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Migration Tendency Delays Distributional Response to Differential Survival Prospects along a Flyway

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ABSTRACT: When populations grow or decline, habitat selection may change due to local density-dependent processes, such as site dependence and interference. In seasonally migrating animals, non-breeding distributions may be determined through these mechanisms of density dependence, which we examine here at a hemispheric scale for a long-distance migrating bird. Using summer and winter resightings of 2,095 Eurasian spoonbills *Platalea leucorodia leucorodia* that were ringed in the Netherlands during 16 years of fast population growth, we show that neither site dependence nor interference fully explains their patterns of survival and winter distribution. Within their three main wintering areas, annual survival decreased with an increase in population size. While survival was consistently higher in the two European wintering areas (France, Iberia), most spoonbills migrated onward to winter in west Africa. The number of birds wintering in Europe increased, but not enough to maximize annual survival. We conclude that a constraint of tradition (their “migration tendency”) inhibits birds from changing their migratory habits. We pose that this phenomenon may similarly constrain other migratory populations from rapidly responding to large-scale climate- and/or human-driven habitat changes at their wintering grounds.

Keywords: climate change, density dependence, habitat change, long-distance migration, multievent mark-recapture modeling, winter site choice.

Introduction

Population regulation is an important theme in ecology, and density-dependent processes are seen to be driving this phenomenon, yet the mechanisms involved remain poorly understood (Begon et al. 2006). Two main mechanisms have been proposed as the cause of density dependence in vital rates: (1) site dependence and (2) interference (Ferrer and Donazar 1996; Rodenhouse et al. 1997). The site dependence hypothesis predicts that ani-

mals utilize available sites in a preemptive manner and distribute according to the ideal preemptive distribution (fig. 1; Kluyver and Tinbergen 1953; Brown 1969; Pulliam and Danielson 1991). This hypothesis assumes that sites differ in suitability for survival and/or reproduction (fig. 1A), leading to density dependence in vital rates as poorer-quality sites are only utilized during times of higher population sizes. Alternatively, it is thought that population regulation may occur through increased levels of interference competition within sites at higher population densities, resulting in a decrease in individual survival and/or reproductive success (fig. 1B). The interference hypothesis predicts that all individuals have equal fitness and distribute according to the ideal free distribution (fig. 1; Fretwell and Lucas 1970).

Both hypotheses lead to the prediction that during population growth there will be a population-level (density-dependent) decrease in vital rates (survival and/or reproduction), as well as a change in the distribution of individuals over habitats when these habitats differ in initial suitability for survival and/or reproduction (hereafter called “habitat quality”). At low population sizes, animals are predicted to choose the highest-quality habitat. With increasing population size, animals are predicted to increasingly occupy lower-quality habitats, either (1) because newly settling individuals are prevented from using the most suitable habitat as it is already occupied by other individuals and are therefore forced to settle in less suitable habitats (site dependence; fig. 1A, 1C) or (2) because interference mechanisms reduced the suitability of the higher-quality habitat to the level of the lower (interference; fig. 1B, 1D). The two hypotheses differ in their predictions with respect to density-dependent changes in vital rates within and between sites. The site dependence hypothesis predicts constant vital rates within sites but differences in these rates among sites (i.e., among individuals in different sites; fig. 1E). The interference hypothesis predicts changes in vital rates within individuals (hence within

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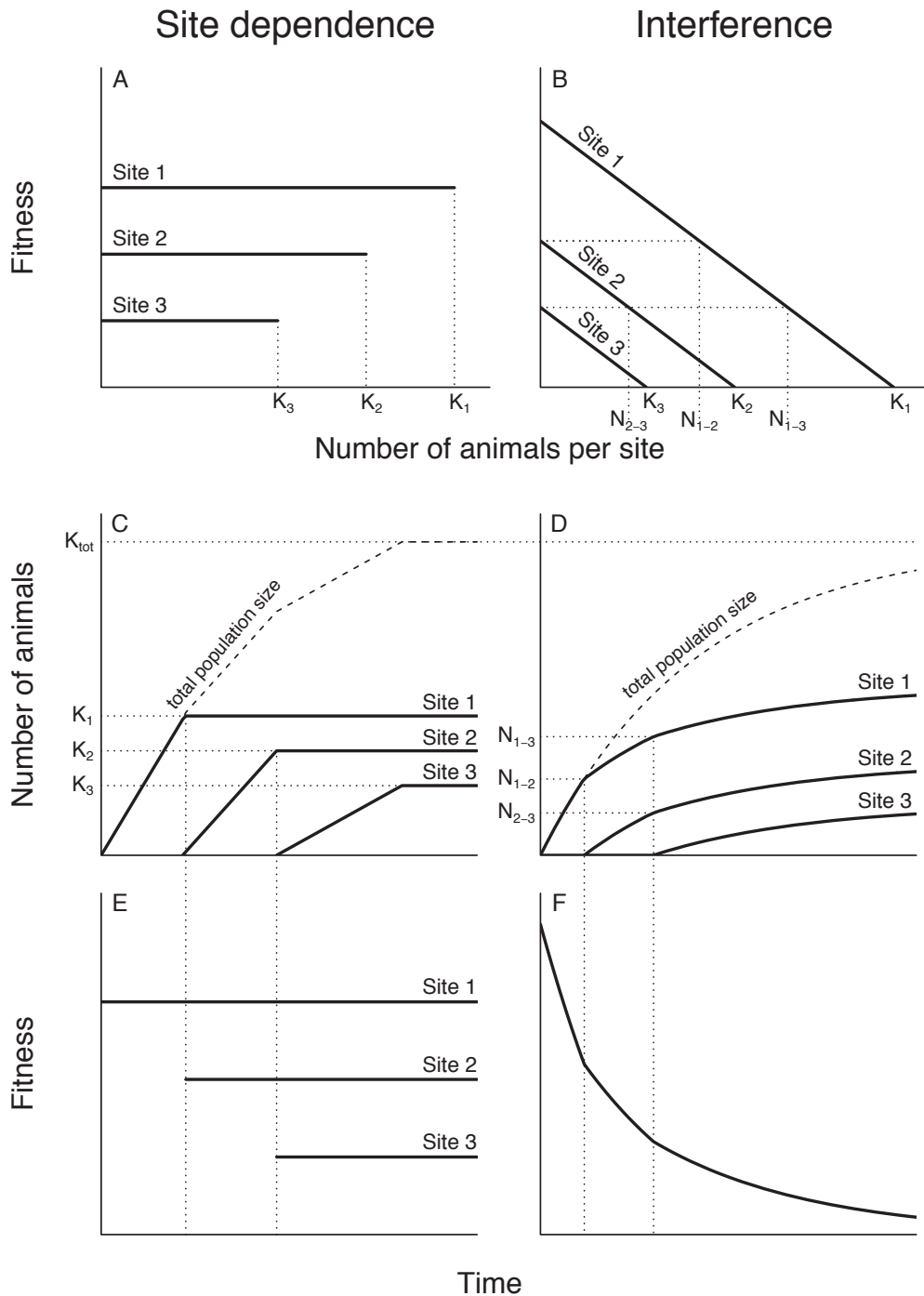


