dominance status increases with age (Townshend 1985), the dominance hypothesis predicts that young

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birds are forced to winter at suboptimal sites but that they gradually move to more suitable sites (with higher fitness prospects) as they get older (Gauthreaux 1978, 1982). The arrival time hypothesis proposes that it is beneficial for reproductively active (adult) birds to winter closer to the breeding grounds, as this will increase their reproductive output, while this benefit is still absent in immature birds. By inherently assuming a cost for immature birds to start wintering close to the breeding grounds, this hypothesis predicts a shift towards wintering closer to the breeding grounds with age (Myers 1981).

One of the major benefits of being site faithful is assumed to be the familiarity with the environment (familiarity hypothesis, Spaans 1977; Greenwood 1980) and predicts birds to show strong wintering site fidelity in areas in which environmental conditions are relatively predictable from year to year. The benefits of familiarity may outweigh the benefits of moving to another wintering site, even when other wintering sites might have become more suitable.

These hypotheses all assume that migratory behaviour is optimal, that is, it maximizes fitness (sensu Stephens & Krebs 1986). To the best of our knowledge, no study has addressed the presumed optimality of age-dependent wintering site choice and fidelity. Using a long-term data set on individual wintering site selection on an intercontinental scale, we analysed the ontogeny of wintering site choice and fidelity in Eurasian spoonbills, *Platalea leucorodia leucorodia*. Through a combination of a large volunteer observer network and dedicated expeditions to infrequently visited areas, 2179 winter resightings throughout the wintering range, covering a latitudinal range of ca. 4000 km, were collected on 1256 birds that were individually marked as nestlings between 1992 and 2009.

Applying a multistate mark–recapture approach, we investigated whether and how wintering site choice and fidelity changed with age. We simultaneously estimated age-specific annual survival per wintering region. Assuming that suitability is determined by survival rather than reproductive prospects, we used annual survival as a measure of wintering site suitability. We predicted that (1) under the dominance hypothesis, individuals would switch to more suitable areas with age; (2) under the arrival time hypothesis individuals would shift towards wintering closer to the breeding grounds with age. Dominance status may increase gradually with age, and wintering close to the breeding grounds is only beneficial for individuals that have become reproductively active, which in spoonbills takes at least 3 years (de le Court & Aguilera 1997; Bauchau et al. 1998). Therefore, the period of increasing fidelity may extend over more than the first year of life, as observed in other long-lived species (Marchi et al. 2010; Marques et al. 2010). To test for this, we compared alternative models with fidelity as a function of two, three and four age classes, and as a linear function of age. Finally, we predicted that (3) the levels of wintering site fidelity would be highest in the most suitable areas.

METHODS

Study Population

This study is based on the breeding population of Eurasian spoonbills in The Netherlands. This population consisted of 1907 breeding pairs in 2008 and represents about 30% of the total western European population (Lok et al. 2009). The population is migratory and winters primarily in river estuaries and intertidal areas situated along the East Atlantic coast of Europe and West Africa (Cramp 1994). Spoonbills only start breeding when 3 years old. Before breeding, some birds may stay on the wintering grounds during summer, while others perform (partial) seasonal migratory movements. Immature birds are regularly observed at the breeding grounds in The Netherlands in summer (unpublished data). Our study population

shows weak migratory connectivity (Webster et al. 2002), with birds from different wintering areas breeding together in the same colony (unpublished data).

Between 1992 and 2009, 5627 spoonbills were ringed as chicks in 19 different colonies (Appendix Table A1). The colour-ring combinations usually consist of a metal ring and a unique combination of either two inscribed PVC plastic colour-rings or five colour-rings without inscription, including a flag, all carried on the upper leg (tibia). The colour-ring combinations can be read through a telescope up to distances of 300 m.

