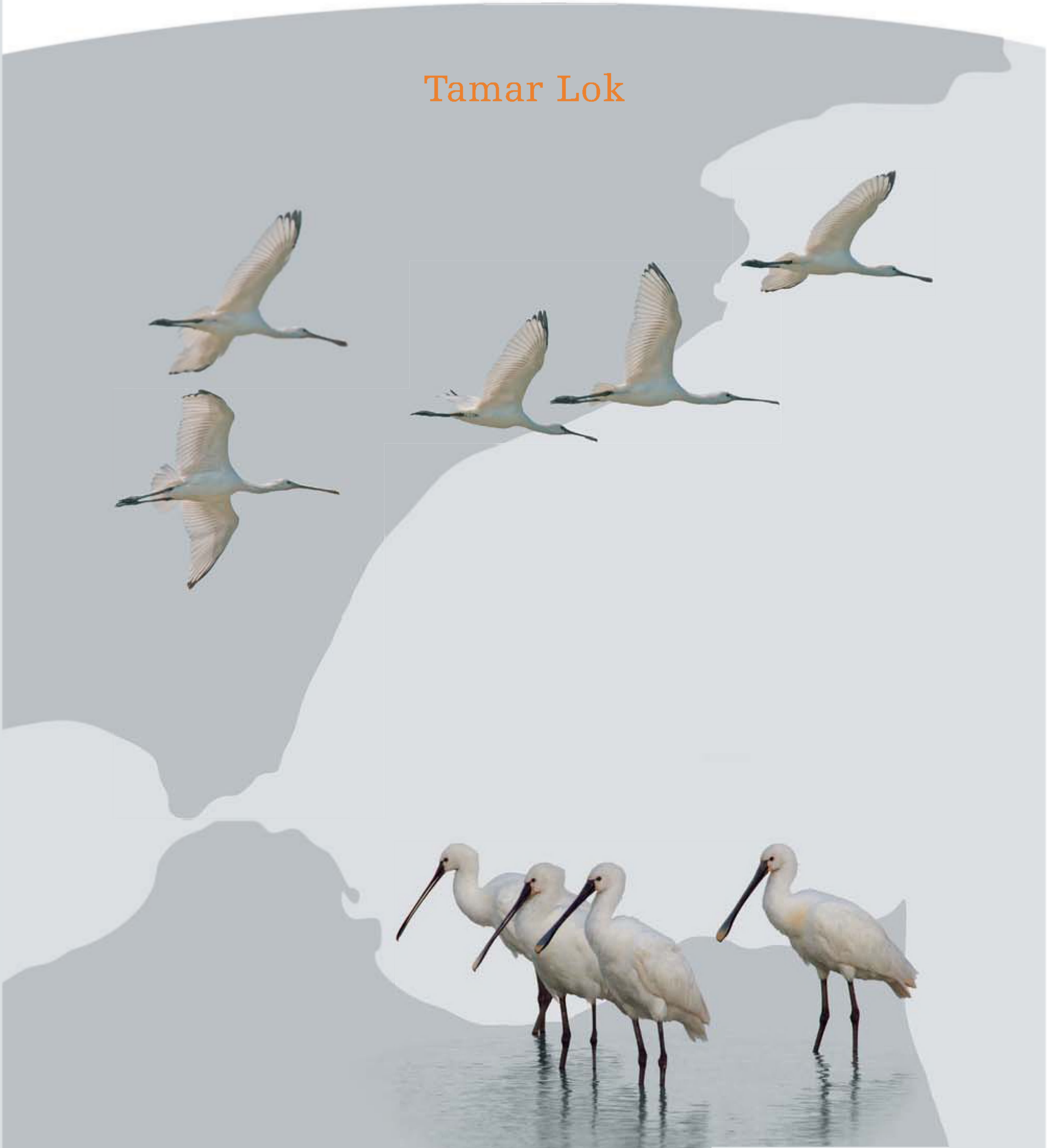
SPOONBILLS AS A MODEL SYSTEM

A demographic cost-benefit analysis of differential migration

Tamar Lok



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A demographic cost-benefit analysis of differential migration

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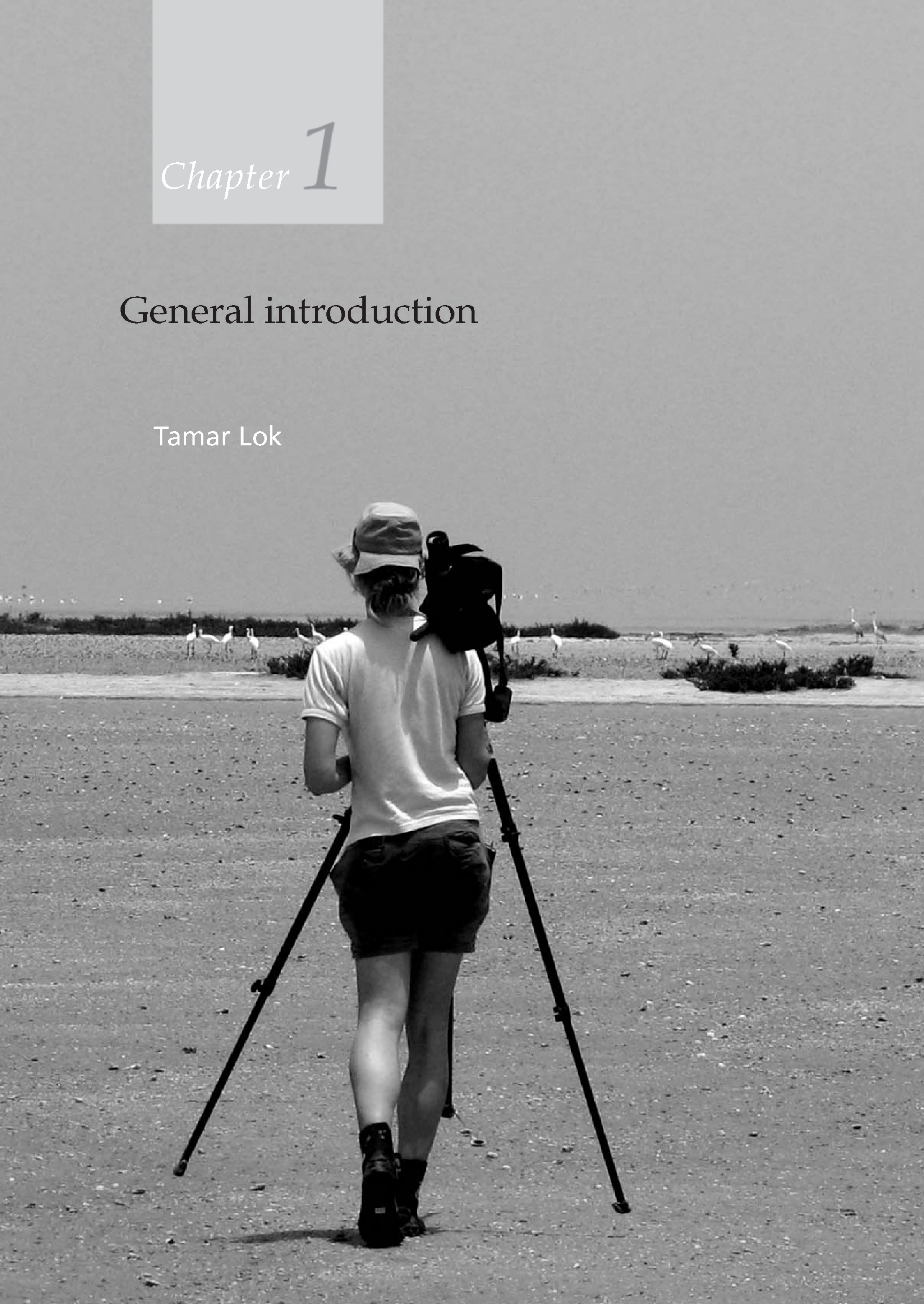
Chapter 1

General introduction

Tamar Lok



EVOLUTION OF MIGRATION

Migration – the regular seasonal movement of individuals, often from a breeding location to a non-breeding location and back – is a common and taxonomically widespread phenomenon in nature (Dingle 1980; Chapman *et al.* 2011). Migration is regarded primarily as an adaptation to exploit seasonal peaks of resource abundance and avoid seasonal resource depression (Alerstam, Hedenstrom & Akesson 2003; Newton 2008). The flight skills of birds allow them to travel over large distances at relatively low costs and exploit resources over vast geographical scales, which would explain why migration is particularly common in birds (Alexander 1998). There is much variation in migration patterns (Alerstam 1990; Newton 2008), not only between species, but also between and within populations of the same species. Theories that try to explain the persistence of variation in migration patterns make assumptions about migration costs, suitability gradients for reproduction and survival and about the role of competition (Ketterson & Nolan 1976; Gauthreaux 1978; Greenberg 1980; Myers 1981; Alerstam, Hedenstrom & Akesson 2003; Bell 2005).

All theories assume that migration is costly, and that this cost increases with migration distance. Migration can be costly in terms of reduced survival or reproductive success. The migratory journey may be associated with high mortality, as shown for a migratory songbird (Sillett & Holmes 2002), but may also have carry-over effects on subsequent survival and/or reproductive success. In the long-distance migrating red knot *Calidris canutus canutus*, most mortality occurred on the wintering grounds, although shortly after arrival from autumn migration (Leyrer *et al.* 2013). This early winter mortality could have been caused by a delayed cost of migration, as individuals arrive with very low body fat stores and may die when refuelling rates are insufficient at the wintering grounds. Carry-over effects, associated with the migratory journey, could similarly reduce survival in early summer, or reduce reproductive success. For example, arriving in low body condition has been shown to result in delayed breeding in the greater snow geese *Chen caerulescens atlantica* which in turn may reduce reproductive success (Bêty, Gauthier & Giroux 2003). Low body condition could also directly reduce reproductive output because of limited resources available for egg production (Drent *et al.* 2003).

Limited information is available on whether seasonal survival and reproductive performance are correlated with migration distance. Some evidence exists for a correlation between migration distance and arrival time at the breeding grounds. Within breeding populations of pied avocets *Recurvirostra avosetta* and great cormorants *Phalacrocorax carbo sinensis*, individuals that wintered further away from their breeding grounds, and migrated longer distances, arrived later on the breeding grounds (Hötker 2002; Bregnballe, Frederiksen & Gregersen 2006). However, the opposite was found in population of Icelandic black-tailed godwits *Limosa limosa limosa*, where individuals that migrated the longest distances wintered in the highest quality areas and were able to overtake short-distance migrating individuals and thus arrive earlier at the breeding grounds (Alves *et al.* 2012).

Besides assumptions about the cost of migration, theories that try to explain variation in migration patterns make different assumptions about the suitability of breeding and wintering areas. In general, it is assumed that suitability for reproduction increases with latitude (Alerstam, Hedenstrom & Akesson 2003), as a result of increasing food availability or decreasing predation risk (McKinnon *et al.* 2010). Concerning the suitability for wintering, some theories assume that it is always beneficial to winter as close to the breeding area as possible (Ketterson & Nolan 1976; Gauthreaux 1978), whereas others assume that wintering in more tropical, lower latitude, areas is beneficial for survival (Baker 1978; Greenberg 1980). Besides environmental factors, the level of competition (which will be density-dependent) may also affect the suitability of breeding and wintering areas as perceived by an individual bird (Lack 1954; Von Haartman 1968; Ketterson & Nolan 1976; Pienkowski & Evans 1985).

AIM OF THIS STUDY

For a better understanding of the evolution of migratory patterns, assessments are needed of the fitness costs and benefits associated with variation in migration distances and wintering areas (hereafter called 'migration strategies'), including the role of density-dependent effects. Such information is necessary to make realistic assumptions that are necessary for testing and developing migration theories. However, quantifying the costs and benefits of migration is difficult because it requires the following of individual migratory animals throughout their annual cycle, often spanning vast geographical ranges.

For a true assessment of the costs and benefits associated with different migration strategies, one would have to experimentally manipulate the migration strategy of individuals to remove the possibility that an individual's quality is correlated with its migration strategy. Experimental manipulation of individual migration strategies will be very challenging, if not impossible. Therefore, we here adopt a comparative approach which provides an important first step into a better understanding of the trade-off that migratory birds make between breeding in temperate and wintering in tropical areas. To avoid confusion about terminology, we used the term **'demographic cost-benefit analysis'** in the title of this thesis to refer to a fitness comparison of individuals with different life history traits, in our case, migration strategies.

The Eurasian spoonbill *Platalea leucorodia* appears a suitable model system for such a study (Dugatkin 2001), since it exhibits variation in both breeding and wintering areas (Fig. 1.1), and can be followed during both the breeding and wintering seasons. To quantify the costs and benefits of different migration strategies, we will compare the seasonal survival and reproductive performance of individuals breeding in the same area (the Netherlands), but wintering in different places. The population is growing rapidly (Lok *et al.* 2009), which allows us to test the role of density-dependent processes in shaping migration patterns.

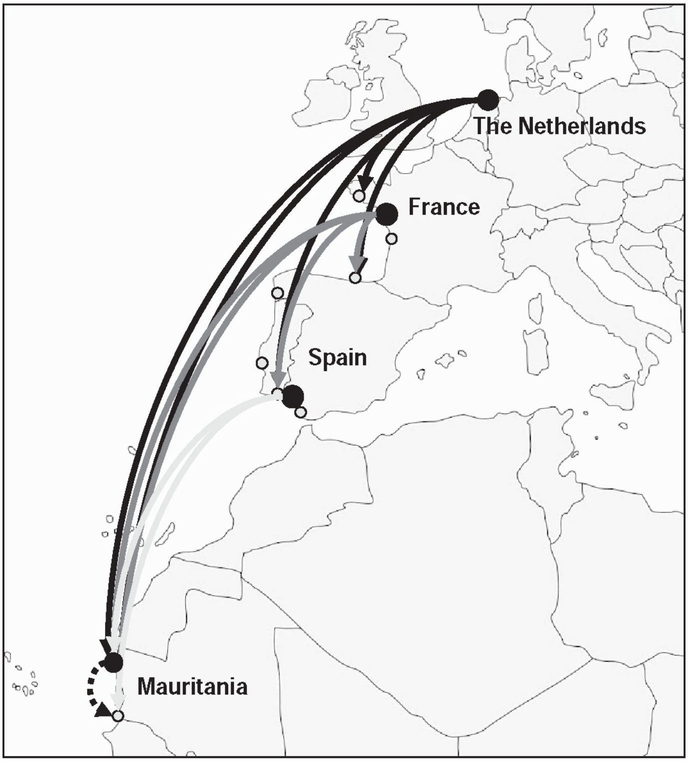


Figure 1.1 Main breeding (black dots) and wintering areas (grey dots) of Eurasian and Mauritanian spoonbills. The arrows roughly represent the migratory connectivity between them (arrows indicate direction during autumn migration).

THE STUDY SYSTEM

Our study population is the Eurasian spoonbill *Platalea leucorodia leucorodia* population that breeds in the Netherlands. This population is migratory and spends the winter mainly in river estuaries and tidal flats along the Atlantic coast between France and Senegal. In winter, it occurs sympatrically with wintering spoonbills from other European breeding populations from Denmark, Germany, Belgium, United Kingdom, France, Spain, and with the Mauritanian spoonbills *Platalea leucorodia balsaci* that are resident to the Banc d'Arguin (Mauritania) (Fig. 1.1). In Senegal, the most southern wintering area of Eurasian spoonbills overlaps with the most northern wintering areas of the African spoonbills *Platalea alba* (O. Overdijk, pers. comm.). Spoonbills feed tactilely on invertebrates living in the water column (e.g. small fish, shrimps and insects) by wading through shallow (10–-30 cm depth) water while sweeping their bills from side to side through the water (Hancock, Kushlan & Kahl 1992). Spoonbills are long-lived birds with high annual survival (0.80-0.90) and delayed age of first breeding (Bauchau, Horn & Overdijk 1998; Lok *et al.* 2009). Spoonbills breed for the first time when (at least) 3 years old, that is, in their 4th calendar year. Most immature spoonbills stay at the wintering grounds until that time.

Due to pollution of surface waters through industrial toxic spills and insecticide use in agriculture, combined with disappearance of suitable foraging and breeding areas, the Dutch breeding population, in concert with other breeding populations in Europe, severely declined to a minimum of 148 breeding pairs in 1968 (Brouwer 1964; Koeman & van Genderen 1966; Niethammer, von Blotzheim & Bauer 1968). Since the prohibition of industrial toxic spilling and organochlorine pesticide use, in combination with strongly enforced protection of foraging and breeding areas (van der Hut 1992), the population has recovered to 2534 breeding pairs in 2012, spread over 38 colonies, of which about two-third breeds on the Wadden islands (Fig. 1.2). The other main breeding populations of spoonbills within the East-Atlantic flyway are the Spanish population, which increased in numbers from ca. 100 to 1500 breeding pairs between 1970 and 2007 (García *et al.* 2009) and the Mauritanian spoonbill population, which declined from 1,610 breeding pairs in 1985 to 750 in 2007 (Triplet *et al.* 2008) (Fig. 1.1).

As part of the conservation plan, a colour-ringing program was started in the 1970s. Just prior to fledging, spoonbill chicks were provided with unique combinations of coloured rings with or without inscriptions or bars. These colour-ring combinations could be read with a telescope up to a distance of ca. 300 m (depending on the light conditions). That spoonbills are large and beautiful birds has probably helped to raise the enthusiasm among many (amateur and professional) ornithologists to read their

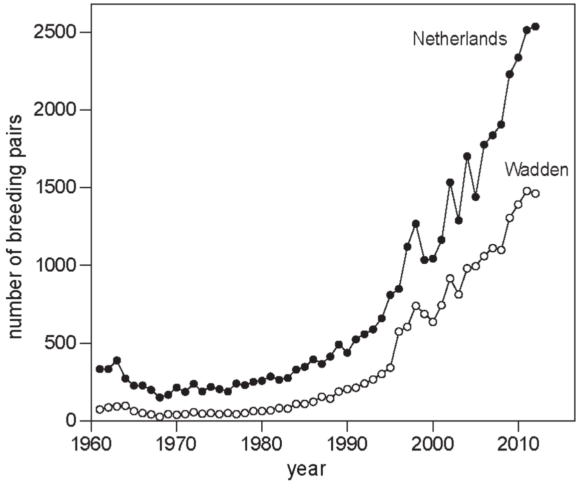


Figure 1.2 Development of the breeding population of spoonbills in the Netherlands (black dots = total number of breeding pairs, open dots = breeding pairs breeding on the Wadden islands).

rings which resulted in Dutch spoonbills being resighted throughout the year and throughout (most of) their geographical range. In addition, regular expeditions have been organized, also as part of this study, to the Banc d'Arguin (Mauritania) and the Senegal delta (Mauritania and Senegal) (e.g. Overdijk, de le Court & Gueye 2001) as these areas turned out to be important wintering areas for the Dutch spoonbills, but were only rarely visited by amateur ornithologists that read their rings. All these combined efforts have resulted in the accumulation of no fewer than 100,000 resightings on over 6,000 birds at present. The winter resightings of colour-ringed birds revealed that the majority of the Dutch breeding population spreads out in winter along the Atlantic coast between France in the north and Senegal in the south, which resulted in variation in individual annual migration distances between 2,000 km and 10,000 km. We studied breeding performance of spoonbills with contrasting migration strategies in the breeding colony on the island of Schiermonnikoog. Since 1997, chicks have been consistently colour-ringed in this colony on a yearly basis. Because spoonbills are likely to return to their natal colony for breeding, this resulted in a considerable proportion (ca. 30%) of breeding birds on Schiermonnikoog being colour-ringed. Resightings of part of these colour-ringed birds in winter showed that even within this breeding colony, considerable variation in migration strategies existed. This provided the observational basis for studying the correlation between migration strategies, breeding performance and (seasonal) survival of spoonbills breeding in the Netherlands.

THESIS OUTLINE

Part I: Some background

European spoonbills that winter in the Banc d'Arguin in Mauritania occur sympatrically in winter with the resident Mauritanian spoonbills. While the Mauritanian spoonbill has been considered a subspecies based on its distinct morphology, this had not yet been confirmed based on DNA. In **Chapter 2**, we show that the level of genetic differentiation of the Mauritanian population from the Dutch population justifies its subspecies status and implies that there is very little genetic exchange between Dutch and Mauritanian spoonbills.

In **Chapter 3**, we studied chick growth of spoonbills, with the practical aims to assess the reliability of different body size measures for estimating the age of a chick, and to derive growth curves of body mass, of which deviations could be used as an index of body condition.

