Animal Behaviour 82 (2011) 837–844

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Tamar Lok [a,b,*], Otto Overdijk [c,1], Joost M. Tinbergen [a,2], Theunis Piersma [a,b,2]

[a] Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen
[b] Department of Marine Ecology, NIOZ Royal Netherlands Institute of Sea Research
[c] Werkgroep Lepelaar, The Netherlands

ARTICLE INFO

Article history:
Received 15 February 2011
Initial acceptance 8 April 2011
Final acceptance 6 July 2011
Available online 19 August 2011
MS. number: 11-00136R

Keywords:
age-differential migration
behavioural plasticity
Eurasian spoonbill
exploratory behaviour
intraspecific competition
movement
optimal migration
Platalea leucorodia leucorodia
winter philopatry

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.

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

* Correspondence: T. Lok, Department of Marine Ecology, NIOZ Royal Netherlands Institute of Sea Research, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands.
E-mail address: t.lok@rug.nl (T. Lok).
[1] O. Overdijk is at Knuppeldam 4, 9166 NZ Schiermonnikoog, The Netherlands.
[2] J. M. Tinbergen and T. Piersma are at the Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands.

0003-3472/$38.00
doi:10.1016/j.anbehav.2011.07.019

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.

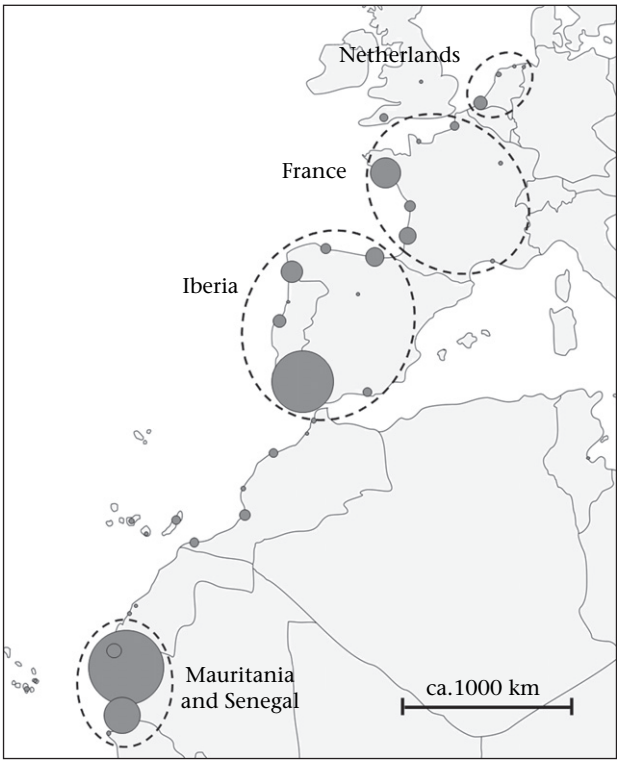

Figure 1. Defined borders of the four regions (dashed circles) and the distribution of winter resightings (dots), where the size of the dots represents the number of different colour-ringed birds observed at each wintering site.