Study Area

The study area covers the breeding area, The Netherlands, and the entire wintering range of the Western European spoonbill population which ranges from France (migration distance ca. 1000 km) along the East Atlantic coast southward to Senegal (migration distance ca. 5000 km). We divided the study area into four regions (Fig. 1), comprising the breeding region, The Netherlands, where the birds are ringed, and three main wintering regions, France, Iberia (comprising Spain and Portugal) and Mauritania and Senegal in West Africa. The vast majority (ca. 96%) of all resightings made during winter originate from these regions ($N = 4230$) and exclude scattered winter observations from The Netherlands ($N = 58$), United Kingdom ($N = 21$), Morocco ($N = 46$), Canary Islands ($N = 24$), Cape Verde Islands ($N = 10$) and Tunisia ($N = 1$). The latter areas do not clearly fall into one of the three main wintering regions, and would require the definition of additional wintering regions. Because of scarcity of data the parameter estimates for these regions would become very inaccurate.
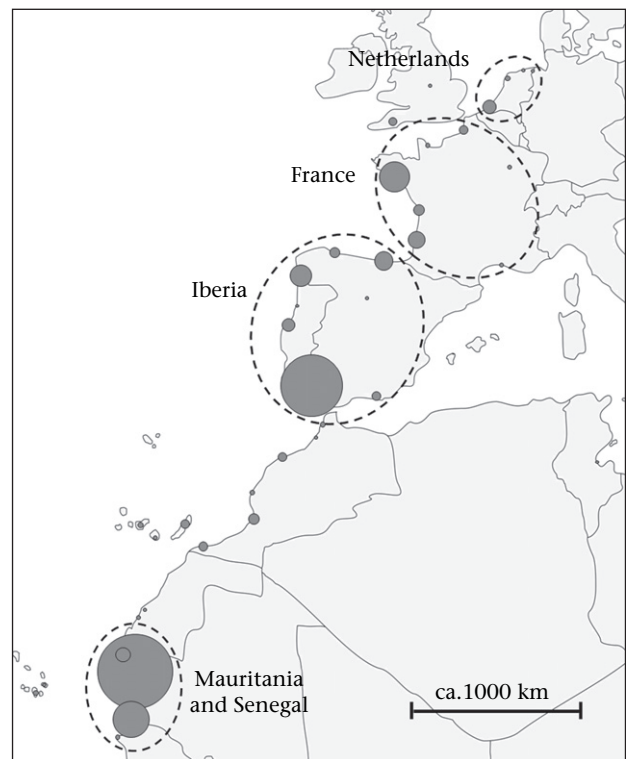

Figure 1. Defined borders of the four regions (dashed circles) and the distribution of winter resightings (dots), where the size of the dots represents the number of different colour-ringed birds observed at each wintering site.

Data Collection and Selection

Observations of colour-ringed spoonbills come from a network of both professional and amateur ornithologists throughout Europe, supplemented by dedicated resighting efforts during expeditions to the Banc d'Arguin National Park in Mauritania (1997–2001 and 2004–2010) and areas in the Senegal delta (Diawling National Park in Mauritania and Guembeul Nature Reserve and Djoudj National Park in Senegal, 1999–2001, 2004, 2008).

The analysis is based on resightings of live birds, which can be treated as recapture data (Lebreton et al. 1992). The first observation refers to the ringing of the bird as a chick in The Netherlands. To select birds at their likely terminal wintering areas, we used resightings between October and February in Mauritania and Senegal, but only the months December and January in France and Iberia, as these sites are known to be used as stopover sites for the birds wintering further south (Navedo et al. 2010). Dead recoveries were excluded from the analysis because they were rare ($N = 12$ birds found in December and January) and because of the uncertainty that these birds actually died in winter.

Ring loss cannot be distinguished from mortality in mark–recapture analyses. However, the fact that spoonbills are ringed with multiple colour-rings, in combination with high resighting probabilities (at least) on the breeding grounds in the Netherlands, makes it likely that ring loss will be detected before all rings are lost. Ring combinations subject to ring loss ($N = 23$) were excluded from the analysis. With these criteria, the data set consists of 1256 spoonbills observed in 2179 bird-winters (Appendix Table A1).

Many birds were observed multiple times (up to 19 times) during single winters (in 742 of the 2179 bird-winters). In 16 of these 742 cases, the same bird was observed in different wintering regions during a single winter. Assuming they were not caused by ring-reading errors, we treated these birds as wintering in the southernmost region where they were observed.

Data Analysis: Multistate Mark–recapture Modelling

We used a multisite (being a specific case of multistate) mark–recapture modelling approach (Arnason 1973; Brownie et al. 1993; Schwarz et al. 1993). This approach is based on individual encounter histories. All individuals start their encounter history when they are ringed on the breeding grounds in The Netherlands. In subsequent winters, individuals may or may not be resighted in one of the three wintering regions, France, Iberia or Mauritania and Senegal. Based on these individual encounter histories, multisite models can estimate site-specific survival probabilities (ϕ_s), that is, the probability of surviving from time i to $i + 1$ given that the individual was on site s at time i, while accounting for potential variation in resighting probabilities between sites (p_s). Survival probabilities reflect local survival, that is, survival within the study area. If there is permanent emigration away from the study area, local survival will be lower than true survival. Moreover, multisite models can estimate transition probabilities ($\psi_{s \cdot d}$, from site s to site d) between all pairs of sites, conditional on survival of the individual. Following Grosbois & Tavecchia (2003), we further separated the transition probabilities between sites into a probability of fidelity to the current site s (f_s) and, conditional on emigration ($1 - f_s$), movement probabilities to any other site d ($\mu_{s \cdot d}$). This allows different parameterizations of fidelity versus movement probabilities. Survival, resighting, fidelity and movement probabilities can further be modelled as a function of, for example, time and age.