In **Chapter 4**, we studied the diet of spoonbill chicks through the breeding season. Based on historical observations, spoonbills were suggested to feed on mainly three-spined sticklebacks *Gasterosteus aculeatus* in freshwater early in the season, and to shift to feeding on brown shrimp *Crangon crangon* later in the season. To test for such a seasonal shift in diet, we analysed the stable isotope composition of longitudinal samples along a flight feather of spoonbill chicks born at different times during the breeding season. This allowed the distinction between within- and between-individual changes in diet, the latter suggesting individual feeding specialization. The seasonal diet shift was confirmed, and it seems that breeding birds show individual specialization with respect to foraging habitat.

Part II: Population dynamics and migration

In **Chapter 5**, we describe population-level (changes in) annual and seasonal survival and permanent emigration from the Netherlands during a 22-year period of rapid population growth. The main aim was to quantify seasonal variation in survival and in density dependence in survival. Because energetic demands and experience may vary with age, we tested whether density-dependent patterns in survival differed between juvenile, subadult and adult birds. We found evidence for density dependence in survival in all age classes with its strength decreasing with age. Survival of adult birds was lowest and decreased most strongly in the second half of the non-breeding season, which included the end of winter and spring migration.

To estimate fitness differences associated with different migration strategies, we need to know whether spoonbills are faithful to a single wintering area, or whether they use different wintering areas in different winters. In **Chapter 6**, we estimate the level of winter site fidelity for different age classes of spoonbills based on 18 years of winter resightings. We used multi-state mark-recapture models to estimate site-specific survival, fidelity and movement probabilities between three main wintering regions: France, Iberia and Mauritania & Senegal. We show that birds wintering in Europe in their first winter still have a high probability to move further south (0.35-0.50), but that from their second winter onward spoonbills become very site faithful (0.92-0.94) to one wintering region. This implies that a single observation of a 2nd year or older spoonbill in winter reveals its lifelong migration strategy.

In **Chapter 5**, we showed that density dependence in adult survival was strongest in the second part of the non-breeding season. In **Chapter 7**, we investigated whether this decrease in survival could be explained by site dependence (at higher population sizes, more birds occupy wintering areas associated with lower survival) or interference competition (survival is similar in all wintering areas, and decreases at the same rate) in the wintering areas. For this, we estimated changes in adult winter site choice and site-specific survival during 16 years of population growth. Combining summer and winter resightings and using novel multi-event mark-recapture models, we were able to estimate winter site choice and site-specific survival of all colour-ringed individuals (also the ones that were never observed in winter), by integrating information on winter region-specific resighting probabilities and survival, which could be estimated for all individuals based on summer resightings. Our results do not confirm the predictions of either the site dependence or the interference hypothesis as an increasing proportion of birds started wintering in Europe, where they had consistently higher annual survival than in Mauritania or Senegal.

Part III: A demographic cost-benefit analysis of differential migration

Between 2005 and 2012, we organized additional expeditions to West Africa to allow the separation of survival estimates during the stationary summer and winter period, and the migratory periods. In **Chapter 8**, we investigate potential survival costs and benefits of different migration strategies by comparing the seasonal survival of spoonbills wintering in France, Iberia or Mauritania & Senegal. Winter survival was not higher at more distant wintering regions, and very low survival during spring migration, but only for birds wintering in Mauritania & Senegal. This suggests that the mortality cost of migration increases with migration distance.

In **Chapter 9**, we investigate whether breeding performance differs between individuals with contrasting migration strategies. Using the information from Chapter 3, we were able to accurately estimate timing of breeding from chick biometry. We test for differences in breeding propensity, timing of breeding, chick body condition, breeding success and post-fledging survival between birds wintering in Europe versus those wintering in Mauritania or Senegal. The long-distance migrating birds that winter in Mauritania or Senegal were found to breed later and produce chicks of poorer condition (probably as a result of their later breeding). At the population level, timing of breeding was negatively correlated with breeding success. Moreover, we show some evidence that long-distance migrants are more likely to skip breeding.

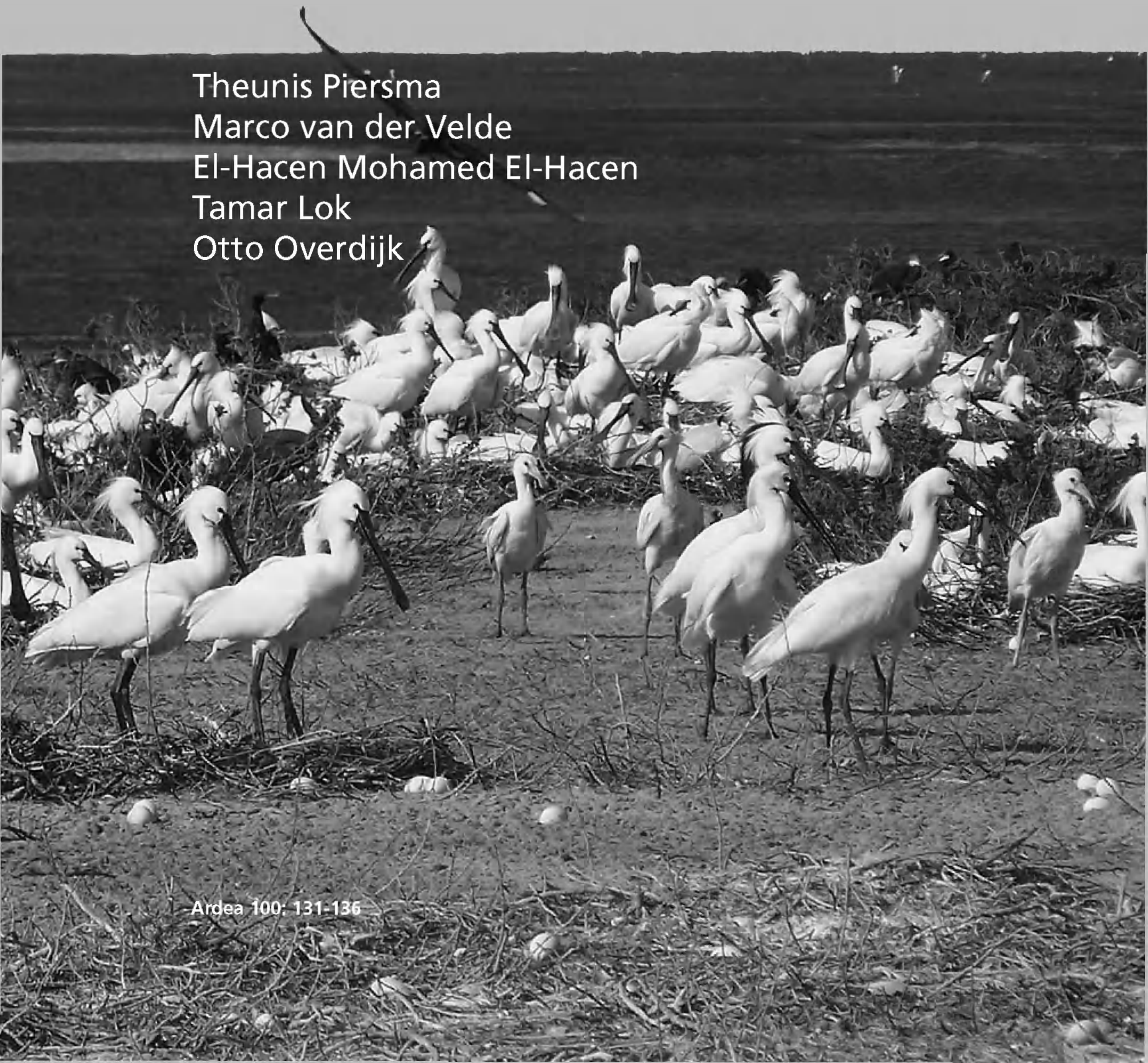
In **Chapter 10**, we synthesize our results and discuss the implications for understanding the evolution of migration in general, and for understanding the role of migration in the population dynamics of spoonbills in particular.

Part I

Some background

Chapter 2

Molecular verification of the subspecies status of the Mauritanian spoonbill *Platalea leucorodia balsaci*



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ABSTRACT

In 1974 R. de Naurois and F. Roux proposed that the distinct morphology of Eurasian spoonbills *Platalea leucorodia* breeding on offshore islands in the Banc d'Arguin, Mauritania, in comparison with the sympatrically wintering northwest European breeding spoonbills *Platalea leucorodia leucorodia*, justifies recognition as a separate subspecies *Platalea leucorodia balsaci*. This proposal is here examined on the basis of variation in nuclear DNA, microsatellites identified earlier for *P. minor* and *P. ajaja*. We show that there is significant variation between spoonbills breeding in Mauritania (N = 25) and the sympatrically wintering conspecifics breeding in the Dutch Wadden Sea (N = 105). Of the total genetic variation among the 130 individuals, 6.3% is attributable to variation between the two breeding areas (93.7% of the variation is within breeding areas). Pairwise F_{ST} values showed low genetic differentiation (F_{ST}'s < 0.012) among breeding colonies within The Netherlands. The level of genetic differentiation indicates that the level of gene flow between The Netherlands and Mauritania is much lower (~ 4–5 individuals/generation) than among the Dutch colonies on separate Wadden Sea islands. Field observations on individually colour-marked birds from The Netherlands indeed suggest extensive dispersal within northwest Europe, with some introgression of *leucorodia* genes into the *balsaci* population. The level of microsatellite distinctiveness between sympatric populations of the two subspecies is similar to what is recorded for other migrant birds, and as such justifies the subspecies status of the Mauritanian spoonbill.

INTRODUCTION

The breeding distribution of Eurasian spoonbills *Platalea leucorodia* along the East Atlantic seaboards of northwest Africa and Europe is rather disjunct (Cramp & Simmons 1977). There is a cluster of colonies in northwest Europe centred in The Netherlands, there are breeding colonies 2000 km further south in southern Spain, and, again separated by a 2000 km gap, a concentration of colonies on Banc d'Arguin, Mauritania, on the very verge of the Western Palearctic (Cramp & Simmons 1977). The Spanish and Dutch breeding birds have been assigned firmly to the subspecies *leucorodia*, birds breeding on the offshore islands of Banc d'Arguin on the basis of their distinct morphology received recognition as a separate subspecies *balsaci* by de Naurois and Roux (1974). Mauritania-breeding birds are somewhat smaller, have less pronounced yellow breast feathers in breeding plumage (de Naurois & Roux 1974, Cramp & Simmons 1977), and adults, but not immatures, have a uniformly black upper bill (O. Overdijk, unpublished data).

Perhaps surprisingly, the proposal for this subspecies distinction has yet to be revisited in the ornithological literature. Here we examine whether the variation in microsatellites that were initially developed for black-faced spoonbills *P. minor* (Yeung *et al.* 2009) and roseate spoonbills *P. ajaja* (Sawyer & Benjamin 2006) is greater between spoonbills breeding in Mauritania and The Netherlands than among spoonbills from a range of breeding islands within the Dutch Wadden Sea. We will reflect on dispersal patterns documented for individually colour-marked birds to interpret the molecular findings.

MATERIALS AND METHODS

The long-term colour-marking project of Dutch spoonbills (a population close to 4000 breeding pairs) that underlies the present study is introduced in Lok *et al.* (2009, 2011). Blood samples were collected from *leucorodia* breeding colonies at four different Dutch Wadden Sea islands: Schiermonnikoog (N = 26), Terschelling (N = 21), Vlieland (N = 40) and Wieringen (N = 18) in June 2011. Blood samples of the *balsaci* subspecies (N = 25), now counting under 1000 breeding pairs (O. Overdijk & E.M. El-Hacen, unpublished data), were obtained at one of the four regular colonies on Banc d'Arguin, at Toufat in October 2007. In all cases we captured chicks before fledging in or near the breeding colonies, and this means that we cannot exclude that we occasionally sampled relatives. Blood was stored on 95% ethanol, and DNA was extracted from these blood samples using a salt extraction method (Richardson *et al.* 2001). As individual breeders may shift between colonies (O. Overdijk & E.M. El-Hacen, unpublished data), the Toufat samples fairly represent the *balsaci* population.

To study genetic variation among the spoonbill samples, initially, six primer sets from *P. ajaja* (Sawyer & Benjamin 2006) and 15 primer sets from *P. minor* (Yeung *et al.*

2009) were tested for amplification and polymorphism in eight samples (four *leucorodia* samples from Schiermonnikoog and four *balsaci* from Banc d'Arguin). Of these 21 microsatellites, 12 were found to amplify a PCR product and to be polymorphic (Table 2.1). Subsequently, all 130 DNA samples were analysed for these 12 microsatellite loci.

Microsatellites were amplified in multiplex PCRs of 3 separate panels (Table 2.1). PCR reactions were carried out in 10 µl volume containing 20–50 ng DNA, 0.2 mM of each dNTP, 10 mM Tris-HCl, 50 mM KCl, 3.0 mM $MgCl_2$, 0.25 U Taq DNA polymerase (Roche Diagnostics GmbH, Mannheim, Germany), and a variable amount of each primer. See Table 2.1 for the amount of each primer in the PCR reaction. PCR program was as follows: 94°C for 1 min, 35 cycles of 94°C for 30 s, 60°C for 60 s and 72°C for 60 s, followed by 72°C for 2 min. Fluorescently labelled PCR products were separated on an AB3730 DNA analyser, and allele-lengths were determined using Genemapper 4.0 software.

Population genetic parameters were estimated using Arlequin 3.1 (Excoffier, Laval & Schneider 2005) and FSTAT 2.9.3 (Goudet 2001).

Table 2.1 Polymorphic microsatellites for Eurasian spoonbills.

Locus	Ta (°C)	Allele range (bp)	N_A	H_O	H_E	Conc. primer (mM)
Panel-1:						
Aaj 1	60	161-204	12	0.84	0.79	0.3
Pm 2-16	60	317-377	13	0.85	0.76	0.6
Pm 2-29	60	223-276	12	0.81	0.81	0.1
Pm 3-20	60	228-240	4	0.57	0.51	0.015
Panel-2:						
Aaj 2	60	194-206	4	0.49	0.57	0.015
Pm 2-62	60	270-399	40	0.96	0.93	0.5
Pm 3-15	60	197-210	2	0.23	0.23	0.03
Pm 3-17	60	149-155	4	0.61	0.61	0.02
Panel-3:						
Pm 2-28	60	225-307	21	0.94	0.91	0.2
Pm 2-37	60	296-402	25	0.92	0.90	0.2
Pm 3-13	60	189-212	6	0.73	0.70	0.1
Pm 3-16	60	197-213	8	0.22	0.23	0.01

Ta = annealing temperature, N_A = number of alleles, and H_O and H_E = Observed and Expected Heterozygosity. Primer conc. = primer concentration in 10 µl volume PCR reaction (n=130).

RESULTS

Microsatellites from *P. minor* and *P. ajaja* showed moderate to high levels of variation in *P. leucorodia*. Number of alleles (N_A) per microsatellite locus ranged from 2-40 and the expected heterozygosity (H_E) ranged from 0.23-0.93 (Table 2.1). Eleven loci showed no significant deviations from HardyWeinberg-equilibrium, the twelfth locus PM2-16 had a significant excess of heterozygotes in birds from the Banc d'Arguin after Bonferroni correction. The mean expected heterozygosity (H_E) was 0.57 for Banc d'Arguin birds and ranged from 0.67–0.69 for the Dutch colonies (Fig. 2.1), even though the difference in H_E among breeding colonies overall was not significant (Kruskal-Wallis ANOVA, $P = 0.74$). A single locus, PM3-16, was monomorphic in Mauritania: it was fixed for allele 201 that had a frequency of 0.83–0.88 in the Dutch populations. Eleven loci showed (rare) alleles unique to either Mauritania or The Netherlands, but these alleles generally had a low frequency (<0.10).

A hierarchical Analysis of MOlecular VAriance (AMOVA) was used to partition the total genetic variation into two components: (1) variation between the source countries Mauritania and The Netherlands (i.e. between subspecies *balsaci* and *leucorodia*), and (2) variation within the breeding sites. The AMOVA revealed significant genetic differentiation between the breeding sites Mauritania (N = 25) and The Netherlands (N = 105), $F_{ST} = 0.063$, $P < 0.00001$. The remaining 93.7% of the variation was due to individual variation within breeding sites. In addition, tests of pair-wise genetic differentiation (F_{ST}) among all possible combinations of breeding colonies (Table 2.2), only showed significant genetic differentiation between the single Banc d'Arguin and each of the Dutch colonies. Genetic differentiation among the Dutch populations was small and not significant.

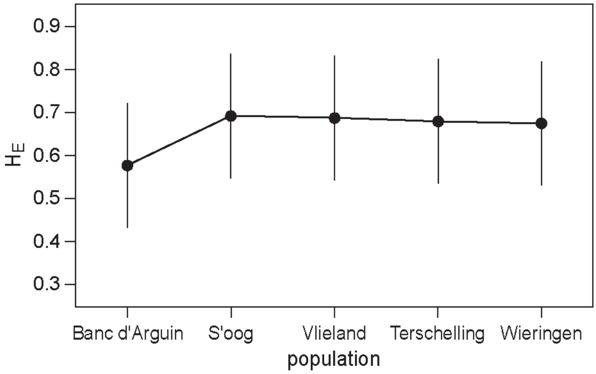

Figure 2.1 Level of genetic variation (mean expected heterozygosity, H_E) within the five sampled populations. Vertical bars denote 0.95 confidence intervals.

DISCUSSION

The birds from Mauritania (*balsaci*) showed somewhat less genetic variation than the Dutch birds (*leucorodia*, Fig. 2.1). Although this might suggest that the Banc d'Arguin population historically has gone through narrower population bottlenecks than the Dutch population, a more likely explanation is methodological: we probably sampled more families (and colonies) in The Netherlands than in Mauritania.

That there is little genetic structure within the *leucorodia*-spoonbills breeding on the Dutch Wadden Sea Islands is consistent with the considerable dispersal between the colonies on different islands. This can be illustrated by observations in the best studied colony on Schiermonnikoog in 1994–2009 of colour-ringed breeding birds born on islands with yearly colour-ringing of spoonbill chicks (Vlieland, Terschelling and, from 1997 onwards, Schiermonnikoog, see Lok *et al.* 2009; O. Overdijk unpubl. data). During this period, 229 colour-ringed birds were observed breeding on Schiermonnikoog of which 85 were born on Vlieland or Terschelling (dispersal) and 144 on Schiermonnikoog (philopatry). In only one case, a bird was known to have previously bred in other colony. Although the level of breeding dispersal is probably biased low due to the lower observation effort in colonies other than Schiermonnikoog, it nevertheless suggests that natal dispersal is more common than breeding dispersal. Figure 2.2 shows that soon after establishment of the Schiermonnikoog colony in 1992 most breeding birds of 2–13 years old were born on Vlieland and Terschelling, whereas in recent years most recruiting birds were locally born individuals (but note that on Schiermonnikoog, about twice as many chicks were yearly colour-ringed compared to Vlieland and Terschelling). This suggests that during establishment of a colony, gene flow is very high but strongly decreases during colony growth when locally born individuals start to recruit. Consequently, genetic differentiation among Dutch colonies may increase in the future.

We observed significant genetic differentiation between *balsaci* breeding in Mauritania and *leucorodia* breeding in The Netherlands. This suggests gene flow between The Netherlands and Mauritania to be much lower than the level of gene flow

Table 2.2 Pairwise genetic differentiation (F_{ST}) between spoonbill colonies and populations. Significant F_{ST} values are bold, $P \leq 0.005$ after Bonferroni correction.

	Banc d'Arguin	Schiermonnikoog	Vlieland	Terschelling
Banc d'Arguin	-			
Schiermonnikoog	**0.071**	-		
Vlieland	**0.061**	0.001	-	
Terschelling	**0.066**	-0.002	0.000	-
Wieringen	**0.085**	0.010	0.011	0.002

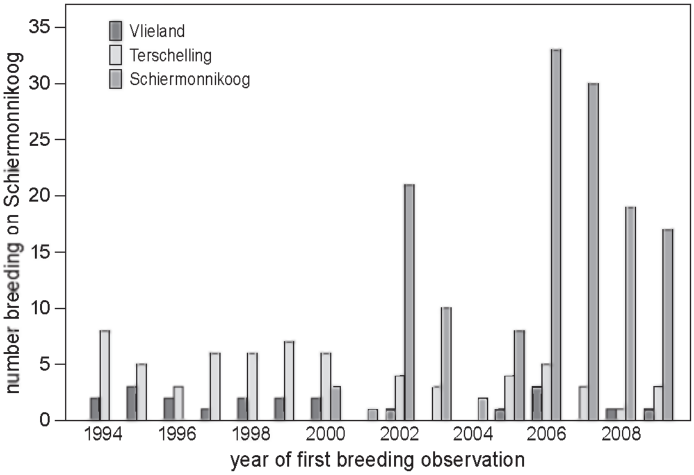

Figure 2.2 Total number of individually colour-marked spoonbills observed breeding on Schiermonnikoog (first established 1992) per source colony and year of first breeding observation. Note that the colour-ringing of chicks on Schiermonnikoog did only start in 1997.