Figure 1: Assumptions and predictions of the site dependence and interference hypothesis (left vs. right columns). *A, B*, Hypothetical relationships between the number of animals and individual fitness are shown for three sites that differ in quality (i.e., in maximum fitness). For graphical clarity, the carrying capacities, that is, the maximum number of individuals that each site can harbor (K_1 , K_2 , K_3) differ between *A* and *B*, but the total maximum number of individuals over all sites (K_{tot} ; see *C* and *D*) is the same. The interference hypothesis predicts that fitness decreases within individuals (and consequently, within sites) and that individuals should distribute in such a way that they have equal fitness. Consequently, individuals should start occupying site 2 when site 1 harbors at least N_{1-2} individuals, and site 3 when site 1 harbors at least N_{1-3} and site 2 N_{2-3} individuals. *C, D*, Predicted distribution of animals over the different sites, and *E, F*, individual fitness within each site over time, that is, during population growth, are shown.

sites) and similar vital rates among sites at any one moment (i.e., at any specific total population size; fig. 1F).

The two hypotheses have been widely tested with respect to small-scale habitat use in territorial animals during either the breeding or nonbreeding season. Both site dependence (with territories or habitat types defined as sites) and interference mechanisms have been proposed to explain density dependence in reproductive success (Morris 1989, 1991; Ferrer and Donazar 1996; Rodenhouse et al. 2003; Gunnarsson et al. 2005b; Nevoux et al. 2011) and survival (Holbrook and Schmitt 2002; Latta and Faaborg 2002; Studds and Marra 2005; Nevoux et al. 2011). While interference mechanisms, operating through local interactions between individuals, will be detected in such small-scale studies, the site dependence hypothesis may be incorrectly rejected when it occurs beyond the spatial scale of territories. The few studies investigating the two hypotheses at larger scales have focused on the distribution of migratory birds during the nonbreeding season. Gill et al. (2001) found evidence of site dependence in winter in a growing population of Icelandic black-tailed godwits *Limosa limosa islandica* across southern England. In this study, sites that were occupied last were associated with lower survival rates and later arrival on the breeding grounds (correlated with lower breeding success; Gunnarsson et al. 2005a). Although covering intersite distances of between 100 and 500 km, the Gill et al. study examined only part of the entire wintering range, which extends from the United Kingdom to Portugal (Alves et al. 2012). In contrast, Quaintenne et al. (2011) used predicted intake rates as a surrogate measure of fitness and established that the distribution of red knots *Calidris canutus islandica* throughout western Europe most closely resembled an ideal free distribution. Although covering an entire wintering range, the spatial scale was relatively small (intersite distances up to 1,000 km) compared to the hemispheric wintering ranges of many migratory birds (Alerstam 1990; Newton 2008).

In the study reported here, we investigated whether the two kinds of density-dependent processes could be applied at the scale of an entire hemispheric flyway. Rather than fitness surrogates (e.g., intake rate), we estimated survival (a direct component of fitness) from mark-recapture data of the rapidly growing Dutch breeding population of Eurasian spoonbills *Platalea leucorodia leucorodia*. These birds winter along the Atlantic coast from France in the north to Senegal in the south, spanning a latitudinal range of 4,000 km (Lok et al. 2011). During the 16-year study period from 1994 to 2010, the number of breeding pairs has increased almost fourfold to approximately 2,300; a growth that was accompanied by density-dependent decreases in adult survival (Lok et al. 2009). This decrease manifested itself mainly during the end of winter and the actual north-

ward migration (T. Lok et al., unpublished manuscript), suggesting that, similar to the Icelandic godwits (Gill et al. 2001), density-dependent effects on survival occurred during the nonbreeding season.

For our study, we divided the wintering range into three regions (France, Iberia, and Mauritania and Senegal) and investigated whether either the site dependence hypothesis or interference hypothesis can explain the hemispheric winter distribution of adult spoonbills along the east Atlantic flyway. Applying the recently developed multievent mark-recapture modeling technique (Pradel 2005; Choquet et al. 2009) allowed us to simultaneously estimate region-specific survival and distribution over these regions to test the predictions that at low population sizes, most birds winter in the highest survival region (both hypotheses: fig. 1C, 1D; prediction 1); and to distinguish among the two hypotheses, that either survival differs among regions, with individuals wintering in more recently occupied regions having lower survival (site dependence: fig. 1E; prediction 2) or survival is the same in all occupied regions and decreases at equal rates within regions (interference: fig. 1F; prediction 3).