To restrict the number of parameters in the models, we assumed all probabilities to be constant over time, with the exception of resighting probability in Mauritania and Senegal, which was allowed to differ between years with dedicated expeditions to either or both

Mauritania and Senegal (1997–2001, 2004–2010) and years without expeditions (e). Survival of young birds is often lower (Francis et al. 1992; Nisbet & Cam 2002) and therefore survival was modelled separately for two age classes (a2): juveniles and older birds. Following the proposed notation of Lebreton et al. (1992), our general model was $\phi_{s \cdot a2} f_s \mu_{s \cdot d} p_{s \cdot e}$.

There are a number of assumptions associated with the mark–recapture modelling approach (Lebreton et al. 1992). Most importantly, it is assumed that there is no heterogeneity in survival, resighting and movement probabilities that has not been accounted for in the general model. Violation of these assumptions will reduce the model fit. To account for this, we assessed the goodness-of-fit of the general model using the median-$\hat{c}$ approach provided by program MARK (White & Burnham 1999). MARK does not allow separate parameterizations for fidelity and movement probabilities, but only for the combination, that is, the transition probabilities ($\psi_{s \cdot d}$, see above). Therefore, the general model did not include an effect of age on fidelity, so that we could rewrite the model as $\phi_{s \cdot a2} \psi_{s \cdot d} p_{s \cdot e}$. The level of overdispersion ($\hat{c}$) was estimated to be a mean $\pm$ SE of 1.59 ± 0.02 and we adjusted $\hat{c}$ accordingly.

As we were interested in survival, fidelity and movement probabilities in relation to wintering region rather than in post-fledging survival between fledging (time of marking) and the first winter, we restricted our analysis to birds that were observed at least once in their wintering area. Nevertheless, the individual encounter histories start with the ringing event as this enables the estimation of first-winter movement probabilities from The Netherlands to each wintering region. Survival between ringing and first-winter observation (with 44% being observed for the first time in their first winter and less than 8% after their sixth winter) is therefore fixed to 1.

Starting with the general model $\phi_{s \cdot a2} f_s \mu_{s \cdot d} p_{s \cdot e}$, we proceeded in three steps. First, we tested whether including an age effect in the fidelity function increased the model fit by comparing fidelity functions with no age classes (.) to up to four age classes (from a2, distinguishing first and >first winter, to a4, distinguishing first, second, third and >third winter birds) as well as a linear effect of age (alin). Furthermore, we assessed whether fidelity differed between wintering regions, either as an additive effect or in interaction with age class, resulting in 14 fidelity functions: $f_{s \cdot a4}$, $f_{s \cdot a3}$, $f_{s \cdot a2}$, $f_{s \cdot alin}$, $f_{s + a4}$, $f_{s + a3}$, $f_{s + a2}$, $f_{s + alin}$, f_{a4}, f_{a3}, f_{a2}, f_{alin}, f_s and $f.$.

During the second step, we tested the significance of the age and region effect on survival, by constraining the best supported model from step 1 by removing either or both the age and the region effect from the survival function, and by testing whether the effect of region differed between juveniles (juv) and older birds (older), or was only present in one of these age classes. This resulted in seven survival functions: $\phi_{s \cdot a2}$, $\phi_{juv + s.older}$, $\phi_{s.juv + older}$, $\phi_{s + a2}$, ϕ_{a2}, ϕ_s and $\phi.$. If multiple fidelity functions found similar support during step 1, we checked the generality of the results of this second step for all these functions.

As a third step, we assessed whether movement probabilities from The Netherlands (NL) to each wintering region during the first winter were different by testing a model in which these probabilities differed between the three wintering regions against a model in which these probabilities were constrained to be the same, i.e. 1/3 for moving to each of the three wintering regions ($\mu_{NL \rightarrow France} = \mu_{NL \rightarrow Iberia} = \mu_{NL \rightarrow Mauritania and Senegal} = 1/3$), starting from the best supported model from step 2. Moreover, we tested for each wintering region whether emigration probability was biased towards one of the remaining two wintering regions by testing a model in which subsequent movement probabilities differed between the two remaining regions and a model in which these probabilities were constrained to be the same, i.e. 0.5. If multiple survival functions found similar support during step 2,

we checked the generality of the results of this third step for all these functions.