Table 2.3 Evidence for natal dispersal by *leucorodia* spoonbills into the *balsaci*-breeding population on the Banc d'Arguin, Mauritania, based on the notebooks of O. Overdijk. In addition there are five cases of birds in *balsaci* breeding colonies showing the symmetric yellow spots on the upper spatula characteristic of *leucorodia*.

Date	Breeding island	Details of the observations
24 April 2000	Zira,	Bird ringed in Netherlands in 1996 copulated with local breeder
2 May 2000	Nair	Bird ringed in Netherlands in 1996 copulated with local breeder on nest
2 May 2000	Nair	Bird ringed in Netherlands in 1996 fed chicks
19 June 2000	Nair	Bird ringed in Netherlands in 1996 copulated with local breeder
17 May 2002	Cheddid	Bird ringed in Netherlands in 1994 copulated with local breeder
21 May 2002	Arel	Bird ringed in Netherlands in 1998 copulated with at least three different local breeders
4 June 2004	Zira	Bird ringed in Netherlands in 2000 sharing nesting materials with *balsaci* female
17 May 2005	Cheddid	Male ringed in Spain in 2000 copulated with more than one local breeder
23 May 2002 & 18 May 2010 & 30 June 2010	Nair	Bird ringed in Netherlands (Terschelling) in 1997 copulated with more than one local breeder in 2002, was observed on a nest in May 2010 and nursing chicks with a *leucorodia*-looking partner in June 2010

Figure 2.3 A colour-ringed bird born on Terschelling in 1997 standing on its nest on Nair (Banc d'Arguin) on 17 May 2010. A month later it was observed feeding chicks. From the picture it can be clearly seen that its partner (breeding on the nest) has a yellow bill tip. Given that male spoonbills generally have larger bills than females, this bird is probably a male.

among the Dutch breeding colonies. Assuming the movements between the two populations to now be in equilibrium and an island model of migration (Wright 1951; $F_{ST} = (1/4Nm+1)$, the level of dispersers between Wadden Sea and Banc d'Arguin (or *vice versa*) should be about four of five individuals per generation. In fact, there is some equivocal observational evidence for such dispersal, albeit in a single direction only (Table 2.3). There are several cases of European-born spoonbills copulating with *balsaci*-looking local breeders. In 2000 a Netherlands-born *leucorodia* was observed feeding chicks in a *balsaci*-colony on the island of Nair. However, the best documented example of dispersal from The Netherlands to Mauritania (but not necessarily subspecies-crossbreeding) is of a colour-ringed male spoonbill born on Terschelling in 1997 that was breeding on Nair (probably in 2002 and certainly in 2010). When, on 17 May 2010, it was observed on its nest and on 30 June 2010, it was observed feeding chicks, it was paired with a *leucorodia*-looking bird probably of European origin (Fig. 2.3).

Breeding colonies of the subspecies *leucorodia* are widely distributed across the Eurasian continent (Cramp & Simmons 1977). Therefore, genetic differentiation between geographic populations of leucordia, at least in theory, could be larger than the estimate of divergence between the two subspecies based on birds from spoonbills breeding in Mauritania and The Netherlands. This question would need additional work, but the question whether the genetic differentiation found is high enough to support a distinction into two subspecies, *balsaci* and *leucorodia*, can be answered. As a gauge, we can compare the level of microsatellite differentiation between *leucorodia* and *balsaci* observed ($F_{ST} = 0.06$) with values found in other microsatellite studies on avian subspecies. A sample of studies on migrant bird species, although generally using a slightly smaller sets of microsatellite loci, showed rather comparable levels of differentiation; in order of increasing F_{ST}: dunlin *Calidris alpina* (three subspecies, 7 loci, $F_{ST} \leq 0.010$; Marthinsen, Wennerberg & Lifjeld 2007), Canada goose *Branta canadensis* (two subspecies, 6 loci, $F_{ST} = 0.021$; Mylecraine *et al.* 2008), bluethroat *Luscinia svecica* (seven subspecies, 7-11 loci, $F_{ST} = 0.042$; Johnsen *et al.* 2006), reed bunting *Emberiza schoeniclus* (two subspecies, 6 loci, $F_{ST} = 0.043$; Kvist *et al.* 2011), and piping plover *Charadrius melodus* (two subspecies, 8 loci, $F_{ST} = 0.104$; Miller *et al.* 2010). Thus, the observed genetic differentiation between the two spoonbill subspecies seems to fall in the upper range of values. On the basis of this comparison the subspecies status of *balsaci* seems entirely valid.

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Chapter 3

Growth of spoonbill chicks: applications for estimating age and condition

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ABSTRACT

Chick growth parameters are essential for estimating a chick's age and body condition. Because of logistic difficulties or undesired disturbance to the entire colony, these parameters tend to be poorly known for colonial breeding birds. Body condition may be related to survival, and hence is an important indicator of the quality of a breeding area. Here we assessed rates of growth of chicks of Eurasian spoonbills *Platalea leucorodia leucorodia* from the Wadden Sea area, the Netherlands. Detailed growth curves until fledging of five morphometric variables and body mass were derived from repeated measurements on 12 spoonbill chicks that grew up in small colonies or on isolated nests on the island of Schiermonnikoog. The generality of these growth curves was tested on biometric measurements of 2 to 5 week old chicks of which hatching date was accurately estimated from head-bill length at a very young age (N = 632). Growth of head-bill, bill, wing, tarsus and body mass differed between the sexes, with the most pronounced sex effect on the asymptotic values of tarsus length and body mass: males (1741 g) become 17% heavier than females (1485 g) and will have 22% longer tarsi (167 mm) than females (137 mm). Tarsus and head-bill length were accurate predictors of age for chicks younger than 15 days old, whereas the age of older chicks was better predicted by the length of their 8th primary or entire wing. As an index of body condition we propose to use the proportional deviation from the predicted body mass, which requires knowledge of a chick's age and sex. To assess the body condition of chicks that are colour-ringed (when 2–5 weeks old), we therefore propose to measure at least the 8th primary length to estimate age, the tarsus length to potentially allow sex determination, and body mass.

INTRODUCTION

Chick growth parameters are often poorly known for bird species that breed in dense colonies. One reason is that reaching colonies may be logistically difficult, e.g. for seabirds breeding on isolated islands or steep cliffs (Ricklefs & White 1975; Benson, Suryan & Piatt 2003) and for herons and cormorants that breed in trees (Cramp & Simmons 1977). Another reason is that the multiple visits necessary to acquire chick growth parameters cause repeated disturbance of the entire colony, which is undesirable, especially when the species of concern is protected or endangered. However, especially for protected or endangered species, monitoring their performance is very important for designing and testing the effectiveness of conservation efforts (e.g. Oro, Jover & Ruiz 1996).

Chick growth performance may be an indicator of the environmental conditions during the breeding season, particularly during the chick-rearing phase (Schew & Ricklefs 1998). Chick condition has been shown to be correlated with survival prior to fledging (Dijkstra *et al.* 1990; Kersten & Brenninkmeijer 1995; Ruthrauff & McCaffery 2005) or during the post-fledging phase (van der Jeugd & Larsson 1998; Naef-Daenzer, Widmer & Nuber 2001). Chick condition may have longer-lasting effects and be correlated with the probability of recruitment into the breeding population (Cézilly, Boy & Green 1995) or even adult survival or reproductive success (Metcalfe & Monaghan 2001; Reid *et al.* 2003). As an index of chick body condition, the deviation in body mass from the predicted body mass for a given age is often used, either as absolute value (Beintema & Visser 1989; Schekkerman, Theunissen & Oosterveld 2009; Kentie *et al.* 2013) or proportional to the predicted body mass (Hamer & Hill 1993; Bolton 1995; Quillfeldt *et al.* 2006). To use this method, knowledge is required about the age of a chick and about how body mass increases with age. Moreover, it assumes that body mass is only a function of age and body condition, which may not be true for sexually size dimorphic species, where for a given age, the larger sex will be heavier than the smaller sex. In such a case, sex should be measured independently and sex-specific growth curves for body mass should be used.

As part of a long-term research effort on the population biology of Eurasian spoonbills *Platalea leucorodia leucorodia* (e.g. Lok *et al.* 2009; 2011; Lok, Overdijk & Piersma 2013), the aim of this study was to find out which morphometric variables are most accurate in predicting age, and to derive a reliable estimator of chick body condition. To do so, we determined (sex-specific) growth curves for several morphometric variables and body mass of chicks by collecting high-resolution growth data of 12 chicks from small colonies (to minimize disturbance) to estimate growth curves. The generality of the growth of these 'growth curve chicks' was then tested with data from ('reference') chicks of 2 to 5 weeks old (n = 632) of which their age was accurately estimated from head-bill length within two weeks after hatching.

METHODS

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 - 2009. A total of 208, 232, 217 and 223 nests were counted during these years (including some re-nesting attempts), spread over 11 or 12 colonies (with inter-colony distances of 100 m to 3 km), varying in size from 1 to 60 nests. Most spoonbills on Schiermonnikoog breed on the ground in saltmarsh habitat. Adult birds forage on small fish and shrimps in shallow fresh- and saltwater creeks within 20 km from the colony (El-Hacen *et al.* in revision).

The breeding season of spoonbills on Schiermonnikoog is long, with egg-laying occurring between late March and early July. Spoonbills usually lay an egg every 2nd day and have a clutch size of 3 to 4 eggs (T. Lok, personal observation; Cramp & Simmons 1977). Incubation usually starts one or two days after the first egg has been laid and causes asynchronous hatching, especially for the 3rd and 4th chick in the nest (pers. obs.). Incubation of the eggs takes 25 to 26 days (N = 4) and the chicks are altricial (Cramp & Simmons 1977; Starck & Ricklefs 1998). Spoonbill chicks fledge when ca. 35 days old, after which they are still fed by their parents for at least another month (Cramp & Simmons 1977).

Growth measurements

For regular growth measurements, we selected colonies of 3 or 4 nests in 2006 and 2007, resulting in N = 35 chicks from 11 nests (5 in 2006 and 6 in 2007). During the hatching period, nests were checked daily to determine the hatching date of each chick in the nest. In these small colonies, chick growth parameters were measured every 3rd day (with some exceptions, due to adverse weather), starting at the day of hatching (age 0). Recorded morphometric variables include the length of head-bill, bill, tarsus, wing (from the wrist up to the longest primary, flattened and straightened) and the 8th primary feather (flattened and straightened, starting from the basis between the 8th and 9th primary feather up to the tip of the 8th primary feather) (± 1 mm). In addition, we measured body mass using 500, 1000 and 2500 g Pesola spring balances (± 1, 5 and 10 gram), depending on the weight of the chick. We only started measuring the 8th primary feather halfway the breeding season of 2006, and with all males being from 2006, we only have data on 8th primary feather growth of males of 18 days and older.

Growth models

For each biometric measure, we assessed whether its growth was best described by either of two classical growth functions (Ricklefs 1968) that are often applied to chick growth (Tjorve & Tjorve 2010): the logistic growth curve, $y_t = y_\infty / (1+\exp(-k \cdot (t-T_i)))$, and the Gompertz growth curve, $y_t = y_\infty \cdot \exp(-\exp(-k \cdot (t-T_i)))$. y_t is the biometric response variable, t is the age (in days), y_∞ is the asymptotic value of the response variable, k is the growth rate constant and T_i is the age (in days) at the inflection point. The inflection point occurs at $y(T_i) = y_\infty/2$ for the logistic curve, and at $y(T_i) = y_\infty/e$ for the Gompertz curve. Maximum growth rate (g_{max}) that occurs at the inflection point T_i is calculated as $ky_\infty/4$ for the logistic and ky_∞/e for the Gompertz growth curve.

Assessing the generality of the estimated growth curves

The growth of the regularly measured chicks (hereafter called 'growth curve chicks') was compared with data of (often earlier-hatched) chicks from the other (generally larger) colonies on Schiermonnikoog between 2007 and 2009. The hatching date of these chicks (hereafter called 'reference chicks') was observed or estimated from head-bill length when younger than two weeks. When 2 to 5 weeks old, these reference chicks were colour-ringed and their head-bill, bill, 8th primary length and body mass were measured.

Because chicks are no longer attached to their nest after ca. three weeks, but congregate in crèches, we provided chicks with a temporary label, i.e. a uniquely labelled cotton band, attached around the tibia with a stampler within two weeks after hatching. During this procedure, the length of the head-bill of each chick was measured. To minimize the period of disturbance no other measurements were taken. To prevent undesirable cooling of small chicks (<3 days old, when they are normally still being brooded by their parents) during this procedure, they were covered with a cloth.

To assess hatching dates with minimal disturbance in large colonies, we daily observed the nests from a mobile hide. The observer entered the hide about 100 m away from the colony, and approached, hidden in the hide, the colony up to a distance of 10 m. When approached slowly, birds would not fly up, but only be shortly alert, after which they resumed their normal breeding activities. The date that a small chick was observed in the nest for the first time (i.e. when its orange bill was visible above the nest edge) was taken as the hatching date of the first chick. Hatching dates of subsequent chicks could not be determined, as this would require counting the number of chicks (dead and alive) in the nest. This is not possible from a hide. Due to lack of manpower, daily observations of the nests were not feasible in 2009, and hence, hatching dates were only accurately observed in 2007 and 2008.

We fitted growth curves based on the data of the reference chicks and compared these with the estimated curves based on the 'growth curve chicks'. Due to the absence of data of reference chicks younger than two weeks, head-bill length, bill length and body mass were fixed at 41.2 mm, 20.5 mm and 56.6 gram at hatching ($t_0 = 0$), and the 8th primary length at 17.3 mm at the 9th day ($t_0 = 9$, which was the age at which all chicks had started growing this feather). These were the mean values of the 'growth curve chicks' at these ages. With y fixed to y_0 at $t = t_0$, T_i can be calculated from y_∞ and k as $T_i = \ln(-\ln(y_0/y_\infty))/k + t_0$.

Age estimation

To assess which morphometric variable most accurately predicted age, we rewrote the logistic and Gompertz growth curve with age (t) as a function of biometric measurement y_t. For the logistic growth curve, this is $t = -\ln(y_\infty/y_t-1)/k+T_i$ and for the Gompertz curve this is $t = -\ln(-\ln(y_t/y_\infty))/k+T_i$. We predicted the age using the estimates of the best-supported growth curves for each morphometric variable and calculated the deviation of the predicted age from the real age. We also calculated the accuracy of the mean of the estimated ages from respectively head-bill length and 8th primary length, both standard measurements taken during colour-ringing of spoonbill chicks. Because differences in growth generally become more pronounced at later stages of chick growth, and because chicks can only be colour-ringed when ca. two weeks or older, we separately calculated the accuracy of age prediction from morphometric variables for chicks younger than 15 days and for chicks of 15 days or older.

Molecular sexing

At the time the chick received its unique colour-ring combination, a blood sample of 10–80 ml was taken 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).

Statistical analysis

For modelling growth, we used nonlinear mixed models (Lindstrom & Bates 1990; Pinheiro & Bates 2000). Because chicks are repeatedly measured over time, there is pseudo-replication within chicks. To account for this, chick identity was included as a random effect. In addition, a (first-order regressive) correlation structure was used to account for temporal autocorrelation within chicks (Box, Jenkins & Reinsel 1994; Pinheiro & Bates 2000). We restricted the analyses to chicks that fledged (i.e., that could fly, when ≥ 32 days old) to allow proper estimation of the random effects. Because of a strong correlation among the random effects for y_∞, k and T_i, and – perhaps as a result of this, or because of limited data – convergence problems when two or three random effects were included in the model, we decided to only include a random effect for the asymptotic value (y_∞). We tested for an effect of sex by comparing models with and without a sex effect on each parameter, resulting in $2^3 = 8$ logistic and Gompertz growth models to be compared.

Analyses were performed in program R (version 2.13.0, R Development Core Team 2011) and package nlme for the analysis of non-linear mixed models (Pinheiro *et al.* 2012). We found significant heteroscedasticity in the residuals of body mass for the 'growth curve chicks', but not for the reference chicks. The reason for this heteroscedasticity was that variation in body mass increased with average body mass. However, correcting for this heteroscedasticity by modelling variance as a function of age (Pinheiro & Bates 2000) had the undesirable result that the heavier (older) chicks had less influence on the estimated curve and caused the asymptotic values to become poorly estimated. For this reason, we decided not to correct for the heteroscedasticity of body mass residuals.

Candidate models were run using maximum likelihood estimation and their relative support was evaluated based on the Akaike information criterion, corrected for small sample size (AIC_c, Akaike 1973; Burnham & Anderson 2002). We considered a model to be substantially better supported when its AIC_c value was at least 2 points lower relative to competing models. Restricted maximum likelihood estimates of the best-supported models are reported.

RESULTS

Growth curves

Of the 35 'growth curve chicks', 0, 1, 2 and 3 chicks survived until fledging in respectively 3, 4, 3 and 1 nests, resulting in 13 fledged chicks. Of the 22 chicks that died, 14 chicks (67%) died within the first 10 days and 4 chicks between 10 and 20 days. The remaining 4 chicks died between 20 and 30 days: one was the third chick in a nest that grew much slower than its siblings and probably died of starvation, the other three drowned during a storm tide. This resulted in age-specific chick survival rates of 0.60 from 0 to 10 days after hatching, 0.81 from 10 to 20 days, 0.76 from 20 to 30 days and 1.00 from 30 days to fledging (between 33 and 39 days). We excluded the thirdly hatched chick of the nest in which 3 chicks fledged, because this chick showed considerably reduced growth. Based on the data of the remaining 12 fledged chicks, head-bill, bill, wing and 8th primary length were best described by a Gompertz growth curve, whereas tarsus length and body mass were best described by logistic growth (for model selection results, see Appendix I, Table I.1).

There was substantial support for differences in growth between males and females for bill, wing, tarsus and body mass (removing the sex effects increased AICc between 5.4 (for bill) and 33.4 (for tarsus)), but only minor support for a sex effect on y_∞ for head-bill ($\Delta AIC_c = -0.53$) and Ti 8th primary growth ($\Delta AIC_c = -0.57$) (Table 3.1, Table I.1, Fig. 3.1). Males had larger asymptotic values (y_∞) for bill, wing, tarsus and body mass than females and reached the inflection point (T_i, the age at which maximum growth occurs) at a later age. The most pronounced sex effects were found for tarsus and body mass: males were estimated to become 17% heavier than females and to get 22% longer tarsi (Table 3.1). Only for tarsus growth, k was lower for males than females. To achieve the same maximum growth rate $g_{\max}$, which occurs at T_i and is calculated as $ky_\infty/4$ for logistic and ky_∞/e for Gompertz growth, k should be lower when y_∞ is higher. This was the case for the growth of the tarsus, but not for bill, wing and body mass, implying faster maximum growth rates of these body measures in males than females.

Generality of growth curves

The growth curve for head-bill, as estimated from the 'growth curve chicks', poorly fits the head-bill lengths of the reference chicks whose age was determined from their hatching date observed from a hide (Fig. 3.2A): the actual head-bills were consistently

Table 3.1 Parameter estimates (mean ± S.E.) of the best-supported growth curves (see Table I.1) for five morphometric variables (head-bill, bill, wing, 8th primary and tarsus length (mm)) and body mass (g). Results are based on the 'growth curve chicks' (N = 8 females and N = 4 males).