Our results show that the hemispheric winter distribution of a long-distance migrating bird was neither ideal preemptive (site dependence) nor ideal free (interference) and that the achievement of an optimal winter distribution appears to be constrained by a tendency (tradition) of the birds to migrate long distances. This is an important result, as it suggests an intrinsic reason as to why migratory populations may be limited in their ability to respond to large-scale climate- and/or human-driven habitat changes in winter.

Methods

Study Population, Data Collection, and Selection

This study is based on the data of Eurasian spoonbills that breed in the Netherlands and winter along the east Atlantic coast between France and Senegal (fig. 2). The study population demonstrates a lack of migratory connectivity, with birds from the same breeding colony consistently using different wintering regions. Between 1988 and 2007, 5,092 spoonbills were color-ringed before fledging. The recorded observations of these color-ringed spoonbills come from a large network of voluntary and professional ring-readers throughout Europe, supplemented by dedicated expeditions to major wintering areas in west Africa: the Banc d'Arguin National Park (Mauritania) and the Senegal delta (Mauritania and Senegal).

As the survival rates associated with wintering in a specific area come to light only when birds migrate, our analysis was restricted to adult birds. Immature birds generally

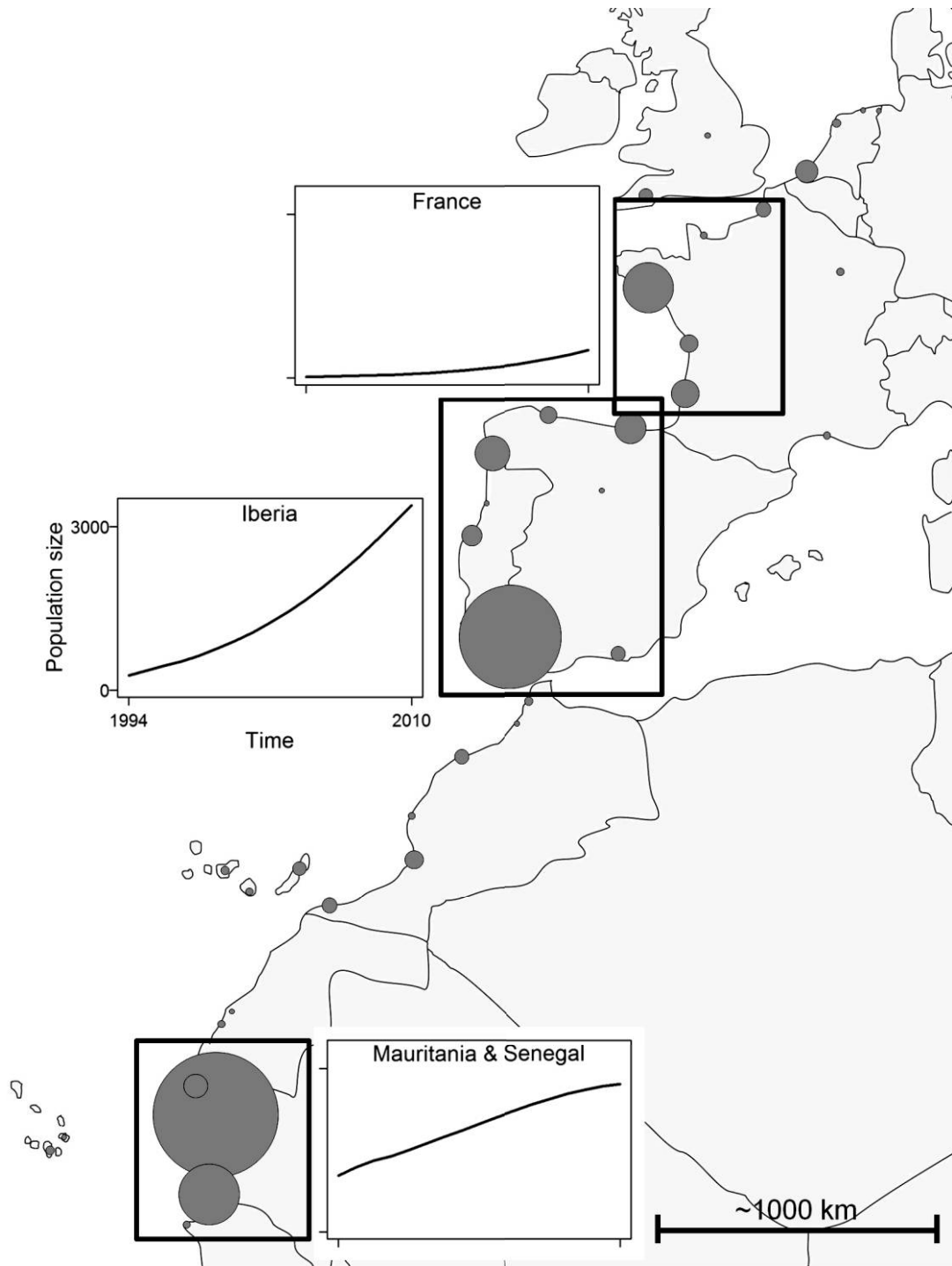


Figure 2: Map of the three wintering regions. The dots represent the sites where birds have been resighted, and the size of the dots reflects the number of different color-ringed birds observed in winter. The graphs show the estimated number of wintering Dutch spoonbills (for assumptions and calculations, see app. B, available online) in each region over time and have the same scales on the axes.