We used program E-SURGE 1.7.1 (Choquet et al. 2009) to obtain maximum likelihood estimates of the parameters and to perform model selection. Because multisite models are sensitive to local minima during the likelihood maximization procedure, we ran each model three times with different initial parameter values to ensure convergence to the lowest deviance (Lebreton & Pradel 2002). Model selection was based on the quasi Akaike information criterion, corrected for small sample sizes and overdispersion (QAIC$_c$, Akaike 1973; Burnham & Anderson 2002). A model was considered to explain the data significantly better when it had at least two QAIC$_c$ points less than competing models. Parameter estimates are derived from the best supported model from step 3.

Obviously, the estimated degree of wintering site fidelity will be a function of the spatial 'grain' of the analysis (Robertson & Cooke 1999). To get an idea of the spatial scale dependence of the level of fidelity estimated by the multisite mark–recapture modelling approach, we performed an additional analysis based on the distribution of between-winter displacement distances. By taking the ratio of the number of displacements within a given distance (for example, 0–20 km) against the total number of between-winter movements (0–4000 km), a rough estimate of fidelity to a certain area (from now on referred to as 'fidelity ratio') can be calculated. Note, however, that the estimated fidelity ratios using this method are sensitive to spatial variation in survival and resighting probabilities. We calculated these fidelity ratios for a range of scales (from fidelity within 0 km to fidelity within 1000 km) and compared these with the values of true wintering site fidelity on a regional level (Fig. 1) to assess the spatial scale dependence of wintering site fidelity of spoonbills.

RESULTS

Models that did not include an age*region interaction in the fidelity function had ΔQAIC$_c$ values of 30.95–44.14 and were not competitive. The model with two age classes (first and >first winter) was unequivocally best supported, as adding more age classes increased the QAIC$_c$ value and the model with a linear effect of age had a ΔQAIC$_c$ > 2 (Table 1). Wintering site fidelity was lower for juvenile birds (fidelity from first to second winter) than for older birds, but only in European wintering regions (Fig. 2a). In Mauritania and Senegal, birds showed high levels of site fidelity throughout life. Adult birds showed high levels of site fidelity in all wintering regions. Resighting probabilities were high in France (mean ± SE = 0.58 ± 0.05) and Iberia (0.40 ± 0.02). Expeditions to Mauritania and Senegal strongly increased resighting probability, from 0.04 ± 0.01 in years without expeditions to 0.37 ± 0.02 in years with expeditions to these West African winter quarters.
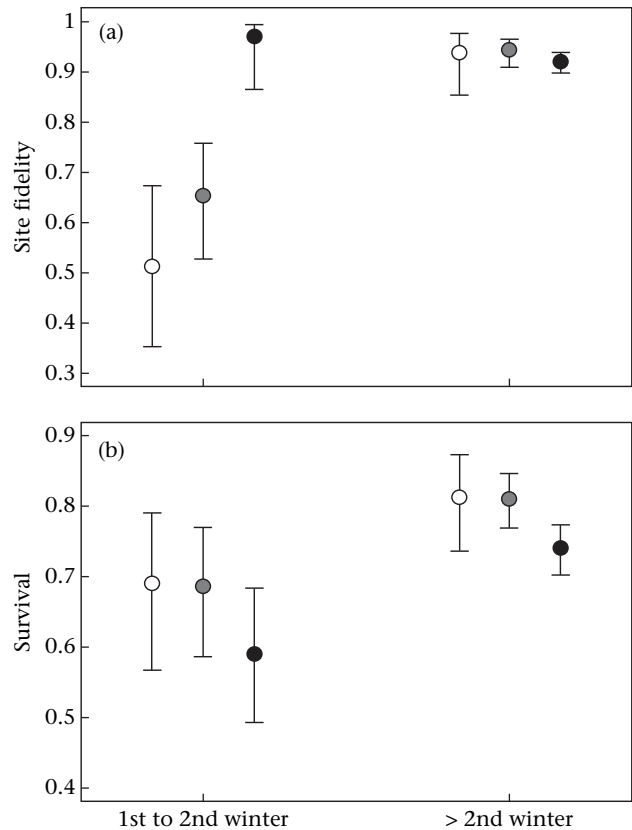

Figure 2. (a) Estimates of wintering site fidelity to France (open dots), Iberia (grey dots) and Mauritania and Senegal (black dots) as a function of age. (b) Estimates of annual survival probabilities in France (open dots), Iberia (grey dots) and Mauritania and Senegal (black dots) as a function of age. Estimates are based on the best supported model (model 3, Table 3). Vertical lines indicate 95% confidence intervals.