		Fixed effects						Random effect	
		y_∞		k		T_i			
Measure (y)	Curve	female	male	female	male	female	male	y_∞	res
Head-bill (mm)	G	184 ± 5	184 ± 5	0.052 ± 0.002	0.052 ± 0.002	7.9 ± 0.6	7.9 ± 0.6	6.0	3.6
Bill (mm)	G	122 ± 4	135 ± 5	0.056 ± 0.003	0.056 ± 0.003	10.4 ± 0.7	12.1 ± 0.8	4.6	2.6
Wing (mm)	G	343 ± 10	366 ± 11	0.095 ± 0.004	0.095 ± 0.004	13.7 ± 0.4	15.6 ± 0.5	0.0	12.2
8th primary (mm)	G	247 ± 10	247 ± 10	0.095 ± 0.005	0.095 ± 0.005	19.7 ± 0.4	19.7 ± 0.4	16.3	6.1
Tarsus (mm)	L	137 ± 2	167 ± 4	0.168 ± 0.007	0.146 ± 0.007	9.1 ± 0.3	12.0 ± 0.5	0.7	5.4
Body mass (g)	G	1434 ± 34	1676 ± 46	0.147 ± 0.007	0.147 ± 0.007	8.9 ± 0.27	10.4 ± 0.31	60.2	82.6

L = Logistic growth: $y_t = y_\infty/(1+\exp(-k*(t-T_i)))$; G = Gompertz growth: $y_t = y_\infty*\exp(-\exp(-k*(t-T_i)))$

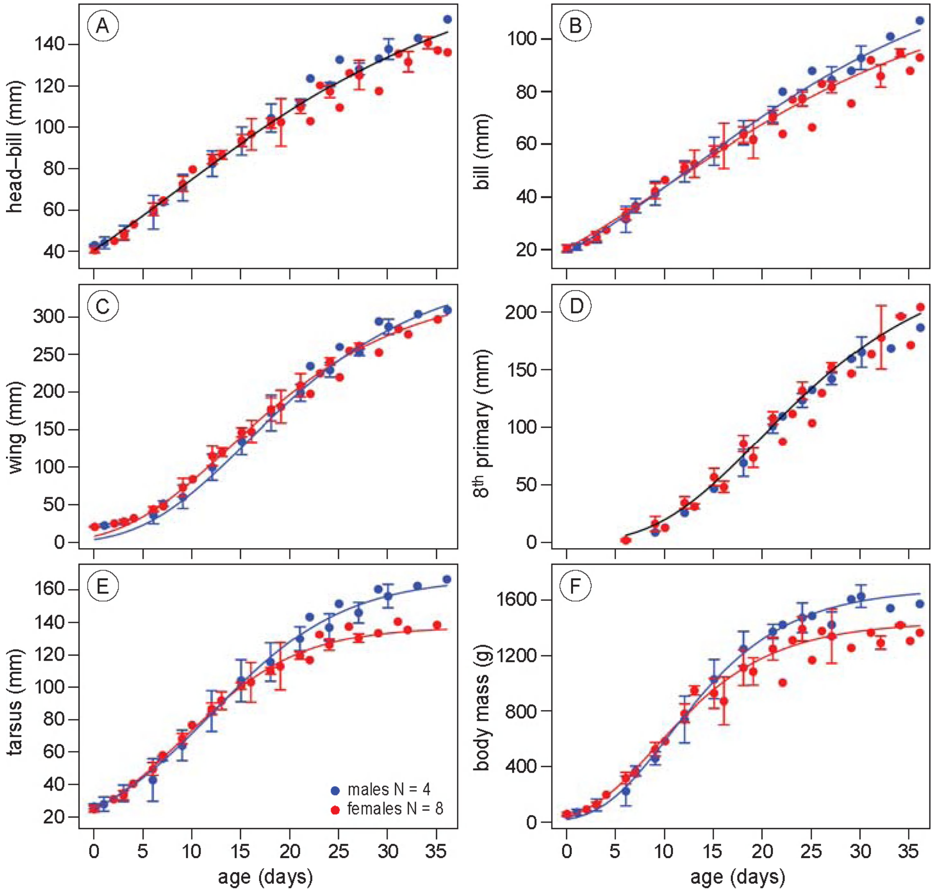

Figure 3.1 Estimated growth curves for five structural size parameters: (A) head-bill, (B) bill, (C) wing, (D) 8th primary and (E) tarsus length; and for (F) body mass based on the 'growth curve chicks'. Estimates are shown as mean ± SD per age and sex, with females in red (N = 8) and males in blue (N = 4). Between 6 and 14 measurements per chick are used for the estimates shown in these graphs. Lines are only separately drawn for the sexes when there was substantial support ($\Delta AIC_c > 2$) for a sex effect on one or more model parameters (see Table I.1).

larger than predicted by the curve. This may be caused by slower growth of head-bill of the 'growth curve chicks' compared to the reference chicks, or because the observed hatching date was later than the actual hatching date. To investigate whether growth rates of the 'growth curve chicks' differed from the reference chicks, we compared the growth of head-bill length between the first measurement (when younger than two weeks) and colour-ringing (when ca. 2–5 weeks old). When estimating the age of the chicks from the head-bill length at the first measurement, the head-bill lengths at colour-ringing were almost perfectly on the curve (Fig. 3.2B). This suggests that the growth rate of head-bill of the 'growth curve chicks' is similar to that of the reference

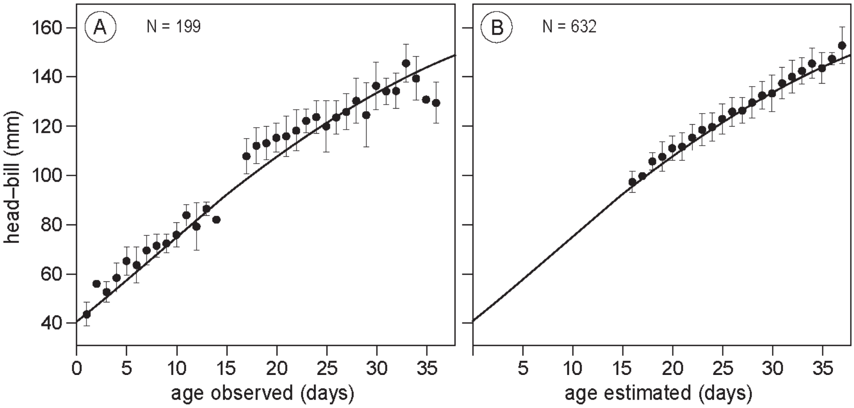

Figure 3.2 The relationship between age and head-bill length (mean ± SD) for reference chicks (A) of which hatching date was accurately observed (i.e., only firstly hatched chicks are included, assumed to have the longest head-bill compared to the other nestlings when younger than two weeks) and (B) of which age was estimated from head-bill length when younger than two weeks (using the estimates in Table 3.1) and their head-bill length was measured again during colour-ringing. In contrast to (A), this is not restricted to firstly hatched chicks. The line represents the Gompertz growth curve for head-bill length estimated from the 'growth curve chicks'. The chicks that survived until ringing occur twice in (A).

chicks, but that hatching probably occurred one or two days before a chick was first observed from the hide.

For further comparison of the growth of the 'growth curve chicks' with that of the reference chicks, we therefore only used reference chicks of which age was accurately estimated from head-bill length within two weeks after hatching. Data and estimated growth curves of the reference chicks, with y_0 fixed, are shown in Table 3.3 and Fig. 3.3 (solid lines) and compared with the estimated growth of the 'growth curve chicks' (dashed lines). While there was only minor evidence for a sex effect on head-bill growth for the 'growth curve chicks' (ΔAIC_c = -0.53, Table I.1; the sex-specific curves are shown in Fig. 3.3A), the sex effect was strongly evident for the reference dataset. Bill growth was sex-specific for both datasets, but the estimated growth curves differed quite substantially. In contrast, 8th primary growth was very similar for the two datasets, with no evidence for a sex effect on any of the growth parameters. Body mass growth was lower for the 'growth curve chicks' than for the reference chicks.

Age estimation

Except for 8th primary and wing length, the age of the 'growth curve chicks' was more accurately estimated from morphometric variables when younger than 15 days rather than older (Table 3.2). For chicks younger than 15 days, head-bill and tarsus length were the best predictors, whereas at older ages, wing length (only measured in the 'growth curve chicks') or a combination of head-bill and 8th primary feather length

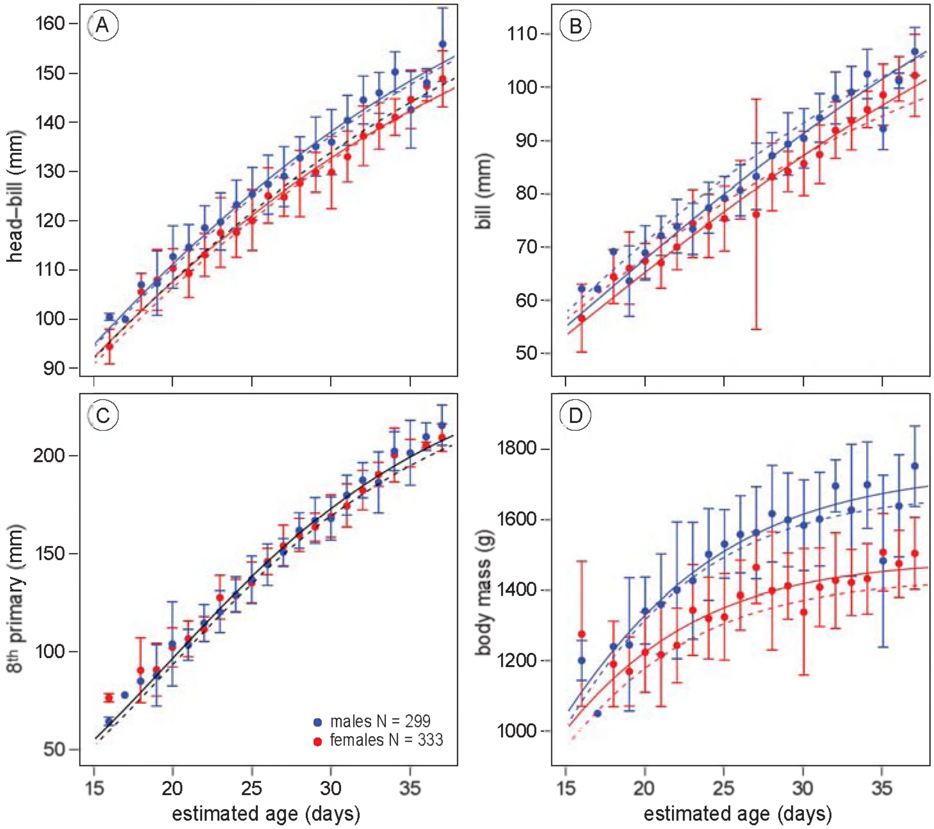

Figure 3.3 (A) Head-bill length, (B) bill length, (C) 8th primary length and (D) body mass of reference chicks, plotted against the estimated age, from the head-bill length measured within two weeks after hatching (using the growth curve parameters for head-bill from Table 3.1). Results are based on N = 333 female (in red) and N = 299 male (in blue) reference chicks. The dashed lines show the growth curves estimated from the 'growth curve chicks', and the solid lines the growth curves estimated for the reference chicks, with head-bill, bill and mass at hatching (age = 0) fixed at the mean of the 'growth curve chicks' (41.2 mm, 20.5 mm and 56.6 gram respectively) and the 8th primary fixed at 17 mm when 9 days old (this was the first day that all 'growth curve chicks' had started growing this feather). Lines are only separately drawn for the sexes when there was substantial support ($\Delta AIC_c > 2$) for a sex effect on one or more model parameters (see Appendix I, Table I.2).

(also measured in the reference chicks) were better predictors of age. The 8th primary feather only started growing ca. one week after hatching (Fig. 3.1) and was the likely cause of the observed delayed growth of the wing in the first week after hatching, as has been suggested to explain the similarly delayed growth of the wing of golden plover chicks *Pluvialis apricaria* (Pearce-Higgins & Yalden 2002). This makes the 8th primary unsuitable and wing unreliable as a predictor of age for chicks younger than one week.

Table 3.2 Accuracy of age estimation (i.e. the mean deviation from the true age) of the 'growth curve chicks' (6-14 measurements on 12 chicks) using the best-supported growth curve for each biometric measure (Table 3.1). Accuracy is separately calculated for chicks younger than 15 days, and for chicks of 15 days or older. For each growth period, the two most accurate estimators of age are shown in bold.

	Accuracy of age estimation (days)		Sex effect
Body measure	<15 days	≥ 15 days	
Head-bill	**0.73**	1.52	No
Bill	0.83	1.57	Yes
Wing	1.64	**1.07**	Yes
8th primary	1.37	1.26	No
Tarsus	**0.66**	1.89	Yes
Body mass	0.83	4.41	Yes
Head-bill + 8th primary	0.86	**1.04**	No

We also assessed which morphometric variables were most accurate for predicting age of the reference chicks at colour-ringing by comparing the estimated hatching date based on head-bill length within two weeks after hatching (using the estimates in Table 3.1) with the hatching date estimated from head-bill length and/or 8th primary during colour-ringing (using the estimates in Table 3.3). This revealed that the 8th primary length most closely resembled the hatching date as estimated from head-bill at young ages (mean deviation = 1.12 days), compared with a deviation of 1.74 days when using sex-specific head-bill length, and 1.24 days when using the combination of 8th primary and sex-specific head-bill length. This conclusion was different from that based on the 'growth curve chicks' of 15 days or older, where the combination of head-bill and 8th primary length more accurately predicted age than 8th primary length alone (Table 3.2). Although for the 'growth curve chicks', wing length turned out as the most accurate age estimator of older chicks (Table 3.2), wing length was not among the standard measures taken during colour-ringing and was thus not measured for the reference chicks. As such, the generality of its growth curve and accuracy for age estimation could not be verified.

DISCUSSION

We have estimated growth curves for several morphometric variables and body mass of spoonbill chicks. We report growth curves from hatching to fledging for 12 chicks that were measured every third day. Their growth was compared with the biometry of chicks at colour-ringing (2-5 weeks old) of which age was accurately predicted from head-bill length within two weeks after hatching. Growth of the 8th primary was very

Table 3.3 Parameter estimates (mean ± SE) of the Gompertz curves for three morphometric variables (head-bill, bill and 8th primary length (mm)) and body mass (g). Results are based on reference chicks of which age was accurately estimated from head-bill length when younger than two weeks (N = 333 females and N = 299 males).

	y_∞		k		T_i		g_{max}	
	Female	Male	Female	Male	Female	Male	Female	Male
Head-bill	179 ± 3	188 ± 3	0.053 ± 0.001	0.053 ± 0.001	7.3 ± 0.4	7.9 ± 0.4	3.5 ± 0.03	3.7 ± 0.03
Bill	146 ± 6	156 ± 6	0.044 ± 0.002	0.044 ± 0.002	15.2 ± 1.0	15.9 ± 1.1	2.4 ± 0.02	2.5 ± 0.02
8th primary	254 ± 3	254 ± 3	0.093 ± 0.001	0.093 ± 0.001	19.7 ± 0.2	19.7 ± 0.2	8.7 ± 0.03	8.7 ± 0.03
Body mass	1485 ± 19	1741 ± 23	0.141 ± 0.005	0.127 ± 0.004	8.4 ± 0.3	9.7 ± 0.3	77.2 ± 2.0	81.4 ± 1.6

For accurate estimation of early growth (despite the absence of data) y_0 was fixed at the mean size of the 'growth curve chicks' at t_0, being respectively 41.2 mm, 20.5 mm and 56.6 g for head-bill, bill and body mass at $t_0 = 0$ and 17.3 mm for the 8th primary at $t_0 = 9$. T_i was calculated as $\ln(-\ln(y_0/y_\infty))/k+t_0$ and the maximum growth rate (g_{max}, which occurs at T_i) as ky_∞/e. Standard errors for T_i and g_{max} were calculated using the Delta method (Cox 1998).

similar for the two datasets (Fig. 3.3C). Growth of the head-bill of the 'growth curve chicks' closely resembled the head-bill growth of female reference chicks (Fig. 3.3A), which could be explained by the fact that this curve was based on more females (N = 8) than males (N = 4). We found some evidence for a sex effect on the y_∞ of head-bill length for the 'growth curve chicks' (Table I.1; 182 and 188 mm for females and males) which provided very similar curves as those estimated for the reference chicks (Table 3.3, Fig. 3.3A). Bill growth of the 'growth curve chicks' did not adequately fit that of the reference chicks. This may be caused by the fact that for the reference chicks, bill length was calculated from the measurement of head-bill and head length, with head length probably being less precisely measured than bill length. For this reason, we choose to measure bill rather than head length of the 'growth curve chicks'. That the body mass growth of the 'growth curve chicks' was slower than of the reference chicks, suggests that the former were in relatively poor condition. The body mass growth was similar to that measured for African spoonbill chicks *Platalea alba* (Kopij 1997).

Our results showed that growth was sex-specific for head-bill, bill and wing length and especially for tarsus length and body mass. Males were estimated to become 17% heavier than females and to get 22% longer tarsi. The more pronounced sex effect on body mass growth compared to several other morphometric variables was also found in chicks of the sexually size-dimorphic shag *Stictocarbo aristotelis* (Velando, Graves & Freire 2000). That the differences in (especially) body mass and tarsus length between males and females were already evident prior to fledging, suggests that male spoonbill chicks have higher daily nutritional demands and hence require more food than female chicks (e.g., Anderson *et al.* 1993; Krijgsveld *et al.* 1998).

A comparison with biometric measurements on adult birds confirms that the wing and 8th primary length only subtly differ between the sexes, but also points out that we considerably underestimated adult male and female head-bill and bill length as well as the sexual size dimorphism in these measures (Table 3.4). This suggests that, while the Gompertz curve appears well able to describe the growth of head-bill and bill of spoonbill chicks during the pre-fledging phase, it poorly predicts the growth during the post-fledging phase. When taking a closer look at Fig. 3.3A, the growth curve appears to be unable to capture the relatively long head-bills of the oldest chicks measured. The growth of head-bill therefore seems to have a longer linear phase than can be captured using a Gompertz growth curve. The full length of the bill is only attained after 3–6 months (Cramp & Simmons 1977). During this period, the difference in bill length between males and females probably also becomes more pronounced.

The estimated asymptotic values for body mass were also much lower than the actual body mass of incubating spoonbills (Table 3.4), despite the fact that body mass already clearly levelled off during the pre-fledging phase (Fig. 3.1, 3.3). Given the enormous variation in body mass among chicks of the same age (Fig. 3.3), a potential explanation is that selective disappearance of the lighter chicks occurs after fledging. Alternatively, the lighter chicks gain additional weight after fledging in a way that is poorly predicted by an extrapolation of the estimated Gompertz growth curve.

Predicting age based on morphometric measurements was generally more accurate for young chicks (<15 days old) than older chicks, probably because variation in growth becomes more pronounced at older ages, either due to structural size differences that become larger when chicks get larger, or because of the cumulative effect of variation in environmental conditions on growth. Growth of the 8th primary was almost identical for the 'growth curve chicks' as for the reference chicks (solid and dashed line in Fig. 3.3C), whereas there was a pronounced sex effect on head-bill growth among the reference chicks. This implies that using sex-specific head-bill growth curves will increase the accuracy of age estimation.

We have derived a growth curve for body mass based on the large dataset of reference chicks of which age was accurately estimated from head-bill length within two weeks after hatching (Fig. 3.3D). The residuals from this growth curve can be used as an index of body condition, preferably proportional to the predicted value (following Hamer & Hill 1993; Quillfeldt *et al.* 2006). Using proportional residuals prevents large deviations from the predicted values, more likely to occur when predicted body mass is also high, to have a disproportionate effect in statistical tests that investigate which variables explain variation in chick body condition. Because males of a given age are heavier than females, assuming this is independent of body condition, sex-specific body mass curves should be used. Spoonbills cannot be reliably sexed based on the biometric measurements that have been usually taken during colour-ringing (head-bill, head, 8th primary length and body mass; de Voogd 2005). Our results suggest that when tarsus length is included, biometry could become reliable for sexing, especially

Table 3.4 Comparison of y_∞ (in mm or grams) estimated from chick growth data with biometric data of adult birds.