remain in the wintering areas and return to the Netherlands only in their third year to begin breeding (Lok et al. 2011). We considered individuals as adult from their third winter, that is, just before their first northward migration to the breeding grounds, and onward. For this study, we selected data of spoonbills that had been color-ringed as chicks in the Netherlands between 1988 and 2007 and who were then resighted as adults between 1994 and 2010 ($n = 2,095$), either in summer in the Netherlands ($n = 1,931$) and/or in winter in one of the three main wintering regions ($n = 783$): France, Iberia (Spain and Portugal), and Mauritania and Senegal (see Lok et al. 2011; for further details, see table A1, available online). Data gathered before 1994 were excluded because resightings in winter were too sparse. On the few occasions where individuals were observed in different wintering regions within a winter, we treated these birds as wintering in the southernmost region where they were observed (see also Lok et al. 2011). To avoid overparameterization of the models, we assumed that individuals do not change between wintering sites. This is supported by the fact that adult birds are highly faithful to their wintering region (Lok et al. 2011). For this reason, the winter resightings of the small number of birds that were observed in different wintering regions in different years were excluded (51 out of 783 adult birds that were observed in winter; for directions of their movements over time, see fig. A1, available online).

Multievent Mark-Recapture Modeling

Multievent mark-recapture models are a special type of multistate models, where observations (“events”) and states are decoupled, resulting in a flexible modeling framework that allows the implementation of state uncertainty (Pradel 2005, 2009). In our case, the state of an individual is related to its wintering area. We defined four states: wintering in France (F), wintering in Iberia (I), wintering in Mauritania or Senegal (MS), and dead (D); and five events: observed in summer in the Netherlands (1), observed in winter in France (2), observed in winter in Iberia (3), observed in winter in Mauritania or Senegal (4), and not observed (0). Some individuals were observed only in summer in the Netherlands, and hence, their wintering state is unknown. However, their probability of wintering in any of the wintering regions can still be estimated by comparing their probabilities of survival (estimated from the summer resightings) and resighting (e.g., the fact that they were never resighted in winter makes it more likely that they wintered in an area with a low resighting probability) with birds with a known wintering state (those observed in winter).

Multievent models have three fundamental types of pa-

rameters: initial state probabilities, transition probabilities, and event probabilities, which are effectively described by matrices (Pradel 2009). Initial state probabilities describe the probability to be in any specific state when first encountered. As no individual starts in the dead state, we have three initial states:

$$\Pi_t = \begin{bmatrix} \pi_F & \pi_I & 1 - \pi_F - \pi_I \end{bmatrix}$$

The transition probabilities describe the probabilities of transition among states, as in multistate models. By enforcing the restriction that individuals do not change wintering sites, the initial state probabilities reflect the probability that an individual will spend the winter in any of the three wintering regions for the remainder of its life. To test whether these probabilities changed over time, that is, during population growth, we modeled them either as constant (c) or as a function of the individual covariate, the year of birth (yb).

Without state transitions, the transition matrix is in fact the survival matrix, with departure states in rows and arrival states in columns:

$$\Phi_t = \begin{matrix} & \begin{matrix} F & I & MS & D \end{matrix} \\ \begin{matrix} F \\ I \\ MS \\ D \end{matrix} & \begin{bmatrix} \phi_F & 0 & 0 & 1 - \phi_F \\ 0 & \phi_I & 0 & 1 - \phi_I \\ 0 & 0 & \phi_{MS} & 1 - \phi_{MS} \\ 0 & 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

Survival is not distinguished from permanent emigration in this model and should therefore be considered “apparent survival” (Lebreton et al. 1992). Nevertheless, the survival estimates presented here will closely resemble true survival rates because we use resightings throughout the geographical range of the population. In all models, survival was estimated for two seasons (summer-winter and winter-summer; see below) and separately for each wintering state. Exploratory analyses showed that data was too scarce to additionally model annual variation in survival. Based on previous results (T. Lok et al., unpublished manuscript), we assumed survival in the summer-winter interval (ϕ_{s-w}) to be constant (c) and survival in the winter-summer interval (ϕ_{w-s}) to be density dependent. The metapopulation of spoonbills (western European and Mauritanian breeding populations mix in winter) has increased over time (T. Lok et al., unpublished manuscript), but accurate annual counts in the wintering areas are lacking. Therefore, we used a linear function of time as a proxy of the increase in population size and modeled ϕ_{w-s} as a linear function of time (T).

We used resightings from two periods: summer and winter. Summer resightings are from the Netherlands during the period March–September (code 1). To exclude

Table 1: Model selection results

Model	Description	K	Δ deviance	Δ QAIC _c	Model weight
1	π (yb, yb, yb) ϕ_{w-s} (T+,T+,T+)	76	.73	.00 ^a	.75
2	π (yb, yb, yb) ϕ_{w-s} (T,T,T)	78	.00 ^b	3.46	.13
3	π (yb, yb, yb) ϕ_{w-s} (c,T,T)	77	3.40	4.34	.09
4	π (yb, yb, yb) ϕ_{w-s} (T,T,c)	77	6.95	7.41	.02
5	π (yb, yb, yb) ϕ_{w-s} (c,T,c)	76	10.96	8.82	.01
6	π (yb, yb, yb) ϕ_{w-s} (T,c,T)	77	13.13	12.73	.00
7	π (yb, yb, yb) ϕ_{w-s} (c,c,T)	76	16.21	13.34	.00
8	π (yb, yb, yb) ϕ_{w-s} (T,c,c)	76	23.56	19.68	.00
9	π (yb, yb, yb) ϕ_{w-s} (c,c,c)	75	26.87	20.48	.00
10	π (c,c,c) ϕ_{w-s} (T,T,T)	76	47.73	40.51	.00

Note: Model selection results for initial state probabilities (π) modeled constant (c) or as a function of year of birth (yb) and survival from winter to summer (ϕ_{w-s}), for each wintering region separately, either constant or as a linear function of time (T). In addition, a model was tested where the rate of decrease in survival was similar in all wintering regions (T+). Survival from summer to winter and resighting probability are modeled as in the full model (ϕ_{s-w} (c,c,c) p_s (t1,t1,t2) p_w (c,t,t)). Results are adjusted for overdispersion ($\hat{c} = 1.16$; see “Methods”).