The best supported survival model included an additive effect of age and region (Table 2, Fig. 2b). Survival of juveniles (from first to second winter) was significantly lower than that of older birds. Moreover, the region effect on survival was significant and seemed similar for juvenile and older birds (model 4 versus model 5), rather than to be different for juveniles and adults (model 1), or to be only present in juveniles (model 3, Table 2). However, the model in which the survival of only older birds differed between regions (model 2) had similar support. This indicates that there is an effect of wintering region on juvenile survival, although not a very strong one. This may be caused by the small sample size, as the estimates of juvenile survival are based on only first-winter birds. Survival was lower in Mauritania and Senegal than in France and Iberia.

Table 1
Model results of site fidelity (*f*) as different functions of site of origin (s) and age

Fidelity function	K	Deviance	ΔQAIC$_c$	Akaike weight
s·a2*	21	12075.26	0	0.55
s·a3	24	12066.79	0.76	0.37
s·a4	27	12063.50	4.78	0.05
s·alin	21	12084.32	5.70	0.03

alin = linear effect of age, a2 = first and >first winter, a3 = first, second and >second winter, a4 = first, second, third and >third winter. Other parameters are modelled as in the general model ($\phi_{s \cdot a2}$ $\mu_{s \cdot d}$ $p_{s \cdot e}$). Only models with an Akaike weight of ≥ 0.01 are shown.
 * QAIC$_c$ = 7636.77.

Table 2
Model results of survival (φ) as different functions of site of origin (s) and two age classes (a2)

Survival function	K	Deviance	ΔQAIC$_c$	Akaike weight
(4) s+a2*	19	12075.48	0	0.45
(2) juv+s.older	19	12076.17	0.44	0.36
(5) a2	17	12087.21	3.34	0.08
(1) s·a2	21	12075.26	3.91	0.06
(6) s	18	12088.05	5.88	0.02
(3) s.juv+older	19	12085.79	6.49	0.02
(7) .	16	12098.68	8.53	0.01

juv = first-winter birds, older = > first-winter birds, (.) = modelled as constant. Other parameters are modelled as in the best supported fidelity model ($f_{s \cdot a2}$ $\mu_{s \cdot d}$ $p_{s \cdot e}$, Table 1).
 * QAIC$_c$ = 7632.86.

First-winter movement probabilities differed significantly between wintering regions (model 2 versus model 1, Table 3) and increased towards the south. Juveniles had the highest probability of migrating to Mauritania and Senegal (0.52 ± 0.03), intermediate to Iberia (0.36 ± 0.03) and lowest to France (0.12 ± 0.01). Between-winter movements were most likely to be directed towards the southernmost remaining region, being significant for Iberia (model 4 versus model 1, Table 3) and Mauritania and Senegal (model 5 versus model 1, Table 3), but not for France (model 3 versus model 1). Birds emigrating from Iberia were most likely to go to Mauritania and Senegal (0.94 ± 0.03) rather than to France and birds emigrating from these West African countries were most likely to go to Iberia (0.90 ± 0.04). Similar results were obtained when step 3 was performed on the second best model from step 2 (model 2, Table 2). The combined processes of age-specific site fidelity and movement probabilities resulted in a geographical range shift between the first and second winter towards more southern wintering regions (Fig. 3).

Fidelity ratios depended on the spatial scale examined and strongly increased up to a displacement distance of 100 km (Fig. 4). Between 500 and 2000 km, comparable to the spatial scale of our study, fidelity ratios approximated our estimated values of true wintering site fidelity, at least for adult birds (0.92–0.94, Fig. 4).

DISCUSSION

During their first southward migration, most spoonbills (52%) migrated to the southernmost wintering region (Mauritania and Senegal) while others moved there from the first to the second winter, owing to a combination of low site fidelity of first-winter birds to European wintering regions and a high probability that these birds moved to Mauritania and Senegal. Adult birds were highly site faithful to all wintering regions. This resulted in most adult birds ending up wintering in Mauritania and Senegal (66% in the second winter, against 7% in France and 27% in Iberia, Fig. 3). Surprisingly, survival probability was estimated to be lowest for birds wintering in this seemingly preferred area.