	Estimated y_∞			Measurements on adult birds						
				Females			Males			
	Females	Males	SSD (%)	Mean	Range	N	Mean	Range	N	SSD (%)
Head-bill	179	188	1.05	231	230-231	2	266	255-283	9	1.15
Bill	146	156	1.07	182	168-191	14	213	195-231	15	1.17
Wing	343	366	1.07	370	360-377	10	394	386-412	13	1.06
8th primary	254	254	1.00	252	252-252	1	262	255-273	3	1.04
Tarsus	137	167	1.22	131	123-141	19	149	140-163	24	1.14
Body mass	1485	1741	1.17	1650	1620-1680	2	1881	1730-1960	9	1.14

SSD = Sexual Size Dimorphism and calculated as Male/Female. The estimated y_∞ of head-bill, bill, 8th primary length and body mass are from Table 3.3, and the y_∞ of wing and tarsus length are from Table 3.1. Adult data on head-bill length, 8th primary length and body mass are from incubating birds (2008-2012, Schiermonnikoog), whereas data on bill, wing and tarsus length come from museum specimen originating from the Netherlands (Cramp & Simmons 1977).

for chicks older than 25 days. A similar result was found for the closely related glossy ibis *Plegadis falcinellus*, where a combination of sex-specific tarsus length and sex-unspecific wing length resulted in 84% of chicks of 2–5 weeks old being correctly sexed (Figuerola *et al.* 2006). Therefore, we propose to include tarsus length as a standard measurement taken during colour-ringing. This eventually allows the evaluation of whether sex determination based on this combination of biometric measurements will be reliable enough to replace expensive and time-consuming (both in the field and in the lab) molecular assays.

The Eurasian spoonbill is a protected species, both nationally (by the Dutch Nature Conservation Act 1998) and internationally (by the Bonn Convention, Triplet *et al.* 2008), and the number of visits that cause disturbance to a single colony should therefore be minimized. We showed here that the age of spoonbill chicks is most accurately predicted from head-bill or tarsus length at a young age (younger than two weeks), for which the estimates in Table 3.1 can be used. However, spoonbill colonies are usually visited only once to ring chicks at the age of ca. 2 to 5 weeks. Although wing length revealed as an accurate estimator of age for the older 'growth curve chicks', wing length was not measured for the reference chicks and the generality of the estimated wing growth curve in Table 3.1 as well as its accuracy for estimating age could therefore, unfortunately, not be verified. Being part of the entire wing and the most accurate estimator of age for the reference chicks, we propose to use the 8th primary and its estimated growth curve reported in Table 3.3 to estimate the age of chicks older than two weeks. For an assessment of the body condition of chicks that are colour-ringed (at the age of 2–5 weeks), we propose to at least measure the 8th primary length for age estimation, the tarsus length for sex determination, and body mass. A body condition index can then be calculated as the proportional deviation in body mass from the predicted sex- and age-specific body mass using the estimates in Table 3.3.

Acknowledgements

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APPENDIX I

Table I.1 Model selection results of logistic and Gompertz growth curves for five morphometric variables (head-bill, bill, wing, 8th primary and tarsus length) and body mass, testing for a sex effect on each growth parameter (y_∞, k, T_i). The models that found similar support ($\Delta AIC_c < 2$) and did not contain uninformative parameters are shown in bold. Results are based on the data of the 'growth curve chicks' (N = 12).

Head-bill

Shape	Sex effects	K	Δ(-2logL)	ΔAIC_c	Akaike weight
Gompertz	**y_∞**	**7**	**2.51**	**0.00**	**0.25**
Gompertz	**-**	**6**	**5.27**	**0.53**	**0.19**
Gompertz	y_∞, T_i	8	1.29	1.04	0.15
Gompertz	k	7	3.85	1.34	0.13
Gompertz	y_∞, k, T_i	9	0.00	2.05	0.09
Gompertz	y_∞, k	8	2.40	2.15	0.08
Gompertz	T_i	7	5.27	2.76	0.06
Gompertz	k, T_i	8	3.68	3.43	0.04
Logistic	y_∞	7	13.69	11.18	0.00
Logistic	-	6	16.54	11.79	0.00
Logistic	y_∞, T_i	8	12.62	12.37	0.00
Logistic	k	7	14.95	12.44	0.00
Logistic	y_∞, k	8	13.25	13.00	0.00
Logistic	T_i	7	16.51	14.00	0.00
Logistic	k, T_i	8	14.53	14.28	0.00
Logistic	y_∞, k, T_i	9	12.59	14.65	0.00

-2logL = 614.46, AIC_c = 631.87

Bill

Shape	Sex effects	K	Δ(-2logL)	ΔAIC_c	Akaike weight
Gompertz	**y_∞, T_i**	**8**	**1.08**	**0.00**	**0.41**
Gompertz	y_∞, k, T_i	9	0.00	1.22	0.22
Gompertz	k	7	5.53	2.18	0.14
Gompertz	y_∞, k	8	4.51	3.44	0.07
Gompertz	y_∞	7	7.19	3.84	0.06
Gompertz	k, T_i	8	5.53	4.45	0.04
Gompertz	-	6	11.00	5.43	0.03
Gompertz	T_i	7	9.44	6.09	0.02
Logistic	y_∞, T_i	8	20.40	19.32	0.00
Logistic	k	7	24.22	20.88	0.00
Logistic	y_∞	7	24.47	21.13	0.00
Logistic	y_∞, k	8	22.31	21.23	0.00
Logistic	y_∞, k, T_i	9	20.39	21.62	0.00
Logistic	-	6	28.32	22.74	0.00
Logistic	k, T_i	8	24.11	23.03	0.00
Logistic	T_i	7	27.84	24.50	0.00

-2logL = 561.79, AIC_c = 580.03

Table I.1 Continued

Wing

Shape	Sex effects	K	Δ(-2logL)	ΔAIC$_c$	Akaike weight
Gompertz	**y_∞, T_i**	**8**	**1.70**	**0.00**	**0.48**
Gompertz	y_∞, k, T_i	9	0.00	0.67	0.34
Gompertz	k, T_i	8	5.52	3.82	0.07
Gompertz	T_i	7	8.29	4.27	0.06
Gompertz	-	6	12.91	6.60	0.02
Gompertz	k	7	10.69	6.67	0.02
Gompertz	y_∞	7	11.66	7.63	0.01
Gompertz	y_∞, k	8	10.67	8.97	0.01
Logistic	y_∞, k, T_i	9	14.17	14.84	0.00
Logistic	y_∞, T_i	8	17.53	15.83	0.00
Logistic	T_i	7	27.68	23.65	0.00
Logistic	k, T_i	8	26.36	24.66	0.00
Logistic	-	6	33.18	26.87	0.00
Logistic	k	7	31.14	27.11	0.00
Logistic	y_∞	7	31.62	27.60	0.00
Logistic	y_∞, k	8	30.87	29.17	0.00

-2logL = 719.65, AIC$_c$ = 738.78

8th primary

Shape	Sex effects	K	Δ(-2logL)	ΔAIC$_c$	Akaike weight
Gompertz	**T_i**	**7**	**1.31**	**0.00**	**0.24**
Gompertz	**-**	**6**	**4.23**	**0.57**	**0.18**
Gompertz	k*	7	2.15	0.84	0.16
Gompertz	y_∞, k	8	0.09	1.20	0.13
Gompertz	k, T_i	8	0.98	2.09	0.09
Gompertz	y_∞	7	3.51	2.20	0.08
Gompertz	y_∞, T_i	8	1.31	2.42	0.07
Gompertz	y_∞, k, T_i	9	0.00	3.59	0.04
Logistic	-	6	31.66	27.99	0.00
Logistic	y_∞	7	30.75	29.44	0.00
Logistic	T_i	7	31.35	30.05	0.00
Logistic	k	7	31.61	30.30	0.00
Logistic	y_∞, k	8	30.42	31.53	0.00
Logistic	y_∞, T_i	8	30.75	31.86	0.00
Logistic	k, T_i	8	31.36	32.47	0.00
Logistic	y_∞, k, T_i	9	29.80	33.39	0.00

-2logL = 581.68, AIC$_c$ = 598.37

Tarsus

Shape	Sex effects	K	Δ(-2logL)	ΔAIC$_c$	Akaike weight
Logistic	**y_∞, k, T_i**	**9**	**0.00**	**0.00**	**0.78**
Logistic	**y_∞, T_i**	**8**	**4.80**	**2.48**	**0.22**
Logistic	y_∞	7	24.00	19.39	0.00
Logistic	y_∞, k	8	23.40	21.07	0.00
Logistic	T_i	7	26.32	21.72	0.00
Logistic	k, T_i	8	24.88	22.56	0.00
Gompertz	y_∞, k, T_i	9	26.41	26.41	0.00
Gompertz	y_∞, T_i	8	29.42	27.10	0.00
Logistic	-	6	40.22	33.37	0.00
Gompertz	Ti	7	39.60	35.00	0.00
Logistic	k	7	40.08	35.48	0.00
Gompertz	k, T_i	8	38.04	35.72	0.00
Gompertz	y_∞, k	8	42.09	39.77	0.00
Gompertz	y_∞	7	49.10	44.49	0.00
Gompertz	-	6	59.17	52.32	0.00
Gompertz	k	7	58.15	53.54	0.00

-2logL = 648.06, AIC$_c$ = 667.61

Body mass

Shape	Sex effects	K	Δ(-2logL)	ΔAIC$_c$	Akaike weight
Gompertz	**y_∞, T_i**	**8**	**0.00**	**0**	**0.71**
Gompertz	y_∞, k, T_i	9	0.00	2.304	0.23
Logistic	y_∞, T_i	8	5.97	5.967	0.04
Logistic	y_∞, k, T_i	9	5.70	8.006	0.01
Gompertz	y_∞	7	12.31	10.04	0.00
Gompertz	y_∞, k	8	11.16	11.15	0.00
Gompertz	k, T_i	8	12.21	12.21	0.00
Gompertz	T_i	7	14.94	12.67	0.00
Logistic	y_∞, k	8	12.74	12.74	0.00
Logistic	y_∞	7	16.11	13.85	0.00
Gompertz	k	7	16.21	13.94	0.00
Gompertz	-	6	22.12	17.62	0.00
Logistic	k	7	20.50	18.24	0.00
Logistic	k, T_i	8	18.71	18.71	0.00
Logistic	T_i	7	21.24	18.97	0.00
Logistic	-	6	26.61	22.11	0.00

-2logL = 1493.25, AIC$_c$ = 1565.81

Table I.2 Model selection results to investigate sex-specific growth of reference chicks of which age was accurately estimated from head-bill length when younger than 2 weeks (N = 333 females and N = 299 males). A sex effect was assessed for the growth parameters y_∞ and k of the Gompertz growth curves for three morphometric variables (head-bill, bill and 8th primary length) and body mass. T_i was calculated from y_∞ and k, using the value set for y_0. The models that received similar support ($\Delta AIC_c < 2$) and did not contain uninformative parameters are shown in bold.

	Sex effects	df	ΔAIC_c
Head-bill			
	y_∞	**4**	**0.00**
	y_∞, k	5	1.93
	k	4	2.87
	-	3	68.65
Bill			
	y_∞	**4**	**0.00**
	y_∞, k	5	1.19
	k	4	1.86
	-	3	29.13
8th primary			
	-	**3**	**0.00**
	y_∞, k	5	1.65
	k	4	1.66
	y_∞	4	1.99
Body mass			
	y_∞, k	**5**	**0.00**
	y_∞	4	3.12
	k	4	56.78
	-	3	172.92

Chapter 4

Seasonal variation in the diet of spoonbill chicks in the Wadden Sea: a stable isotopes approach

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Theunis Piersma
Jeltje Jouta
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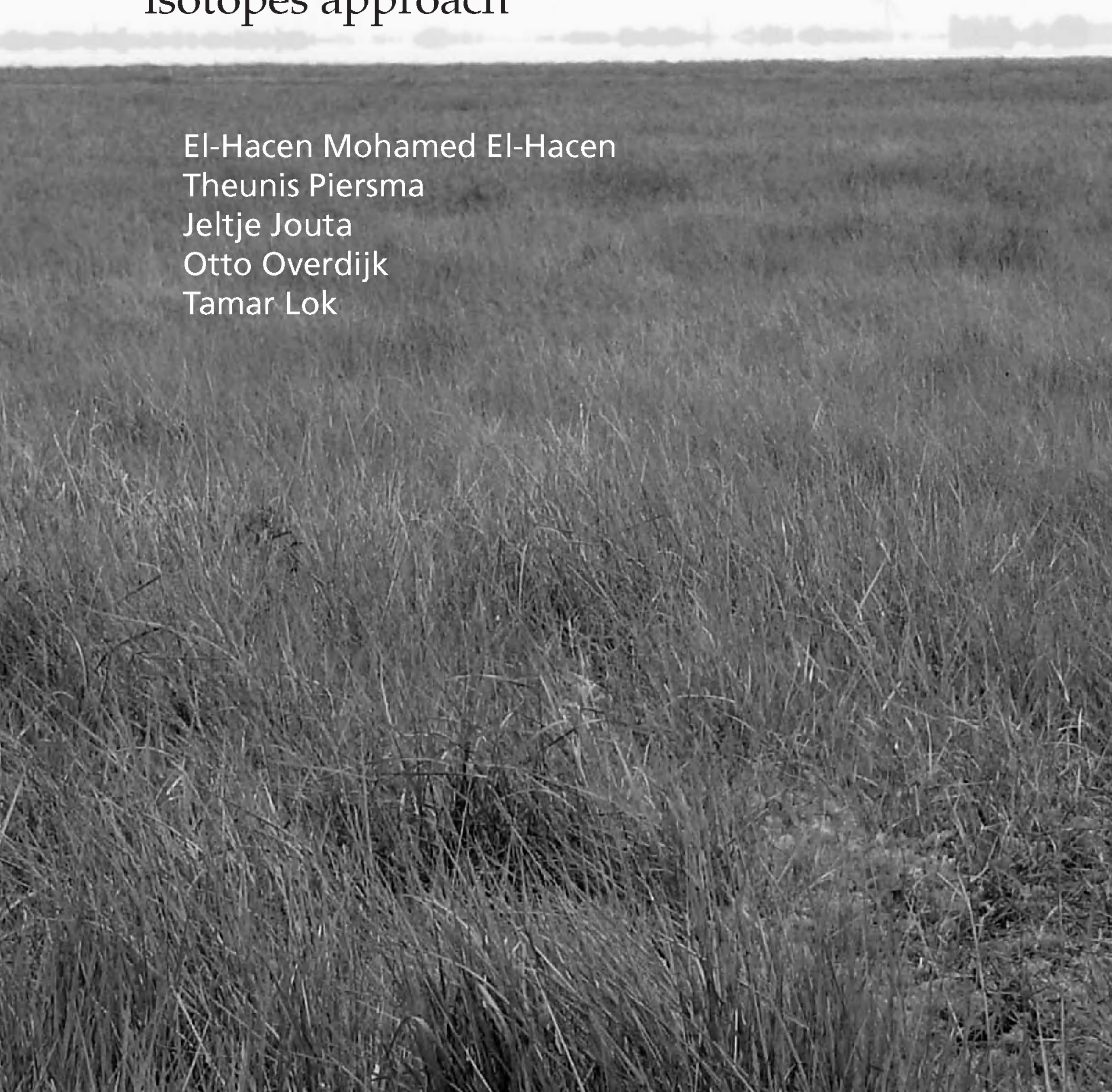
Tamar Lok



ABSTRACT

We used stable isotope tracers in the growing primary feathers of Eurasian Spoonbill chicks (*Platalea leucorodia leucorodia*) to study seasonal variation in their diet on one of the Frisian islands, Schiermonnikoog, The Netherlands. Using growing individual primaries as natural samplers over time, feather-samples were taken along the length of primary feathers to estimate both within- and between-individual variation in diet. Absolute isotopic ratios of feather material ranged from -26.2‰ to -14.7‰ for carbon ($\delta^{13}C$) and from 13.0‰ to 18.7‰ for nitrogen ($\delta^{15}N$). The variation in $\delta^{13}C$ values suggests the use of a variety of feeding habitats, ranging from freshwater to marine. Across the breeding season there was a shift from predominantly freshwater prey early on, to a more marine diet later in the season. Surprisingly, this shift did not occur within the growth trajectory of early born chicks which rather showed the opposite, but it did occur within individual chicks born later in the season. Stable isotope Bayesian mixing-model (SIAR) outcomes demonstrated that the freshwater/brackish prey had the highest isotopic contribution (57%) to the diet early in the breeding season, whereas marine prey contributed most (73%) to the diet later. That chicks fed with either freshwater or marine food items had similar body condition indices suggested that the eating of salty prey did not come at a major cost for growing spoonbill chicks.

INTRODUCTION

Optimal foraging theory predicts that animals will maximize their energy intake by seeking the most profitable prey (MacArthur & Pianka 1966). Many bird species are known to change diet in response to changes in food availability (Bryant *et al.* 1999; Eggers 2000; van Gils *et al.* 2006; Ghosh *et al.* 2011). However, young birds may have additional requirements and possible constraints on food selection, aspects that will change as the chicks turn into fully grown birds (Johnston & Bildstein 1990; Davoren & Burger 1998; Knoff *et al.* 2002; Hannam, Oring & Herzog 2003; Valera *et al.* 2005; Abraham 2008; Beaulieu *et al.* 2010; Steenweg, Ronconi & Leonard 2011). For example, studies have shown that a saline diet may impose physiological stress (Klaassen & Ens 1990; Johnston & Bildstein 1990, Hannam *et al.* 2003; Gutiérrez *et al.* 2011), especially affecting chicks that not yet have fully developed salt glands (Knoff *et al.* 2002; Hannam *et al.* 2003).

Although some species of birds are highly restricted in their choice of food and feeding habitats (the molluscivore Red Knots (*Calidris canutus*) can serve as an example; Piersma 2012), others are able to rely on a variety of foraging habitats to make a living. The Eurasian Spoonbill (*Platalea leucorodia leucorodia*) provides an example of a large wading bird that forages in both freshwater and marine habitats (Hancock, Kushlan & Kahl 1992). Spoonbills are tactile foragers that wade through shallow water and use bill-sweeping to catch their prey (Hancock *et al.* 1992; Matheu & del Hoyo 1992). They feed during both day and night (Piersma 1980; El-Hacen *et al.* 2013) on a wide variety of prey, including fish, crustaceans, molluscs, insects and worms (Cramp & Simmons 1977).

Based on daytime observations of foraging Eurasian Spoonbills in different estuarine habitats in the Netherlands (de Goeij, Kemper & van Wetten 1985; van Wetten & Wintermans 1986), it has been suggested that Spoonbills primarily feed in freshwater habitats at the beginning of the breeding season but gradually shift to feed in intertidal zone (van Wetten & Wintermans 1986; Kemper 1995; Bauchau *et al.* 1998). This diet shift is thought to be driven by an early spring peak in the availability of anadromous Three-spined Sticklebacks (*Gasterosteus aculeatus*) in freshwater habitats (Kemper 1995; Huntingford *et al.* 2001; Östlund-Nilsson 2007) combined with a build-up of the availability of Brown Shrimp (*Crangon crangon*) in the nearby intertidal areas later on (Campos *et al.* 2010; Hufnagl & Temming 2011; Campos *et al.* 2012; Tulp *et al.* 2012). However, since the first descriptions of spoonbill foraging in the 1980s, the Wadden Sea area has been subject to major ecosystem change (Erikson *et al.* 2010), changes that well may have affected the abundance and migration strategies of Spoonbills' potential prey, including sticklebacks and Brown Shrimp.

Feathers consist of keratin that is metabolically inactive once synthesized. Keratin thus reflects the isotope values of the diet during the time when the tissue was formed (Schell, Saupe & Haubenstock 1989; Mizutani *et al.* 1990). Carbon values of marine organisms are typically 7‰ more ^{13}C enriched relative to the freshwater animals

(Craig 1953; Chisholm, Nelson & Schwarcz 1982; Fry, Scalan & Parker 1983). For nitrogen, the ratio of ^{15}N to ^{14}N ($\delta^{15}N$) shows a typical progressive increase of 3.4‰ (on average) at each successive trophic level (Schoeninger & deNiro 1984; Hobson & Welch 1992; Minagawa & Wada 1984; Post 2002; Fry 2006). By not only sampling individuals over the course of the breeding season, but by additionally sampling the material along the length of a single feather (Hobson & Clark 1992; Knoff *et al.* 2002), it is possible to document both inter- and intra-individual seasonal changes in the origin of diets.

Here we verified the occurrence of a seasonal shift in the use of freshwater to marine habitats by characterizing stable isotopes (carbon and nitrogen) in the growing feathers of chicks of Spoonbills breeding on the Wadden Sea island, Schiermonnikoog. We evaluated the relative contributions of several freshwater versus marine prey species in the diet. In an attempt to see whether a marine (i.e. salty) diet might compromise the growth of growing chicks (Knoff *et al.* 2002; Hannam *et al.* 2003), we assessed whether the proportion of marine food in the diet was correlated with body condition.