^a Quasi corrected Akaike Information Criterion (QAIC_c) = 16,198.04

^b Deviance = 18,610.75

stopover resightings, winter resightings in France and Iberia (codes 2 and 3, respectively) are restricted to the months December and January. Resightings in the most southern wintering sites (not used for stopover) in Mauritania and Senegal (code 4) were taken from the months October–February. Given these resighting periods, survival was estimated over two 6-month intervals: mid-June–mid-December and mid-December–mid-June. Birds in all states can be resighted in summer, but birds in a certain wintering state can only be resighted in that particular region in winter, resulting in the following event matrix:

$$\mathbf{B}_t = \begin{matrix} & & 0 & 1 & 2 & 3 & 4 \\ \begin{matrix} F \\ I \\ MS \\ D \end{matrix} & \begin{bmatrix} 1 - p_{s,FI} - p_{w,F} & p_{s,FI} & p_{w,F} & 0 & 0 \\ 1 - p_{s,FI} - p_{w,I} & p_{s,FI} & 0 & p_{w,I} & 0 \\ 1 - p_{s,MS} - p_{w,MS} & p_{s,MS} & 0 & 0 & p_{w,MS} \\ 1 & 0 & 0 & 0 & 0 \end{bmatrix} \end{matrix}$$

Resighting probabilities in winter (p_w) were modeled as a function of year (t) and wintering state. Resighting probabilities in summer (p_s) were modeled as a function of year. As exploratory analyses indicated that resighting probabilities in summer differed between birds wintering in either Mauritania and Senegal (MS), or Europe (France or Iberia; FI), we included this difference in all models. Resighting probabilities in winter were modeled as a function of year (t) for birds wintering in Iberia and Mauritania and Senegal but, due to limited data, constant for birds wintering in France. Resighting probabilities in the Netherlands during winter and in the wintering regions during summer were fixed to zero. Our full model can be written as π (yb,yb,yb) ϕ_{s-w} (c,c,c) ϕ_{w-s} (T,T,T) p_s (t1,t1,t2) p_w (c,t,t), with the parameterizations of each model parameter separately specified for each wintering state in parentheses.

Currently a goodness-of-fit test is not available for multievent models. To get an estimate of the level of overdispersion in our data set, we simplified it by separating individuals that are observed (code 1) or not observed (code 0) and distinguishing 4 groups (g): observed in winter in either France (1), Iberia (2), Mauritania and Senegal (3), or never observed in winter (4). We tested the goodness-of-fit of the Cormack-Jolly-Seber model (Lebreton et al. 1992) $\phi_{s-w}(g)$ $\phi_{w-s}(g \cdot T)$ $p(g \cdot t)$ using the median c-hat approach in program MARK (White and Burnham 1999). In this model, the winter resighting probability of group 4 was fixed to zero. The level of overdispersion, caused by extrabinomial variation, was estimated at $\hat{c} = 1.16 \pm 0.01$ SE.

Given the computational time constraints of these models (see “Statistical Analysis”), we used a stepwise approach to test whether the data could be more parsimoniously modeled by first testing reduced parameterizations for initial state probabilities and then for survival probabilities. When multiple models were supported at step 1 (Δ quasi-corrected Akaike Information Criterion [QAIC_c] <2), we tested the robustness of the results by applying subsequent steps using all of these models.

We first tested whether the initial state probabilities were more parsimoniously modeled as constant or as a function of year of birth. Next, starting from the best-supported parameterization for initial state probabilities, we tested for each wintering region (state) whether winter-summer survival (ϕ_{w-s}) was constant or decreased over time, resulting in eight models to be compared (table 1, models 2–9). In addition, we tested whether the rate of decrease in winter-summer survival was similar in all wintering regions (to test prediction 3) by modeling an additive lin-