Wintering site fidelity was significantly lower in first-winter birds than in older birds, although this difference was only apparent in European wintering regions. Such an age-dependent increase in wintering site fidelity was also found in Greenland white-fronted geese (Marchi et al. 2010) and was suggested to be caused by young birds switching to the wintering site of their partner after pairing outside the wintering grounds. However, this reasoning
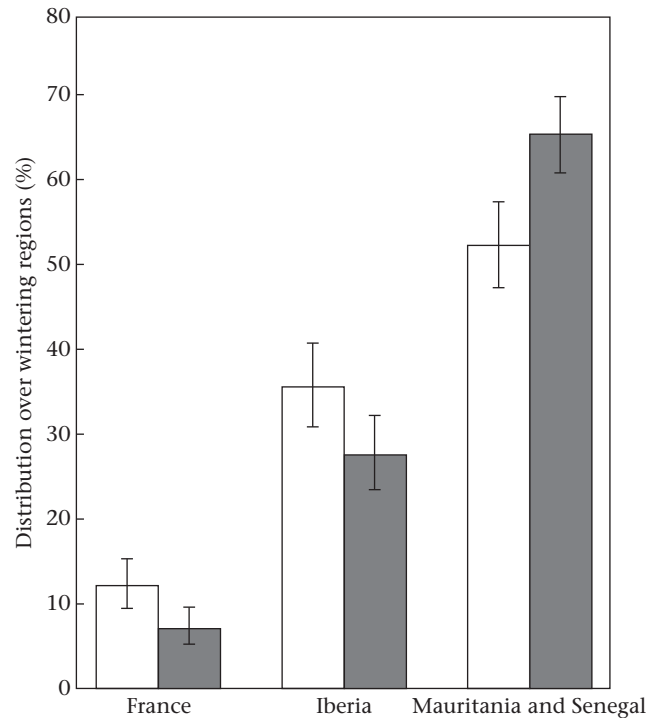

Figure 3. Predicted distribution of first-winter (white bars) and second-winter (grey bars) birds over the three wintering regions. Predictions are based on the estimated probabilities of movement and site fidelity from the best supported model (model 3, Table 3) by assuming constant juvenile survival. Vertical lines indicate 95% confidence intervals calculated using the Delta method (Cox 1998).

cannot hold for spoonbills because they do not form pairs for life (unpublished data).

Our finding that spoonbills move southwards between their first and second winter and stay faithful afterwards means that adult birds winter further away from the breeding grounds than juveniles (Fig. 3). This is opposite to most age-differential migrants
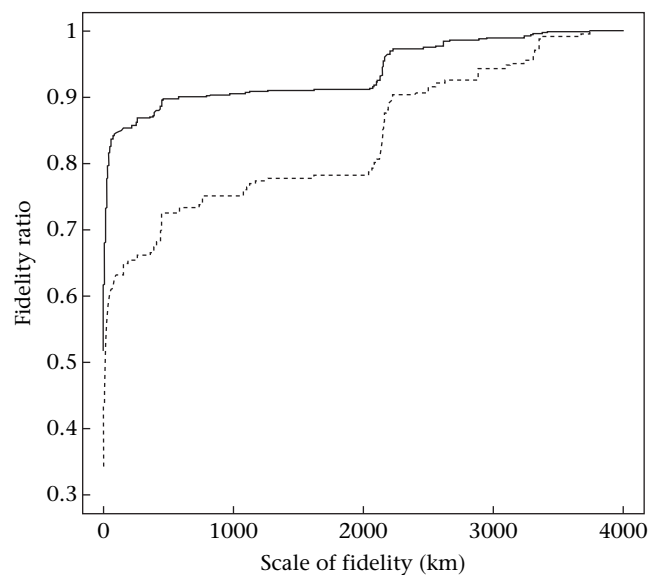
Table 3
Model results of movement (μ)

Model	K	Deviance	$\Delta QAIC_c$	Akaike weight
(3) $\mu^{\text{NL-winter}}_d \; \mu^{\text{between winter}}_{s(I,A)}$*	18	12076.03	0.00	0.70
(1) $\mu^{\text{NL-winter}}_d \; \mu^{\text{between winter}}_{s(all)}$	19	12075.48	1.67	0.30
(5) $\mu^{\text{NL-winter}}_d \; \mu^{\text{between winter}}_{s(F,I)}$	18	12146.28	44.18	0.00
(4) $\mu^{\text{NL-winter}}_d \; \mu^{\text{between winter}}_{s(F,A)}$	18	12146.31	44.20	0.00
(2) $\mu^{\text{NL-winter}}_. \; \mu^{\text{between winter}}_{s(all)}$	17	12232.70	96.51	0.00