METHODS

Feather collection and processing

We studied the Spoonbills breeding on the saltmarshes of Schiermonnikoog, the Netherlands (53°29′N, 6°15′E) during April-June 2010. Colonies were observed from a mobile hide to assess hatching dates. Within two weeks after hatching, chicks received individually labelled cotton bands and head-bill length was measured to accurately estimate age (Lok *et al.* in review, Chapter 3). When 3 to 5 weeks old, 40 of these chicks were recaptured and the 5th primary feather of the left wing was collected. In addition, we collected the 5th primary feather of 6 chicks that were not labelled at a younger age; their age was estimated (somewhat less accurately, Lok *et al.* in review, Chapter 3) from the head-bill length at 4 to 5 weeks old. Age was estimated from head-bill length (HB) using the reversed Gompertz curve: $\text{age } (t) = -\ln(-\ln(HB(t)/HB_{max}))/k+T_i$. Following Lok *et al.* (in review, Chapter 3), we used $HB_{max} = 179$, $k = 0.053$ and $T_i = 7.3$ for females, and $HB_{max} = 188$, $k = 0.053$ and $T_i = 7.9$ for males. Weight (g) was measured for all chicks during feather extraction. For sex determination, a blood sample of 10–80 ml was taken from the brachial vein, stored in 96% alcohol and analysed using molecular assays (Fridolfsson & Ellegren 1999).

Prior to subsampling, the length of the 5th primary feather was measured. Assuming that the feather started to grow immediately after hatching (though not yet visible at the outside), we estimated daily growth rate of the feather by dividing the length of the feather by the estimated age of the chick when the feather was extracted. Average daily growth rate of the feathers was 6.6 ± 0.5 mm (mean ± sd, N = 46). Between 3 and 5 weeks after hatching, the growth of the 5th primary feather is approximately linear (Fig. 4.1). Although this may not be entirely true for the first few weeks

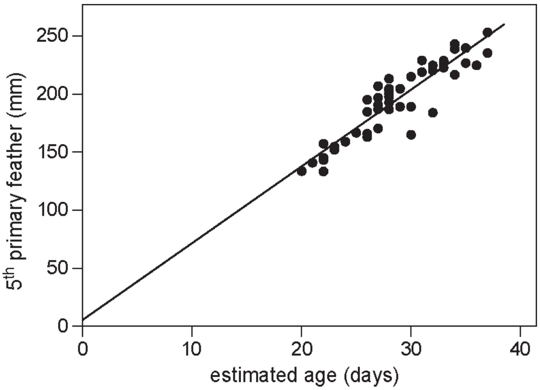


Figure 4.1 The length of the 5th primary feather (in mm, measured after pulling, therefore including the entire shaft) as a function of chick age which was estimated from head-bill length.

(Lok *et al.* in review, Chapter 3), a linear growth of 6.6 mm/day fitted nicely through the origin and the points, with the age of the chicks estimated from their head-bill length (Fig. 4.1).

Feathers were cleaned with warm water and rubbed to remove dirt and external contamination, then dried in an oven at 60°C. After drying, feather subsamples were taken along the length of the right side of the vane. The subsampling protocol was to cut a 6 mm (assimilated over approximately one diurnal cycle) longitudinally every 25 mm (resulting in a time interval of approximately four days). The number of longitudinal subsamples of a feather was only determined by its length, varying from 2 to 7 subsamples per feather, resulting in a total of 203 subsamples of 46 feathers.

Prey item collection and processing

In April – May 2012, prey items were sampled with a fishing net at locations where foraging Spoonbills originating from the breeding colonies of Schiermonnikoog were regularly observed. All collected prey items were stored frozen at -20°C. Biometrics (total length and weight) were measured, after which the samples were freeze-dried.

Stable isotope analysis

The dried feather and prey samples were ground with a pestle and mortar. After the sample preparation was completed, we used a microbalance (Sartorius CP2P) to weigh 0.8 - 1 mg of the ground material into 5 × 9 mm tin capsules. Finally, capsules containing the fine fragments were analysed with the elemental analyser (EA) isotope ratio mass spectrometer (IRMS) (Flash EA, 1112, Flash 2000). Two additional internal laboratory standards (Acetanilide and Urea) plus a blank tin capsule were analysed every tenth sample, allowing for drift correction. Stable isotope ratios are reported in the δ (delta) notation relative to Vienna PeeDee belemnite for carbon and atmospheric

N2 for Nitrogen. A replicate sample was examined every tenth sample to verify the precision of the isotopic measurements. The two samples were expected to be identical. The difference in the isotope values between a sample and its replicate ranged between 0.011‰ and 0.23‰ (with the majority less than 0.1‰) and reflected a measurement error of ≤ 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Statistical analyses

The variation and correlation between $\delta^{13}C$ and $\delta^{15}N$ values were examined visually. To investigate within- and between-individual changes in reliance on freshwater habitats (reflected mainly by $\delta^{13}C$) over the breeding season, we used a mixed-effects model with random individual variation in intercept (u_{0j}~N(0,σ_0^2)) and slope (u_{wj}~N(0,σ_W^2)). We applied the "within-subject centering" approach described by van de Pol and Wright (2009) to distinguish between within- (β_W) and between-individual (β_B) changes in $\delta^{13}C$. In addition, we allowed for changes in within-individual patterns over the season ($\beta_{W.B}$), resulting in the following model: $y_{ij} = (\beta_0 + u_{0j}) + (\beta_W + u_{wj})(x_{ij} - \bar{x}_j) + \beta_B(\bar{x}_j) + \beta_{W\cdot B}(x_{ij} - \bar{x}_j)(\bar{x}_j) + \varepsilon_{0ij}$ where y_{ij} is the $\delta^{13}C$-value of the ith feather section of individual j with x_{ij} referring to the actual assimilation date and x_j to the mean assimilation date of that individual.

Data were checked for collinearity and the isotope values were tested for outliers and departure from normality using graphical inspection with QQ plots. Parameter values and approximate 95% confidence intervals of the above model were estimated using the package nlme (Pinheiro & Bates 2000) in the statistical software R (version 3.0.1, R Development Core Team 2009). Significance of the parameters was assessed using Wald test statistics (Pinheiro & Bates 2000).

The relative contribution of several potential prey species to the diet of Spoonbill chicks was estimated using a Bayesian isotopic mixing model programmed in the R-package SIAR (v 4.0, Parnell *et al.* 2010). The SIAR model requires the isotopic composition of both the predator (consumer) and the prey species (sources), plus the trophic enrichment factors (TEFs). Brown Shrimp, Gobies (Gobiidae) and Righteye Flounder (Pleuronectidae) were selected as sources because these prey species/families contributed the most in the biomass of 7 regurgitates that were spontaneously produced by the chicks during ringing sessions in June-July 2011-2012 (i.e, late in the breeding season, Fig. 4.2). European Smelt (*Osmerus eperlanus*) was excluded from the analyses, since it only occurred accidentally in the regurgitates but because of its large size and weight, its contribution to the diet in terms of biomass was disproportionally high (Fig. 4.2). Moreover the $\delta^{15}N$ values of the sampled individuals were higher than the consumer values and hence out of the range of potential prey species. Chameleon Shrimp (*Praunus flexuosus*) were additionally included as a source in the model as they were abundant in 6 regurgitates produced in June 2010 (Fig. 4.2) and since Palaemoninae are highly abundant on forage locations of Spoonbills during early season (pers. obs.). Because Three-spined Sticklebacks are known to be an important prey species for Spoonbills in this area in the early season (de Goeij *et al.* 1985; van

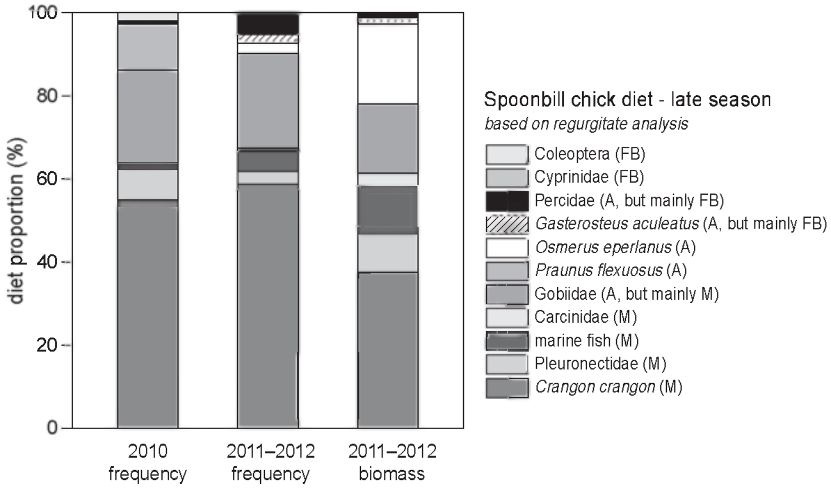


Figure 4.2 Relative abundance of prey species in the spoonbill chick regurgitates in terms of frequency (regurgitates of 2010 (n=6) versus 2011-2012 (n = 7)) and biomass (only determined for the 2011–2012 regurgitates). Letters between brackets denote the expected origin of the prey: (FB) = freshwater/ brackish habitat, (M) = marine habitat and (A) = both habitat categories.

Wetten & Wintermans 1986; Kemper 1995) they were also included as a source in the model. We used the trophic enrichment factor (TEF) estimated for feathers of marine birds, being 2.16 ± 0.35‰ for $\delta^{13}C$ and 3.84 ± 0.26‰ for $\delta^{15}N$ (Caut, Angulo & Courchamp 2009). The estimated diet composition was compared between the early and late season, splitting up the feather data at 10 May, when a rapid increase in the number of foraging spoonbills in marine habitat was observed in the study area in multiple years (pers. obs.).

To assess whether the proportion of marine food in the diet of a chick affected its body condition, we correlated the $\delta^{13}C$ value of the most recently assimilated feather section with chick body condition. As an index of body condition, we used the residual body mass divided by the predicted body mass, using the sex-specific Gompertz curves for body mass estimated by Lok *et al.* in review (Chapter 3; females: $y_\infty = 1485$, $k = 0.141$, $T_i = 8.4$, males: $y_\infty = 1741$, $k = 0.127$, $T_i = 9.7$).

RESULTS

The 46 primary feathers from Spoonbill chicks exhibited a wide range of $\delta^{15}N$ and $\delta^{13}C$ values (Fig. 4.3). The $\delta^{15}N$ values ranged between 13.0‰ and 18.7‰, $\delta^{15}N$ values varied mostly within the freshwater habitat and were almost identical in the marine habitat category (Fig. 4.3). The $\delta^{13}C$ values ranged between -26.2‰ and -14.7‰ which indicates that the diet originated from a variety of habitats ranging from freshwater to

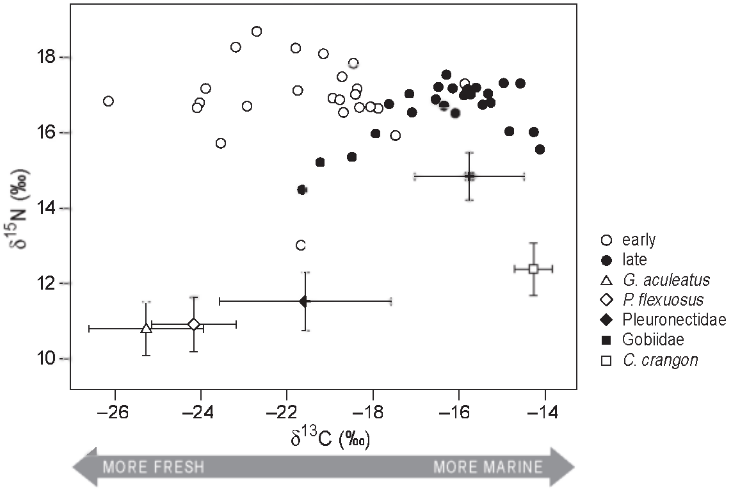


Figure 4.3 $\delta^{13}C$ and $\delta^{15}N$ values of chick's feathers in the early and late season and of selected prey sources: Three-spined Sticklebacks (*G. aculeatus*, n = 11), Chameleon Shrimp (*P. flexuosus*, n = 9), Righteye Flounder (Pleuronectidae, n = 11), Gobies (Gobiidae, n = 19) and Brown Shrimp (*C. crangon*, n = 10).

marine sources (Bearhop *et al.* 1999). $\delta^{13}C$ values from feather samples differed significantly between early and late breeding stages (t-test: $t = -7.02$, $df = 47$, $p < 0.001$).

The statistical model describing the within- and between-individual changes in $\delta^{13}C$ pattern showed that, at the population level, there was a shift towards higher $\delta^{13}C$ values through the season, indicating an increasing reliance on marine prey (Table 4.1, Fig. 4.4). Moreover, there was a significant interaction between within-individual slopes and season. Whereas the change in $\delta^{13}C$ values within chicks born in May showed a similar pattern as that of the population, chicks born in April showed the opposite trend.

The SIAR mixing model confirmed an increasing reliance on marine prey through the breeding season (Fig. 4.5). The model estimated that the chicks received 57% of their diet from freshwater/brackish sources (Three-spined Sticklebacks and Chameleon Shrimp) early in the season and 73% from marine sources (Gobiidae, Brown Shrimp and Righteye Flounder) later in the season. We did not find a significant correlation between the body condition index at the time when the feather was collected and the proportion of marine food in the diet (reflected by the $\delta^{13}C$ value of the most recently assimilated feather section; $F_{1,44} = 0.56$, $P = 0.46$).

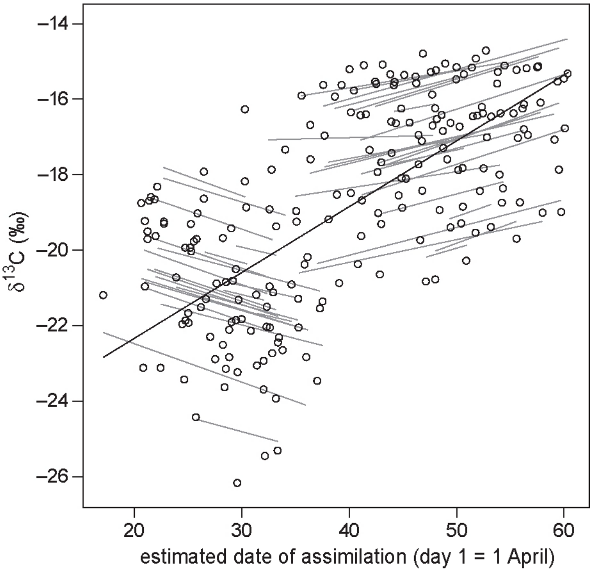


Figure 4.4 $\delta^{13}C$ values as a function of the estimated assimilation date, which assumes that the feather grows linearly by 6.6 mm per day (see Fig. 4.1). Open circles represent the 203 subsamples from the 46 feathers. The black line shows the between-individual slope and the grey lines the individual slopes, estimated by the model shown in Table 4.1.

Table 4.1 Parameter estimates and approximate 95% confidence intervals from the 'within-subject centering' mixed-effects model.

		95% CI			
	Estimate	Lower	Upper	F-value	P-value
Fixed effects					
β_0	-25.82	-27.86	-23.79	644.30	<0.001
β_B	0.17	0.12	0.23	47.23	<0.001
β_W	-0.31	-0.49	-0.11	11.18	0.002
β_{WB}	0.008	0.003	0.012	12.43	0.001
Random effects					
$\sigma^2_{u_{0j}}$	2.85	1.82	4.56		
$\sigma^2_{u_{Wj}}$	0.014	0.006	0.035		
$\sigma^2_{e_{0ij}}$	0.68	0.51	0.91		

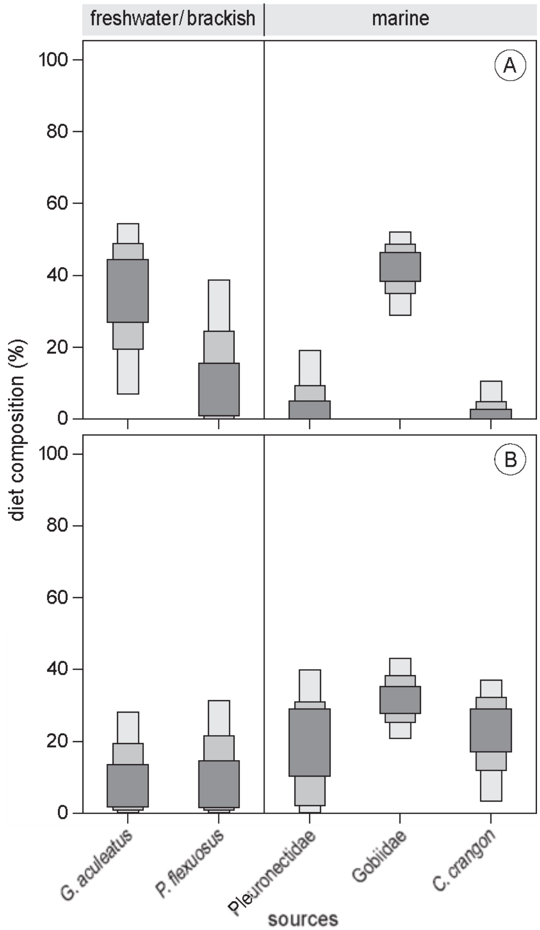


Figure 4.5 Bayesian mixing model (SIAR) results showing the estimated diet composition (95, 75, and 25% credibility intervals) of Spoonbill chicks in the (A) 'early' feather samples (assimilated before 10 May) and (B) 'late' feather samples (assimilated after 10 May).

DISCUSSION

We analysed stable isotopes in the feather material of chicks to investigate changes in the reliance of Spoonbills on freshwater versus marine prey for feeding. It has been reported that the use of only a small section of the feather or the homogenisation of the entire vane leads to great loss of spatiotemporal information about the dietary during the feather growth (Hobson & Clark 1992; Knoff *et al.* 2002; Wiley *et al.* 2010). Taking multiple samples from the same feather is becoming more common in the isotopic studies on the feeding biology of birds (Thompson & Furness 1995; Knoff *et al.* 2002; Wassenaar & Hobson 2006; Smith, Donohue & Dufty 2008; Wiley *et al.* 2010; Quillfeldt, Voigt & Masello 2010; Jaeger *et al.* 2010; Jensen *et al.* 2012; Wiley *et al.* 2012). However, to our best knowledge, this is the first time that the longitudinal sampling involves the daily growth rate of a feather allowing us to track temporal variation in the diet of individual Spoonbill chicks. In this way we could test whether a population-level change in diet over the breeding season was caused by within- and/or between-individual changes. We have shown that within-individual trends did not follow the overall trend line early in the breeding season (Fig. 4.4).

We found a spatio-temporal diet shift in Spoonbills from freshwater/brackish habitat early in the breeding season to marine habitat later on (Table 4.1, Figs. 4.4, 4.5). This shift mirrors the observation of increasing numbers of Spoonbills foraging in the Wadden Sea through the breeding season made in earlier years (de Goeij *et al.* 1985; van Wetten & Wintermans 1986; Kemper 1995; Bauchau *et al.* 1998). The SIAR mixing model demonstrated that Spoonbill chicks were fed predominantly with freshwater/brackish prey early in the season and mostly marine prey later in the season (Table 4.1, Figs. 4.4, 4.5). In early spring – from March until May – Brown Shrimp are not yet available in the shallower areas of the Wadden Sea (Beukema 1992; Birdlife Netherlands 1997). In the meantime, freshwater prey such as sticklebacks may provide good food (de Goeij *et al.* 1985; van Wetten & Wintermans 1986; Altenburg & Wymenga 1997; Birdlife Netherlands 1997). In the study area, two types of non-migratory sticklebacks, Ten-spined Sticklebacks (*Pungitius pungitius*) and Three-spined Sticklebacks, and the anadromous migratory Three-spined Sticklebacks, concentrate in the freshwater ditches early in spring to reproduce (de Goeij *et al.* 1985; Altenburg & Wymenga 1997). Later in spring, after spawning, the adult anadromous Sticklebacks die and their numbers decrease dramatically in freshwater bodies (Kemper 1995). Moreover, growing vegetation closes the ditches in such a way that Spoonbills may not be able to forage there anymore and are forced to seek food elsewhere. While Spoonbills could still forage in nearby open freshwater habitats on prey species such as Common Roach (*Rutilus rutilus*), Common Rudd (*Scardinius erythrophthalmus*), European Perch (*Perca fluviatilis*), Common Carp (*Cyprinus carpio*) and Beams (*Abramis* spp) (Altenburg & Wymenga 1997; Birdlife Netherlands 1997), Brown Shrimp are meanwhile becoming available in high numbers in the surrounding intertidal areas in the Wadden Sea (Campos *et al.* 2010; Hufnagl & Temming 2011; Campos *et al.* 2012; Tulp *et al.* 2012).