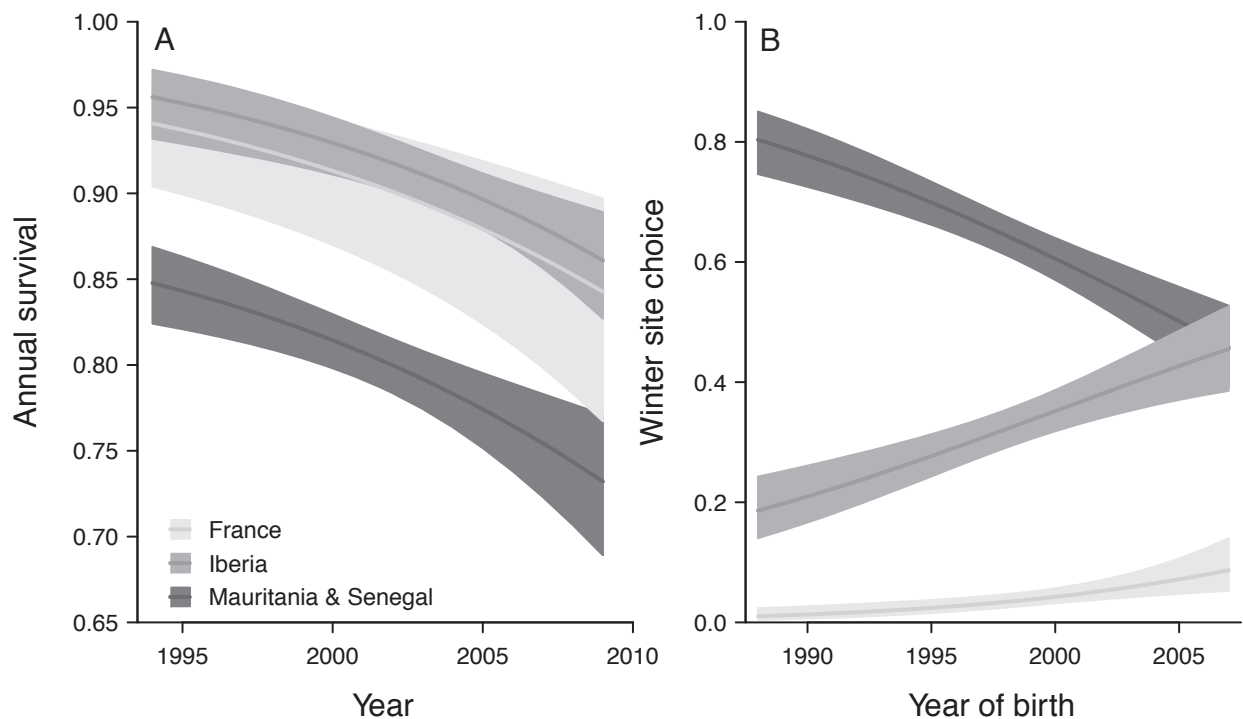


Figure 3: Annual survival (A) and initial state probabilities (B), the probabilities to choose to winter in France, Iberia, or Mauritania and Senegal, as a function of year and year of birth, estimated from the best-supported model (model 1; table 1). Lines and shaded areas represent means and 95% confidence intervals. Annual survival is calculated from the seasonal survival estimates, using the delta method to derive 95% confidence intervals. Confidence intervals are corrected for overdispersion ($\hat{c} = 1.16$; see “Methods”).

ear time trend for all wintering regions (T+). Annual survival per wintering region was derived from the seasonal survival estimates, using the delta method to derive 95% confidence intervals (Cox 1998).

Statistical Analysis

We used E-Surge to build multievent mark-recapture models (Choquet et al. 2009). Multievent models are (more so than multistate models) prone to local minima (Choquet et al. 2009). Each model was therefore run 20 times using different random initial values. Model selection was based on the Akaike Information Criterion, corrected for small sample size and overdispersion (QAIC_c; Burnham and Anderson 2002). We considered a model to be substantially better supported when its QAIC_c value was at least 2 points lower when compared to another model (Burnham and Anderson 2002). Reported standard errors and confidence intervals were also adjusted for overdispersion.

Results

Survival from winter to summer (ϕ_{w-s}) decreased with time in all wintering regions. The best-supported model included an additive linear effect of time on winter-summer survival (table 1), suggesting that the rate of decrease in winter-summer survival was similar in all wintering regions. Annual survival was similar in France and Iberia but, given the lack of overlap in 95% confidence intervals, annual survival in Mauritania and Senegal was substantially and consistently lower (fig. 3A). This difference was mainly caused by lower survival from summer to winter of birds wintering in Mauritania and Senegal when compared to birds wintering in Europe (see fig. A2, available online). This was demonstrated by the fact that removing the effect of state for summer-winter survival from model 1 (table 1; using model 2 gave similar results) substantially reduced the model fit ($\Delta\text{QAIC}_c = 9.68$), whereas removing the state effect for winter-summer survival did not ($\Delta\text{QAIC}_c = -0.44$). When testing for each wintering state separately, there was substantial evidence for a decrease in winter-summer survival (model 2; table 1) for Iberia and West Africa (Iberia: model 2 vs. model 6, $\Delta\text{QAIC}_c = -9.27$; Mau-

ritania and Senegal: model 2 vs. model 4, $\Delta\text{QAIC}_c = -3.95$; table 1), but not for France (model 2 vs. model 3, $\Delta\text{QAIC}_c = -0.88$; table 1).

The migrating bird's choice of where to spend the winter (i.e., the initial state probabilities) changed over time. In the early years of the study period, most young birds ended up wintering in Mauritania and Senegal, a region where survival was lowest. More recent generations of spoonbills were observed to be more likely to go to the higher-survival areas, France, and especially Iberia (model 2 vs. model 10, $\Delta\text{QAIC}_c = -37.06$; table 1; fig. 3B).

Discussion

Our investigation is directed at the question of whether, during a period of rapid population growth, either the interference hypothesis or the site dependence hypothesis could explain the hemispheric winter distribution of spoonbills along the east Atlantic flyway. Given the absence of winter region effects on breeding success (T. Lok, unpublished data), we can use annual survival as a direct measure of winter site suitability. Instead of choosing to winter in the highest-quality (highest-survival) area at low population sizes (i.e., at the start of the study period), most birds chose to winter in Mauritania and Senegal, where survival prospects were lowest. This leads us to reject prediction 1 (both hypotheses) that birds would winter in the highest-survival area at low population sizes. During the study period (i.e., during population growth) increasingly more birds began wintering in the higher-survival areas (Iberia and France). This leads us to reject prediction 2 (the site-dependence hypothesis) that more birds would start wintering in lower-survival areas during times of population growth. Although decreasing at similar rates, survival differed among wintering regions. As a consequence, we also reject prediction 3 (the interference hypothesis) that survival rates would be similar among wintering regions. As all three predictions were rejected, we conclude that the hemispheric winter distribution of spoonbills during our study period was neither ideal preemptive nor ideal free.