First-winter movements ($\mu^{\text{NL-winter}}$) are modelled as a function of site of destination (d) or as constant (.), i.e. equal ($1/3$) for all three wintering region. Subsequent between-winter movements ($\mu^{\text{between winter}}$) from each site of origin (s) to either of the two remaining wintering regions were modelled to be different ($\neq 0.5$) for all sites, s(all), or to be equal (i.e. 0.5), separately modelled for each site (s(I,A), s(F,A) and s(F,I)). For example, the model $\mu^{\text{between winter}}_{s(I,A)}$ implies that only for birds leaving France, subsequent movements to Iberia and Mauritania and Senegal were constrained to be equal (0.5). Other parameters are modelled as in the best supported survival model ($\phi_{s+a2} f_{s \cdot a2} p_{s \cdot e}$, Table 2).
  * $QAIC_c = 7631.19$.

Figure 4. Fidelity ratios for site fidelity within 0 km up until fidelity within 4000 km between the first and later winters (dashed line) and between later winters (solid line). Multiple between-winter movement distances of the same individuals are included in the calculations.

(Cristol et al. 1999; Marques et al. 2010) and indicates that the arrival time hypothesis, stating that it is beneficial for reproductively active birds to winter closer to the breeding grounds, does not apply to spoonbills.

The dominance hypothesis predicts that young birds, because they become more dominant in the course of their life, should gradually move towards more suitable wintering areas, that is, areas with better survival prospects. The pattern observed is precisely the opposite. Most movements between the first and second winter are away from Europe to the wintering region with the lowest survival probability (Mauritania and Senegal). By the second winter, most birds are wintering in Mauritania and Senegal (66%, Fig. 3) and remain faithful to this wintering region. Therefore, the prediction from the dominance hypothesis is also rejected, as is the prediction that wintering site fidelity should be highest in the areas associated with the highest survival.

We used the annual survival probability of birds in a wintering region as a measure of the suitability of the wintering site but ignored the possible effect of wintering site on reproductive output. Although, in practice, spoonbills wintering in Mauritania and Senegal could compensate for lower survival by higher reproductive rates, we are not aware of any studies that have found a positive relationship between migration distance and breeding success. In fact, Hötker (2002) showed that in pied avocets, *Recurvirostra avosetta*, along the same flyway with approximately the same variation in wintering destinations, the shorter-distance migrants arrived earlier at the breeding grounds than the longer-distance ones, with early arrival being positively correlated with breeding success. No relationship between migration distance, arrival time and breeding success was detected in a population of Icelandic black-tailed godwits, *Limosa limosa islandica* (Gunnarsson et al. 2006).

If birds wintering in Mauritania and Senegal indeed have lower fitness, the observed movements could still reflect an adaptive behavioural choice if individuals differed in the costs and benefits associated with wintering site choice. This could be the result of differences in individual 'quality'. Such 'quality' can refer to competitive ability, with birds wintering in Mauritania and Senegal being competitively excluded from the more suitable wintering sites in Europe. This seems in contradiction with the observation that a considerable number of juveniles stay in France and Iberia in their first winter but move to Mauritania and Senegal in the subsequent winter. But perhaps these are the poor-quality juveniles that cannot escape competition with the older birds in France and Iberia, for example because they hatched relatively late in the season. If this were the case, birds that move further south between the first and second winter are predicted to have a lower survival probability than birds that are site faithful throughout life. Currently, sample sizes are still too low to test this prediction.

Alternatively, some birds may be physiologically better capable of coping with the relatively harsh wintering conditions in France and Iberia than others, for example because of individual differences in body size (Ketterson & Nolan 1976). Such birds would be better off by not having to pay the survival cost of migrating across the Saharan desert. In this case, the southward movement of birds from the first to the second winter could be the result of deteriorating conditions in Europe during the first winter or subsequent autumn, causing birds that are unable to handle these harsher wintering conditions to winter further south in their second winter.