Intriguingly, the seasonal trend towards higher $\delta^{13}C$ values as the breeding season progressed was shown by the chicks born later in the season, but not by the chicks born early (Fig. 4.4). As anadromous Sticklebacks move from marine to freshwater in early spring, which will lead their isotopic values to gradually change from a marine to a freshwater signal (Bearhop *et al.* 2002), this surprising change in the direction of individual time-trends may reflect the changes over time in isotopic values of the consumed migratory sticklebacks. Alternatively, Spoonbills may gradually include more true freshwater prey in their diet, because the anadromous Sticklebacks, who probably have an intermediate freshwater-marine isotope values, may become less available over time as suggested above.

In some birds young chicks suffer from a salty diet (Harriman 1967; Barnes & Nudds 1991; Dosch 1997; Knoff *et al.* 2002; Hannam *et al.* 2003). Spoonbill chicks fed mainly marine prey (i.e. the later born chicks) were not in poorer condition than chicks fed freshwater prey. As sticklebacks and Brown Shrimp are of similar (relatively low) nutritive value (Massias & Becker 1990), this suggests that a high proportion of marine food (a salty diet) did not come with major physiological costs for spoonbill chicks of the age of 3 to 5 weeks old. This also helps explain why Mauritanian Spoonbills (*P. l. balsaci*) are able to successfully breed in an entirely marine environment (the Banc d'Arguin, Mauritania) where no freshwater is available.

There was hardly any seasonal overlap between the early chicks that had a low and generally decreasing $\delta^{13}C$ signal and the later chicks that on average had a higher and slightly increasing $\delta^{13}C$ signal (Fig. 4.4). Rather than being caused by an arbitrary selection of chicks for this study, there were in fact no chicks raised in the intermediate period. If this gap would turn out to be a systematic feature of the timing of breeding of Spoonbills in the Wadden Sea, this would indicate some degree of individual food specialization among breeding birds related to breeding time. Assuming that freshwater food (mainly sticklebacks) is more abundant early in the season, in contrast to marine food resources (mainly shrimp) that become more abundant later on, freshwater habitat specialists are expected to breed earlier than marine habitat specialists. This hypothesis now requires testing by observations in multiple breeding seasons, and the tracking of individual spoonbills breeding early and late to investigate their foraging habitat usage in relation to diet and the availability of freshwater and marine food resources.

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Part II

Population dynamics and migration

Chapter 5

Seasonal variation in density dependence in age-specific survival of a long-distance migrant

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Joost M. Tinbergen
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Ecology *in press.*

ABSTRACT

Density dependence in vital rates is key to population regulation. Rather than being constant, the strength of density dependence may vary throughout the year, but empirical evidence is limited. Based on 22 years of data of colour-ringed birds from a recovering population of Eurasian Spoonbills *Platalea leucorodia leucorodia*, we show, for the first time, seasonal variation in density dependence in survival of a long-distance migrating bird. Combining resightings and dead recoveries at breeding, stopover and non-breeding areas enabled us to (1) separate true survival from permanent emigration from the breeding area, and (2) estimate survival in three seasons: summer, early winter (including autumn migration) and late winter (including spring migration). Accompanying the rapid population growth, juvenile annual survival initially increased, manifested in early winter, but thereafter, at high population sizes, strongly decreased, through a combination of decreasing survival in all seasons. Annual survival of subadult (2nd and 3rd year) and adult birds more gradually decreased with increasing population size, with density dependence occurring in respectively early and late winter. Thus, the shape and strength of density dependence in survival varied with age and season. Understanding the seasonal timing of density dependence, especially with reference to underlying mechanisms, is important for the design of effective conservation strategies.

INTRODUCTION

Density dependence is key to the regulation of wildlife populations (Lack 1954). Detecting density dependence has mostly been done on an annual basis, using time-series analyses of population sizes (reviewed in Newton 1998; Brook & Bradshaw 2006), or correlating population size with annual reproductive output (e.g., Both 1998; Rodel *et al.* 2004; Armstrong *et al.* 2005) or annual survival (e.g., Achord, Levin & Zabel 2003; Armstrong *et al.* 2005; Owen-Smith, Mason & Ogutu 2005; te Marvelde *et al.* 2009). Yet, rather than being constant, the strength of density dependence may vary throughout the year (Runge & Marra 2005; Ratikainen *et al.* 2008) as a result of seasonal variation in food availability (Skogland 1985; Martin 1987; Sherry, Johnson & Strong 2005), nutritional demands (Bryant & Tatner 1988; Doherty, Williams & Grubb 2001; Tinbergen & Williams 2002), disease risk (Nelson *et al.* 2002) or even predation risk, assuming they act in a density-dependent manner. This may result in seasonal variation in the strength of density dependence in (especially) survival and is likely to be particularly pronounced in animals living in strongly seasonal environments and in migratory animals that visit multiple sites during the year.

Although the population consequences of seasonal variation in density dependence in survival have been investigated theoretically (Runge & Marra 2005; Ratikainen *et al.* 2008), notably to predict the effects of harvesting (Kokko & Lindström 1998; Boyce, Sinclear & White 1999), empirical evidence of this phenomenon is limited. This is probably due to the difficulties inherent to the collection of the necessary data, as it requires long-term monitoring of populations that vary considerably in size, or studies in which population size is experimentally manipulated in all seasons (Runge & Marra 2005). The few studies that investigated seasonal variation in density dependence in survival mainly focussed on exploited species. In juvenile Atlantic salmon *Salmo salar*, density dependence in survival was strongest in autumn, the season where energetic demands were presumably highest (Bailey *et al.* 2010). In Willow Ptarmigan *Lagopus lagopus*, experimental harvesting regimes were compared, revealing that harvesting mortality during autumn was partially compensatory (Sandercock *et al.* 2011). This suggests that survival was density dependent during autumn, but in the absence of hunting in other seasons, the presence of density dependence in survival could not be evaluated for all seasons.

Here we present, for the first time, strong evidence for seasonal variation in density dependence in survival of a fully protected and non-game long-distance migrating bird. For this, we used 22 years of mark-recapture data of the Eurasian Spoonbill *Platalea leucorodia leucorodia* population that breeds in the Netherlands and increased almost 6-fold from 415 to 2338 breeding pairs during the study period (1988-2010). Combining resightings (N = 25,177) and recoveries (N = 152) at the breeding, stopover and non-breeding areas enabled us to (1) separate annual true survival from permanent emigration from the breeding area, and (2) estimate survival in three different seasons: summer, early winter (including autumn migration) and late winter (including spring migration). We evaluate patterns of density dependence in annual and seasonal survival, while allowing for age effects (Eberhardt 2002), and discuss potential explanations for the patterns observed.

Estimates of density-dependent effects on population parameters in natural populations have, in the majority of studies, been based on effects of natural variation in density. Strictly speaking such analyses leave the question of causality open because the cause for the variation in density may be the same that caused the variation in the parameters studied. In continuously growing populations as discussed here, population size is also confounded with time. Yet, at this moment it is the closest we can get to model density-dependent processes as a function of age and season (or location) in a long-distance migrant.

MATERIALS AND METHODS

Study population and data collection

Our study is based on the breeding population of Eurasian Spoonbills in the Netherlands. This population is migratory and winters along the East-Atlantic coast between France and Senegal (Lok *et al.* 2011). Due to pollution of surface waters through industrial toxic spills and insecticide use in agriculture, combined with disappearance of suitable foraging and breeding areas, the breeding population severely declined to a minimum of 148 breeding pairs in 1968 (Brouwer 1964; Koeman & van Genderen 1966). Since the prohibition of industrial toxic spilling and organochlorine pesticide use, in combination with strongly enforced protection of foraging and breeding areas (van der Hut 1992), the population has recovered to over 2300 breeding pairs in 2010, spread over 35 colonies (Figs. 5.1, 5.2). The number of breeding pairs is accurately estimated by counting all used nests in the Netherlands during, or shortly after, the breeding season.

Between 1988 and 2010, 6482 spoonbills were colour-ringed just before fledging. Resightings and recoveries came from a large network of amateur and professional ornithologists in and outside the Netherlands (for details, see Appendix II, Table II.1).

Number of breeding pairs as proxy for population size

We used the number of breeding pairs in the Netherlands to approximate the size of the population at the scale at which density-dependent processes may take place. Previous analyses showed that colony size was not a better predictor than total population size in the Netherlands for adult survival (Lok *et al.* 2009) or juvenile survival (unpublished data), suggesting that the main density-dependent processes did not occur locally around the breeding colonies. We did not include juvenile, subadult and non-breeding adult birds into our estimates of population size, because counts of these classes were generally incomplete and unreliable. However, the overall size of the population should strongly correlate with the size of the breeding population. In addi-

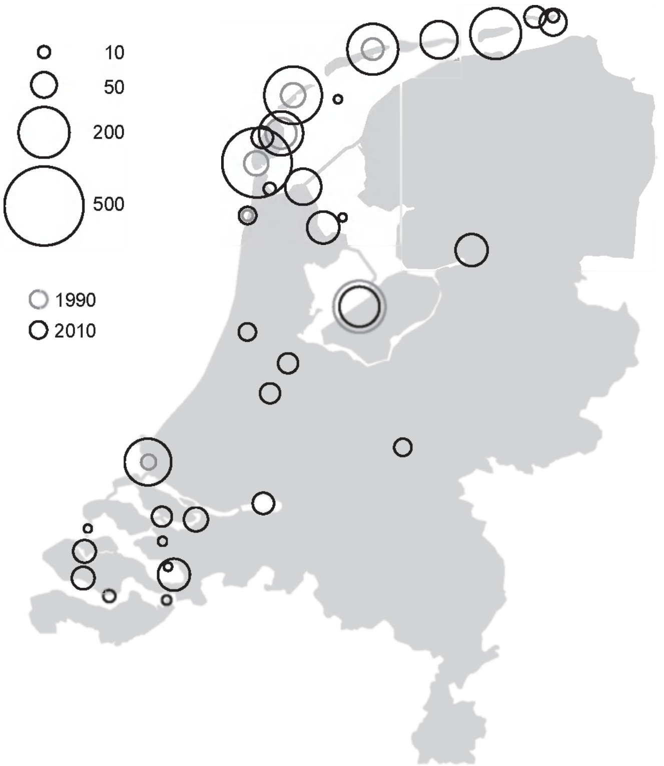

Figure 5.1 Map of the Netherlands with the location and size (number of breeding pairs) of all breeding colonies.

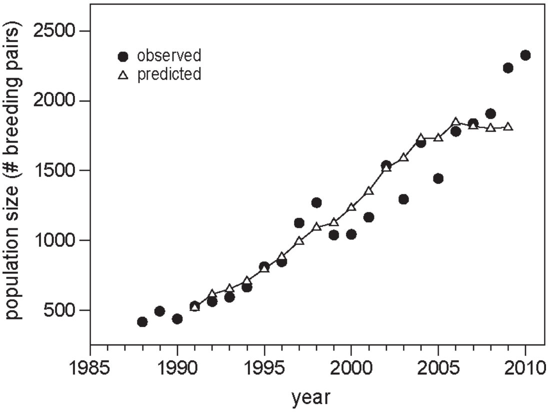

Figure 5.2 Observed and predicted population size in terms of number of breeding pairs of Eurasian Spoonbills in the Netherlands over the years.

tion, the Dutch population mixes with other populations from Western Europe and Mauritania during the non-breeding period. After the Netherlands, Spain harbours the largest breeding population of spoonbills, and together they account for ca. 80% of the Western European population (O. Overdijk, pers. comm.). The Spanish population increased from ca. 500 to 1500 breeding pairs in 1988-2007 (García *et al.* 2009). In contrast, the population of Mauritanian Spoonbills *Platalea leucorodia balsaci* resident on the Banc d'Arguin (Mauritania) (Piersma *et al.* 2012) has declined from ca. 1600 breeding pairs in 1985 to ca. 750 in 2007, a decrease that appears to be mainly driven by lack of reproductive output due to predation and flooding (Triplet *et al.* 2008). Overall therefore, the Western Palearctic metapopulation of spoonbills has increased, though at a relatively lower rate than the Dutch population.

Annual true survival and permanent emigration

Annual true survival was estimated using the Barker model (Barker 1997). In contrast to conventional Cormack-Jolly-Seber (CJS) models where mortality is confounded with permanent emigration (Lebreton *et al.* 1992), the Barker model combines resightings in a core study area with resightings and recoveries from the entire geographical distribution of the species to derive estimates of both true survival and (permanent) emigration away from the study area (Barker 1997). Since immature spoonbills tend to stay on the non-breeding grounds before they start to breed when 3 years old or older (Lok *et al.* 2011), using the additional data from outside the breeding area increases the accuracy of survival and fidelity estimates of especially immature birds.

The Barker model estimates the following probability parameters: S = true survival, F = fidelity to the core study ('capture') area, p = resighting during capture occasions, r = dead recovery, R = resighting during interval (see below), R' = resighting during interval before death and F' = immigration. As we are interested in permanent rather than temporary emigration, we fixed $F' = 0$. Consequently, F gives the probability of permanent emigration (Barker, Burnham & White 2004) and the probability that an animal is temporarily absent becomes a component of the – now apparent – resighting probability p. In this study, a capture occasion is defined as the breeding season (April-July) in the Netherlands (capture area), whereas the interval includes resightings in the Netherlands during the remaining period (August-March) and resightings elsewhere throughout the year (June-May). Recoveries throughout the year are included.

The majority of spoonbills only return to the Netherlands to breed when 3 years old, although some already return, but do not breed, when 1 or 2 years old (Lok *et al.* 2011). To account for this temporary emigration of immature birds, apparent resighting probability p in the Netherlands was modelled separately for three age classes (age 1, age 2, age ≥ 3). Annual survival was modelled separately for four age classes: 1st (juvenile), 2nd, 3rd and ≥4th year (adult) birds. With only a single bird colour-ringed in 1995, age-specific survival rates could not be estimated for this cohort and were fixed to 0. Due to limited data because only few birds return to the breeding grounds when immature, 1st, 2nd and 3rd year birds were pooled to increase the precision of the estimate of fidelity of immature birds (F_{012}) versus that of older birds ($F_{\geq3}$). F_{012} can be seen as an estimate of natal philopatry, i.e., the probability that a bird recruits in the Netherlands. We started with between-year variation in all (age-specific) model parameters. Adopting the notation used by Catchpole *et al.* (2000) and Loison *et al.* (2002), separate symbols were used for each age-specific parameter and parameters that varied in parallel over time were placed between brackets (Catchpole *et al.* 2000, Loison *et al.* 2002). The fully time-dependent model was therefore written as S_0(t) S_1(t) S_2(t) $S_{\geq3}$(t) F_{012}(t) $F_{\geq3}$(t) F'(0) p_1(t) p_2(t) $p_{\geq3}$(t) r(t) R(t) R'(t). Optimization of this model turned out to be problematic and the simulated annealing algorithm in program MARK (White & Burnham 1999) was necessary to find the global maximum (which took 3 days on a fast 12-core workstation). Inspection of the parameter estimates revealed that there were many boundary estimates (N = 24), of which 13 were among the yearly estimates of immature and adult fidelity. Because boundary estimates reflect poorly estimated parameters and may be the reason of the problematic optimization of the fully time-dependent model, we removed the between-year variation from the parameters F_{012} and $F_{\geq3}$ and modelled them as linear functions of population size (N_{lin}), which resulted in a more parsimonious model (Appendix II, Table II.2). Moreover, explorative analysis showed that recovery probability could be more parsimoniously modelled as constant, rather than as variable between years (Table II.2). The new full model now becomes S_0(t) S_1(t) S_2(t) $S_{\geq3}$(t) F_{012}(Nlin) $F_{\geq3}$(Nlin) F'(0) p_1(t) p_2(t) $p_{\geq3}$(t) r(.) R(t) R'(t). This model properly converges to the global maximum using the regular optimization routine of program MARK.

Goodness-of-fit of this model was assessed using the median $\hat{c}$ approach in program MARK (White & Burnham 1999). During this approach, datasets with different levels of overdispersion (extra-binomial variation) are simulated using the parameter estimates of the model of interest and then optimized with the model structure of that model. The level of overdispersion is then estimated at the value for which half of the simulated model $\hat{c}$ are above the actual model $\hat{c}$. The level of overdispersion was estimated at $\hat{c} = 1.16 \pm 0.01$ S.E.

Starting from the full model, we investigated support for density dependence in age-specific survival and fidelity. For this, survival was modelled as a linear or a quadratic function of population size (N_{lin}: $\beta_0 + \beta_1 N_t$ or N_{quad}: $\beta_0 + \beta_1 N_t + \beta_2 N_t^2$) or as constant. Fidelity was only modelled as constant or as a linear function of population size, because we do not expect an initial increase in fidelity when population size is low (perhaps at the colony level, but not at the scale of the Netherlands), but only a decrease in fidelity with increasing population size. To reduce computational time, and to facilitate comparison of support for the different parameterizations within a single age class, we compared the different parameterizations for each age-specific survival or fidelity parameter while modelling the other biological parameters as in the full model.

For long-term mark-recapture datasets, models with between-year variation in parameters are often preferred over constant or covariate models (Frederiksen *et al.*

2008). Testing the effect of covariates in such cases is preferably done while accounting for random between-year variation (Link 1999). Random effect methodology for mark-recapture analyses has been developed by Burnham and White (2002) and has been implemented in program MARK (White & Burnham 1999). In short, the method of moments is used to separate process and sampling variation from a series of parameter estimates (in our case, yearly estimates of annual survival). Despite the suggested advantages of information-based model selection among mixed-effects mark-recapture models, we were unable to find an application for a real dataset (Grosbois *et al.* 2008). Using the above described random effects methodology, age-specific survival was modelled as constant or as linear or quadratic functions of population size, while accounting for random between-year variation.

Seasonal survival

Seasonal apparent survival (Φ) and resighting probabilities (p) were estimated using only live resightings and CJS models (Lebreton *et al.* 1992). Using resighting periods during the start of the summer (*s1*, Feb-May), the end of the summer (*s2*, Jul–Oct) and in winter (*w*, Dec-Jan in Europe and Oct-Feb in West Africa), survival was estimated in three seasons: the breeding season (summer (*s*), April–August, 5 months), the first half of the non-breeding season including autumn migration (early winter (*w1*), September-half December, 3.5 months), and the second half of the non-breeding season including spring migration (late winter (*w2*), half December-March, 3.5 months). As winter resightings were scarce in most years, survival during the migratory seasons could not be separated from survival in winter. Although CJS models estimate apparent survival which is confounded with permanent emigration ($\Phi = SF$), the estimates will closely resemble true survival because resightings in both breeding and wintering areas are used, i.e., birds that permanently emigrated away from the Netherlands (to breed elsewhere), as accounted for in the Barker models, can still be resighted at their wintering grounds. Moreover, whereas resightings in the Netherlands for the Barker model analysis were restricted to the core breeding period (April–July), in the seasonal survival analysis we also included the months during which the Netherlands is used during spring and autumn migration by more northern breeding birds (Feb–May, Jul–Oct).

Due to the relatively low sample sizes and because of their similar behaviour and annual survival (see Results), 2nd and 3rd year old birds were pooled into one subadult age class to get more precise estimates of their seasonal survival and resighting probabilities. Birds were considered adult from the *late winter* season in their 3rd year onwards. Juvenile summer survival reflects the post-fledging period from ringing (mean ringing date = 11 June) until the end of August, covering ca. 2.5 months.

To ensure that mortality during the migratory periods was included in the early and late winter seasons, only resightings in the Netherlands were selected for juvenile and adult birds for the summer periods. Because they stay at the non-breeding grounds year-round, resightings of subadult birds were not restricted to the Netherlands for the summer periods. Resighting probability p was modelled as a function of age and time during the summer periods (*s1* and *s2*) and only as a function of time during the winter period (*w*). Resighting probability p in period *s2* was constrained to vary in parallel over time for juvenile and adult birds, because their resightings during this period are confined to the Netherlands. During the summer resighting periods, most subadult birds are resighted at their non-breeding grounds, and summer resighting probabilities were therefore allowed to vary differently over time than those of juvenile or adult birds.