Assuming no heterogeneity in habitat quality, the decrease in survival within wintering regions would support the interference rather than the site dependence hypothesis. Given the large extent of the three wintering regions, this assumption is unlikely to be entirely valid, and the decrease in survival within wintering regions may also be the result of site dependence on a smaller scale. For example, Gill et al. (2001) showed evidence of site dependence within southern England for wintering Icelandic black-tailed godwits. Similarly, a small-scale study (within 5 km) on red knots *Calidris canutus canutus* wintering on Banc d'Arguin, Mauritania (which is also an important

wintering area for the spoonbills considered here) found evidence for the preemptive occupation of "high survival" sites, according to the order of arrival (Leyrer et al. 2012). This suggests that site dependence may occur on a small scale, even in group-living nonterritorial migrant birds such as spoonbills. Smaller-scale studies will be required to provide better insights into the role of interference and small-scale site dependence underlying the within-region decline in survival of spoonbills.

We found that birds wintering in Mauritania and Senegal had lower resighting probabilities in summer than birds wintering in Europe (fig. A2, available online). At this stage we can only speculate about the reasons for this difference. Birds wintering in Mauritania and Senegal are possibly more time constrained due to their longer migratory journey and hence arrive later and depart earlier from the breeding grounds, resulting in a shorter period in which they can be observed. Alternatively, birds wintering in Mauritania and Senegal may more often skip breeding than European winterers, for example, if they are in too poor condition or when adverse weather conditions during passage over the Sahara causes them to abort their northward migration and return to their wintering grounds to wait another year before attempting to breed.

Given that the proportion of spoonbills choosing to winter in France and Iberia increased over time (fig. 3B), the birds did in fact show a distributional response to the better survival prospects in these northern wintering regions. The strong mismatch between the optimal (ideal preemptive or ideal free) and the actual winter distribution at the start of the study period, combined with this subsequent distributional response, suggests that at some point before the onset of the study survival must have been higher in Mauritania and Senegal than in Europe. Between that point and the start of this study, survival could have decreased in Mauritania and Senegal through density dependence or other factors, causing survival to become higher in France and Iberia at some point. Alternatively, conditions for wintering may have improved in France and Iberia before the study period. The European Union's birds and habitats directives (initiated in 1979 and 1992, respectively) led to improvements in habitat and species protection throughout the European wintering range (Donald et al. 2007). Another factor may be that in the 1990s water management in Spain was changed in response to severe droughts in both Spain and Portugal, with an accompanying increase in the extent of suitable wintering habitat (e.g., Novo and Cabrera 2006). Winter temperatures in France and Iberia have also increased over the last decades (Tank et al. 2002), which will have reduced the costs of thermoregulation and may also have increased food availability (prey may become more active in the water column at higher temperatures), inducing the kind

of climate-related northward shift of winter range recently predicted for black-faced spoonbills *Platalea minor* (Hu et al. 2010).

Many studies have now shown changes over time in the wintering distribution of migratory birds and correlated these changes with natural, human-induced, or climate-related changes in environmental conditions (reviewed in Sutherland 1998; Visser et al. 2009). However, few studies have investigated whether the changes were sufficient to maximize fitness. For example, Visser et al. (2009) have shown that many migratory birds that breed in temperate areas have reduced their migration distance over recent decades and have explained this shortening of migration distances as a means for the birds to better adjust their arrival time at the breeding grounds to the advancing onset of spring. Whether such a reduction in migration distances actually resulted in adequately timed earlier arrivals was not discussed. In fact, Both (2010) recently showed that, despite earlier passage through northern Africa, pied flycatchers *Ficedula hypoleuca* were unable to arrive earlier at the breeding grounds and bred later than would be optimal (cf. Both and Visser 2001). This appeared to be due to the fact that during their northward migration temperatures in southern Europe were still low enough to limit food availability (Both 2010). Hence, a northward shift of the wintering distribution may not always translate into adaptive advancement of arrival at the breeding grounds.

In addition to the potential benefit of earlier arrival at the breeding grounds, our study suggests that a northward shift of the wintering range may also be mediated by the increased survival prospects of wintering in more temperate regions. The results show however, that the change in distribution was not sufficient to maximize survival. To quantify this, we estimated the distribution of adult spoonbills over the three wintering regions (fig 2; for assumptions and calculations, see app. B, available online) in order to calculate the actual population-level decline in survival. We then compared these estimates with the survival that could have been achieved if the birds had distributed ideally and freely (fig. 4; app. C, available online). The comparison demonstrates that with the actual survival converging over time towards the maximum achievable when individuals are ideal free distributed, the winter distribution of spoonbills has indeed shifted closer to an ideal free distribution.

We now turn to the question of what may have prevented a more rapid response to the better survival prospects in France and Iberia. Spoonbills, among other birds (Robertson and Cooke 1999; Lindberg et al. 2007; Williams et al. 2008), choose their wintering site early in life and tend to remain site-faithful thereafter (Lok et al. 2011), which probably hinders a flexible response to short-term (within a lifetime) change in winter habitat suitability. In