We should also consider the possibility that wintering site choice in many spoonbills (i.e. those wintering in Mauritania and Senegal) is suboptimal. What could cause spoonbills to choose the wintering site in which birds have the lowest survival? Young birds may have an explorative period during which they make their decision where to spend the winter (Baker 1978, 1982). If, during this period, individuals do not face the suite of environmental conditions that overall determine the suitability of a wintering region, they may make the wrong decision. For example, to reach wintering sites in Mauritania and Senegal, spoonbills have to cross the Sahara. During southward migration, weather conditions are generally favourable as migrating birds benefit from the trade winds blowing in a southwest direction at altitudes at which spoonbills are known to fly during southward migration (unpublished data from GPS transmitters). Moreover, the climate and perhaps also the food conditions may be good in Mauritania and Senegal. However, crossing the Sahara on their way back will be much harder. During this flight the trade winds cause a high incidence of headwinds at low altitudes of flight (Piersma & van de Sant 1992; Shamoun-Baranes et al. 2010); this reduces migration speed and increases energy demands (Liechti & Bruderer 1998; Shamoun-Baranes et al. 2003). Since some of the immature spoonbills remain on the wintering grounds for 1 or 2 years (before breeding when 3 years old), birds will face the supposedly harsh spring migration conditions only after some years. This late experience may prevent birds switching to more favourable wintering sites as they may have lost behavioural flexibility by then, as indicated by the strong site fidelity shown from the second winter onwards (Baker 1978, 1982). Such a scenario would cause spoonbills to get 'trapped' in suboptimal wintering sites south of the Sahara.

Suboptimal wintering site choice may also occur when the relative suitability of wintering regions has changed over time, but the evolutionary response of spoonbills has been too slow to adjust to these changes. An increasing proportion of spoonbills have started wintering in Europe over the last few decades (unpublished data). Moreover, climate change has been predicted to cause a northward shift of the wintering distribution of the black-faced spoonbill, *Platalea minor* (Hu et al. 2010). This suggests that wintering sites in the northern part of the wintering range may have become more suitable over time.

Spoonbills do not migrate in family formation (as inferred from colour-ring readings of both parents and their offspring during the migratory period; unpublished data) and, therefore, wintering site choice is not socially inherited from the parents. However, it is still possible that immature birds follow older, more experienced, birds during migration (Avital & Jablonka 2000). First-year birds generally migrate later than older birds (Navedo 2008), suggesting that some are unable to use the experience of older birds during their first southward migration. Yet, during the subsequent autumn these birds may decide to join older birds flying towards more southern wintering sites than where they had spent their first winter, which could explain the southward movement of spoonbills between their first and second winter. Such social inheritance could result in suboptimal wintering traditions when wintering site suitability is changing.

Alternatively, suboptimal wintering site choice may arise when an individual's wintering site is primarily genetically determined (Berthold 2001) and the rate of natural selection, favouring European winterers, is slower than the rate of environmental change. However, the fact that many spoonbills switch wintering sites between their first and second winter makes it rather unlikely that the wintering site of an individual is primarily genetically determined.

Although most spoonbills currently end up wintering in Mauritania and Senegal, a considerable part of the adult spoonbill population (34%, Fig. 3) does winter in Europe. If they are of 'good quality' or have 'good genes' and raise offspring that will also winter in Europe, or if, through social inheritance, they encourage

young spoonbills not to cross the Sahara, this behavioural option is expected to increase in the future.

Acknowledgments

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APPENDIX

Table A1
The number of spoonbills ringed, resighted in winter and resighted per wintering region, specified per year of birth, and the number of different birds resighted per winter

Year of birth	Ringed	Resighted in winter	Resighted per wintering region			Winter	Number of different birds resighted per winter		
			France	Iberia	Mauritania and Senegal		France	Iberia	Mauritania and Senegal
1992	279	50	4	19	33	'92–'93	0	7	0
1993	271	58	8	19	37	'93–'94	5	8	0
1994	300	67	4	30	39	'94–'95	8	13	11
1995*	0	0	0	0	0	'95–'96	3	7	7
1996	233	92	15	34	61	'96–'97	12	30	42
1997	221	91	10	26	71	'97–'98	15	34	87
1998	214	83	3	17	68	'98–'99	9	30	141
1999	330	114	12	35	74	'99–'00	16	25	118
2000	195	55	9	28	26	'00–'01	16	19	123
2001	265	73	21	39	23	'01–'02	25	38	1
2002	184	41	2	26	17	'02–'03	12	39	10
2003	301	66	5	36	29	'03–'04	17	91	32
2004	393	78	8	46	32	'04–'05	15	94	11
2005	395	109	9	29	78	'05–'06	12	104	68
2006	460	110	18	46	51	'06–'07	28	63	87
2007	483	65	5	37	26	'07–'08	34	122	137
2008	592	80	10	22	48	'08–'09	31	82	129
2009	511	24	6	12	6	'09–'10	17	62	32
Total	5627	1256	149	501	719		275	868	1036

*No spoonbill chicks were ringed in 1995.