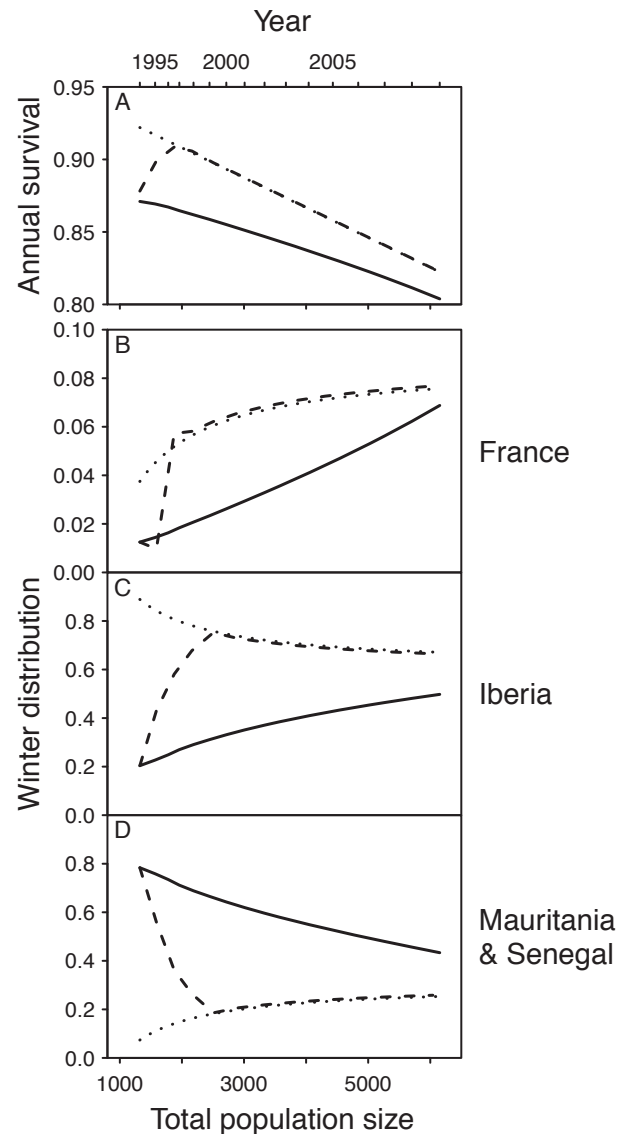


Figure 4: Adult survival and winter distribution over time and during population growth. The solid lines represent the estimated actual (A) population-level annual survival and proportion of adult birds wintering in France (B), Iberia (C), and Mauritania and Senegal (D; for assumptions and calculations, see app. B). The dotted lines represent survival and distribution if birds had been ideal free distributed over the three wintering regions (see app. C, available online). Starting from the estimated actual winter distribution in 1994, the dashed lines show the predicted survival and distribution when the winter site choice of young birds is ideal free, but adult birds remain site faithful (i.e., they are not free and their distribution remains ideal only if conditions do not change). Note that under this scenario the population-level survival, that is, the survival averaged over all individuals, becomes equal to that under an ideal free distribution before the ideal free distribution is even reached (in 1999). Yet only from that point onward, survival is equal for each individual in each wintering region.

such species, a distributional response to rapid changes in winter site suitability relies mainly on changes in the winter site choice of young birds, but our results show that this change is slower than optimal in spoonbills. If these young birds had made an ideal and free winter site choice, with older birds remaining site faithful, an ideal free distribution would have been achieved within approximately 5 years time (dashed line in fig. 4).

One explanation as to why this did not occur is that competitive interactions with other breeding populations in winter dictated the wintering distribution of Dutch spoonbills (Lundberg and Alerstam 1986) and restricted any redistribution. The western Palearctic spoonbill metapopulation consists of three main breeding populations, situated in northwest Europe (Netherlands and Germany), Spain, and Mauritania (Cramp and Simmons 1977). While the two European breeding populations are migratory, with their main wintering areas located in Mauritania and Senegal (de le Court and Aguilera 1997; Lok et al. 2011), the breeding population in Mauritania is resident (Cramp and Simmons 1977). Therefore, competition among these populations in winter is expected to be strongest in Mauritania and Senegal and if important, would be expected to have driven, rather than restricted, a northward shift of the wintering distribution of the Dutch breeding population.

Alternatively, the slow distributional response may be caused by winter site choice (and migration tendency) having a genetic basis (as shown for blackcaps *Sylvia atricapilla*; Pulido and Berthold 2010). What may be occurring is an evolutionary change through natural selection of the better-surviving birds wintering in Europe. However, the lack of association between wintering regions of parent and offspring (in only 16 of the 29 cases where wintering region of both parent and offspring was known, being either Iberia or Mauritania and Senegal, they wintered in the same region) lends little support for a genetic basis of migration tendency in spoonbills.

As a final explanation of our results, we consider the fact that social cues may be used by the birds when choosing a wintering site. Young spoonbills do not migrate south with their parents (Lok et al. 2011). Yet, because spoonbills often migrate in mixed-age flocks (T. Lok, personal observation), the young spoonbills may tend to follow older (and more experienced) individuals. Young spoonbills may also use the presence of wintering conspecifics along their migratory route as a cue for the suitability of a site for wintering. The fact that a preferred wintering area is chosen early in life, combined with their long life span, would make such social cues unreliable in a rapidly changing world.

In conclusion, we have shown that the response of a long-distance migrant bird to differential survival pros-

pects along the wintering range exhibits a lag which appears to be constrained by a tradition to migrate over long distances (their “migration tendency”). Such an intrinsic constraint could also limit the response of other migratory birds to rapid large-scale, climate- or human-driven, habitat changes on the wintering grounds (e.g., van Gils et al. 2006). The winter distribution of spoonbills appears to slowly shift closer toward an ideal free distribution over the time span of this observational study. However, only the continuation of this monitoring program will allow a verification as to whether the geographical wintering distribution of spoonbills will eventually converge to such an ideal free distribution. Further work is also required to reveal the proximate mechanisms (i.e. the importance of genetic, ontogenetic, social, and environmental factors) mediating such large-scale distributional responses as well as their constraints (e.g., Sutherland 1998; Piersma 2011).

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Spoonbills, Banc d'Arguin, Mauritania, taken December 9, 2004. Photograph credit: Jan van de Kam.