When there was substantial support for a correlation between population size and annual survival from the Barker models (see Results), we investigated in which of the seasons this relationship was present. This resulted in the comparison of three parameterizations for juvenile survival (constant, N_{lin} and N_{quad}) and two parameterizations for subadult and adult survival (constant and N_{lin}) for each season. Because annual survival is now divided into seasonal components, the available data per season is less. Consequently, sampling variation was large when seasonal survival rates were allowed to vary from year to year, and many parameters were inestimable (Appendix II, Fig. II.1). This resulted in covariate models being consistently preferred over between-year variation in age- and season-specific survival (Appendix II, Table II.6, step 1). Since the method of moments performs poorly when sampling variation is large relative to process variation (Burnham & White 2002), we only considered fixed effects models in this seasonal survival analysis. Using similar model notation as for the Barker model, the full seasonal survival model was $\Phi_{0,s}(N_{quad})$ $\Phi_{0,w1}(N_{quad})$ $\Phi_{0,w2}(N_{quad})$ $\Phi_{12,s}(N_{lin})$ $\Phi_{12,w1}(N_{lin})$ $\Phi_{12,w2}(N_{lin})$ $\Phi_{\geq 3,s}(N_{lin})$ $\Phi_{\geq 3,w1}(N_{lin})$ $\Phi_{\geq 3,w2}(N_{lin})$ $(p_{0,s2}\ p_{\geq 3,s2})(t)$ $p_{12,s1}(t)$ $p_{\geq 3,s1}(t)$ $p_{12,s2}(t)$ $p_{w}(t)$. Using the median $\hat{c}$ approach in program MARK (White & Burnham 1999), the level of overdispersion was estimated at $\hat{c} = 1.61 \pm 0.003$ S.E.

To reduce computational time, we proceeded in three steps. First, we checked whether resighting probability could be more parsimoniously modelled by removing age effects or between-year variation. As this substantially reduced the model fit (Table II.6, step 2), we kept the parameterization for p as in the full model in the subsequent steps. We then investigated for each age-specific seasonal survival parameter (while keeping the other parameters as a function of population size) whether the model became less supported when removing the effect of population size. For this, the criteria was used that when $QAIC_c$ decreased when a parameter was removed from the model (also when less than 2 points, Arnold 2010), this parameter had a negligible effect and was removed in step 2. When removal of a parameter from the model increased $QAIC_c$, but less than 2 points, the models with and without this parameter were considered to both have some support and both parameterizations were included in step 2. When $QAIC_c$ increased more than 2 points, the parameter was considered to have a substantial effect and was always included in step 2. In the third step, all combinations of parameterizations that were supported in the second step were compared.

Statistical analysis

We used program R (version 2.13.0, R Development Core Team 2011) and the package RMark (Laake 2011) to construct mark-recapture models for running in program MARK (White & Burnham 1999). To build the random effects models, we followed the approach described by Burnham & White (2002) and implemented in program MARK. In short, the method of moments is used to derive shrunken estimates at which the fixed effects likelihood is then evaluated. This gives the likelihood of the random effects model. The number of parameters associated with the random effects model can be calculated as $K_{re} = tr(G) + \ell$, where $tr(G)$ is the dimension of parameter space associated with the random component of the model, and ℓ is the number of remaining parameters (fixed effects) to be estimated. The random effects models were fitted on a probability scale because boundary parameters will inflate sampling and process variation when estimated on a logit scale (Burnham & White 2002). All other probability parameters (fixed effects) were estimated on a logit scale.

To check that all Barker models had converged to the global maximum (likelihood), models were rerun using different initial values. Some reduced models (only three) turned out not to have converged properly (the estimated deviance varied depending on the initial values used), and the global maximum of these models was verified using simulated annealing. Shrunken estimates were imported into R to enable time-efficient parallel running of the random effects Barker models on a 12-core workstation. Model selection was based on Akaike information criterion, corrected for small sample size and overdispersion ($QAIC_c$, Burnham & Anderson 2002). Reported standard errors and confidence intervals are also adjusted for overdispersion.

Table 5.1 Estimates of parameters, process variation (σ^2) and residual variation (σ^2_{res}) of the intercept (μ) and best-supported density dependence (N_{lin} or N_{quad}) random effects mark-recapture model, by age, for annual true survival of Eurasian Spoonbills.

Annual survival	Intercept model		Best-supported density dependence model					
	$\hat{\mu}$	$\hat{\sigma}^2$	$\hat{\beta}_0$	$\hat{\beta}_1$	$\hat{\beta}_2$	$\hat{\sigma}^2_{res}$	R^2	$\Delta QAIC_c$
1st year	0.56 ± 0.03	0.012	0.67 ± 0.02	-0.036 ± 0.02	-0.165 ± 0.02	0.003	0.77	-3.20
2nd year	0.92 ± 0.01	0.003	0.91 ± 0.01	-0.046 ± 0.02		0.002	0.40	-1.34
3rd year	0.95 ± 0.01	0.001	0.95 ± 0.01	-0.032 ± 0.01		0.001	0.40	-1.44
≥ 4th year	0.88 ± 0.01	0.001	0.89 ± 0.01	-0.039 ± 0.01		0.0006	0.51	-1.42*

N_{lin}: $\beta_0+\beta_1 \cdot N_z$ and Nquad: $\beta_0+\beta_1 \cdot N_z+\beta_2 \cdot N_z^2$, where $N_z = \frac{N-\bar{N}}{sd}$ with N = the number of breeding pairs, $\bar{N} = 1175$ and sd = 585. Estimates are given as mean ± S.E. The percentage of variation explained by the density dependence model, as compared to the intercept model, (R^2) is calculated as $1 - \frac{\sigma^2_{res}}{\sigma^2}$ (Loison *et al.* 2002). $\Delta QAIC_c$ is calculated as $QAIC_c$ (best-supported random effects covariate model) - $QAIC_c$ (random effects intercept model). For an overview of all the fixed and random effects models compared, see Table II.3.

* Note that the survival of ≥ 4th year old birds was by far best described by the fixed-effects N_{lin} model (see Table II.3).

RESULTS

Annual true survival and permanent emigration

Model selection results of the fixed and random effects Barker models are shown in Appendix II, Table II.3. Annual survival and fidelity of all age classes were best described as a function of population size (Table II.3, parameterizations in bold), with random between-year variation in 1st, 2nd and 3rd year survival, but not in adult survival. 1st year annual survival was best described by a quadratic function of population size, whereas annual survival of 2nd, 3rd and ≥4th year birds was best described by a linear function of population size (Table II.3). On average, survival increased from the 1st to the 3rd year, but was somewhat lower in adult birds (Table 5.1). The decrease in survival with population size was strongest for juveniles, though only at high population sizes, and weakest for 3rd year and adult birds (Fig. 5.3, Table 5.1). Fidelity of immature birds was lower and decreased more strongly with population size (from 0.94 ± 0.008 (mean ± S.E) in 1988 to 0.87 ± 0.012 in 2008) than that of adult birds (from

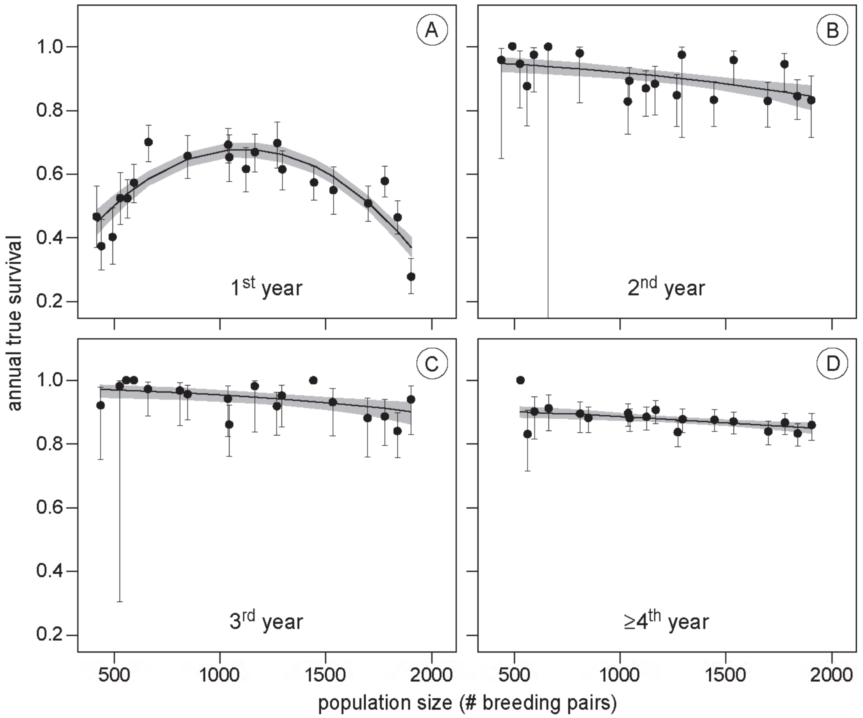

Figure 5.3 Estimates of annual true survival of (A) 1st year, (B) 2nd year, (C) 3rd year and (D) adult (≥4th year) birds in relation to population size. The black dots represent the yearly estimates from the full model. The lines represent the estimates of the best-supported fixed-effects model per age class (Table II.3). Error bars and grey areas represent 95% confidence intervals adjusted for overdispersion ($\hat{c}$ = 1.16, see Methods).

0.99 ± 0.004 to 0.95 ± 0.010). Shrunken estimates of survival and maximum likelihood estimates of fidelity, resighting and recovery probabilities are shown in Appendix II, Table II.4 and II.5.

Seasonal survival

The seasonal differences in survival varied with age. On average, juvenile survival (reported as year^{-1}) was lowest in early winter (0.33 ± 0.03), higher in late winter (0.58 ± 0.05) and highest in summer (0.71 ± 0.02). Similarly, subadult survival was lowest in early winter (0.79 ± 0.04), higher in late winter (0.85 ± 0.07) and approaching unity in summer (1.00 ± 0.00). Adult survival was lowest in late winter (0.68 ± 0.03), higher in early winter (0.89 ± 0.03) and also approaching unity in summer (1.00 ± 0.00).

The effect of population size on seasonal survival also varied with age (Fig. 5.4). Model selection results are shown in Table II.6. There was substantial support for an effect of population size ($\Delta QAIC_c > 4$ when the effect was removed) on juvenile survival during the post-fledging period and early winter, on subadult survival during early winter, and on adult survival during late winter. Juvenile survival decreased with population size during the post-fledging period, with the quadratic and linear effect having similar support ($\Delta QAIC_c = 0.24$ when removing the quadratic term), whereas the quadratic effect was clearly supported during early winter ($\Delta QAIC_c = 3.47$): after an initial increase, early winter survival of juveniles decreased at high population sizes. Subadult and adult survival decreased with population size in respectively early and late winter. There was some support for an initial increase with population size in subadult survival in summer ($\Delta QAIC_c = 2.40$ when the effect was removed) and for a decrease in juvenile survival during late winter ($\Delta QAIC_c = 1.19$). Estimates of season- and age-specific resighting probabilities from the best-supported model (model 14, Table II.6) are presented in Appendix II, Fig. II.2. Age-specific annual survival, when calculated from the seasonal survival estimates, was very similar to the annual true survival estimates from the Barker model (Appendix II, Fig. II.3).

DISCUSSION

Survival was correlated with population size, with the shape of the relationship varying among age classes and seasons. Juvenile annual survival initially increased with growth of the population, but then decreased with further population growth. Annual survival of older birds decreased with population size throughout the study period. The initial positive effect of population size on juvenile survival was manifested in early winter, whereas at high population sizes, juvenile survival decreased with population size in all seasons. Subadult and adult survival decreased with population size in early and late winter, respectively.

To investigate seasonal density dependence in survival in the absence of accurate counts of population size in winter, we related survival in each season to the preceding

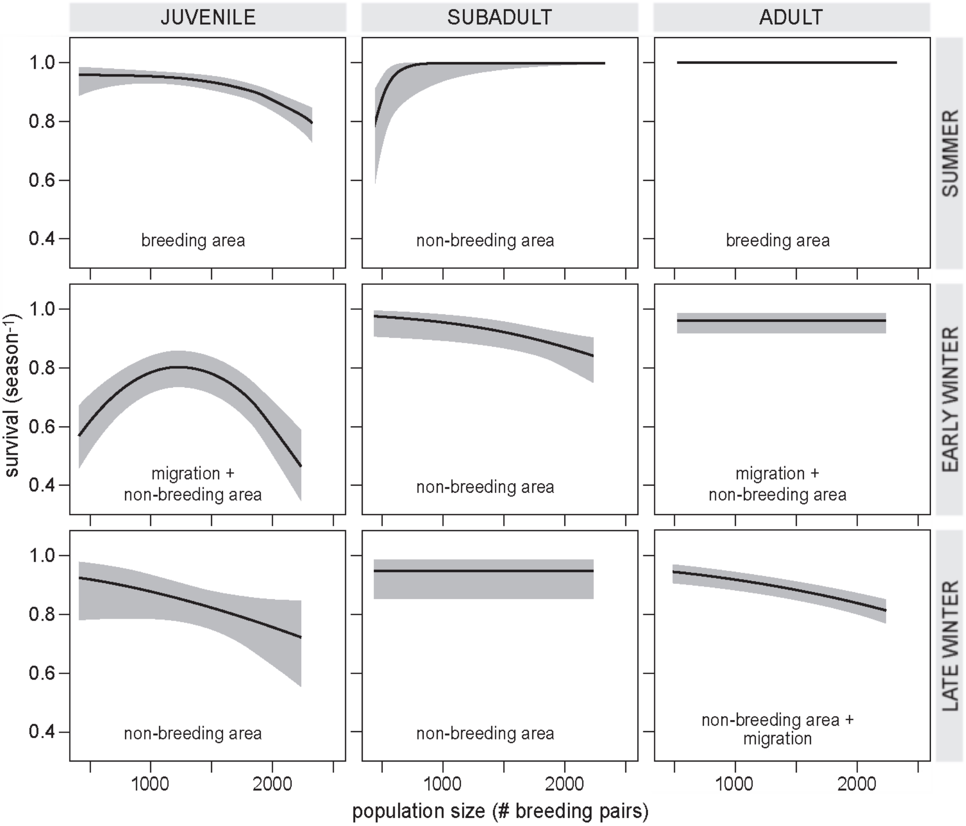

Figure 5.4 Estimates (solid lines) of the relationship between population size and seasonal survival of juvenile, subadult (2nd and 3rd year birds combined) and adult birds from the best-supported model (model 29, Table II.6). Grey areas represent 95% confidence intervals adjusted for overdispersion ($\hat{c}$ = 1.16, see Methods).

number of breeding pairs in the Netherlands. By doing so, we did not account for seasonal changes in abundance due to mortality. For example, after a season of high mortality (whether or not density dependent), population size is reduced, and density dependence in a subsequent season may be relaxed (Ratikainen *et al.* 2008). Using the estimates of seasonal survival allows us to estimate the seasonal changes in abundance in a post-hoc fashion and adjust the interpretation of the results where needed. In our case, because juvenile survival was especially low in early winter, the number of juveniles in late winter is reduced, and consequently, the strength of density dependence in the late winter season is underestimated to some extent. Since adult survival is lowest in late winter, the largest reduction in the number of adult birds occurs between winter and summer which is accounted for by evaluating the adult population size in summer (by counting the number of breeding pairs). And since subadult survival is high and similar in all seasons, the number of subadult birds decreases slowly and gradually over the year.

Permanent emigration increased with population size, potentially to escape from increased competition (for food or space) during the breeding season in the Netherlands and is consistent with the northward expansion to Germany and Denmark (O. Overdijk, personal observation). Permanent emigration has especially increased for immature birds (Table II.4), suggesting that natal dispersal has been more important than breeding dispersal as a mechanism of this range expansion. The estimated age-specific survival and emigration rates (Table II.4), together with an assumed constant reproductive output ($f = 0.62$, see Appendix II, Section II.1 for calculations), resulted in a reasonable fit between predicted and observed number of breeding pairs in the Netherlands until 2008 (Fig. 5.2). This suggests that reproductive output is not (yet) density dependent at the scale of the Netherlands, at least not at the level which would have a pronounced effect on population growth rates. As Lok *et al.* (2009) found that reproductive output was strongly density dependent at the level of a single colony, the apparent absence of density dependence in reproductive output at the scale of the Netherlands suggests that the range expansion of spoonbills has coincided with the discovery of new suitable breeding habitats (Fig. 5.1). In fact, the deviation between observed and predicted population growth from 2008 to 2009 could have been partly caused by some preceding years with exceptionally high reproductive output. In addition, the fact that fidelity was forced to be a linear function of population size may have resulted in an overestimation of the proportion of birds that permanently emigrated during recent years of high population sizes.

At present, we can only speculate about the mechanisms underlying the relationships between population size and age-specific survival rates. We cannot exclude the potential role of density-independent factors that changed with time and thus covaried with population size over the study period. For example, many migratory bird populations have declined during the last decades and this has been correlated with climate change (Newton 2004) and (human-induced) habitat alterations (Kraan *et al.* 2009). However, because the season of the strongest effect of population size differs among age classes, it is unlikely that the declining survival rates are primarily caused by density-independent changes in the environment in any particular season. Below we will elaborate on potential reasons for the most pronounced patterns of density dependence in seasonal survival.

Age effects on strength and seasonal timing of density dependence

Juvenile survival initially increased steeply with population size, but showed a sharp decrease at higher population sizes. The positive effect of population size on survival at low population sizes was only apparent in juveniles but not in older birds (Fig. 5.3). Earlier studies on Mediterranean Gulls *Larus melanocephalus* and Dalmatian Pelicans *Pelicanus crispus*, both colonial breeders as well, also found evidence of inverse density dependence in juvenile annual survival, but not in adult survival (te Marvelde *et al.*

2009; Doxa *et al.* 2010). In colonial breeders, inverse density dependence in juvenile survival might occur during the rearing period when the presence of conspecifics reduces predation risk and thermoregulatory costs (Courchamp, Clutton-Brock & Grenfell 1999; Doxa *et al.* 2010). Rather than during the post-fledging period, however, we show that the initial increase in juvenile survival occurs in early winter (Fig. 5.4). Possibly, this increase in early winter survival resulted from carry-over effects from positively density-dependent effects during the post-fledging period (Lindström 1999; Harrison *et al.* 2011). Alternatively, the presence of conspecifics is particularly important for juveniles in early winter. As spoonbills migrate in groups, consisting of both juvenile and adult birds, the inexperienced juveniles may benefit from social information for navigation and stopover site use during their first autumn migration (Henningsson & Karlsson 2009). Moreover, spoonbills may use V-formation flight during migration so that the presence of others may reduce flight costs during migration (Cutts & Speakman 1994). However, this would also benefit adult birds where inverse density dependence in survival did not occur.

After the initial increase, the subsequent decrease in juvenile annual survival with population size was much stronger than in older birds, decreasing from ca. 0.70 to 0.50 between 2000 and 2008. Stronger density dependence in juvenile than adult annual survival was also confirmed by other studies (Fowler 1987; Arcese *et al.* 1992; Gaillard, Festa-Bianchet & Yoccoz 1998; Armstrong *et al.* 2005; Bailey *et al.* 2010). Here we show that survival of juveniles, occurring together with adults in summer and early winter, was density dependent in those seasons whereas adult survival was not (Fig. 5.4). This may be explained mechanistically by food availability having declined most strongly for juveniles because they are competitively inferior (Townshend 1985; Sandell & Smith 1991), or because they are less efficient foragers (Groves 1978). Although juvenile and adult survival appeared similarly density dependent in the late winter season, this comparison is not very meaningful, since juveniles stay at the non-breeding grounds, whereas adults migrate back to their breeding grounds and prepare for breeding. As population growth rate is generally more sensitive to changes in adult survival than immature survival (Saether & Bakke 2000), the stronger density dependence in juvenile compared to adult survival (though only at high population sizes) is in accordance with the commonly observed pattern that the strength of density dependence in demographic parameters decreases with increasing sensitivity of population growth rate to changes in a demographic parameter (Eberhardt 2002). That density dependence in subadult survival was not (much) stronger than in adult survival may be explained by the higher energetic and nutritional demands of adult birds that migrate and breed compared to subadult birds that generally remain on their non-breeding grounds year-round.

Potential mechanisms of seasonal density dependence in adult survival

Adult survival was independent of population size in summer and early winter but decreased with population size in late winter. The strong decline in adult survival in late winter may find its cause on the wintering grounds or during spring migration. This decline may be caused by food limitation, and be density dependent when *per capita* food availability is a function of population density. Sillett and Holmes (2002) have argued that during migration periods density-independent factors, such as adverse weather conditions and collisions, will be more important than density-dependent factors in causing mortality. While this may be true for migratory passerines, density-dependent factors during migration could be important for migratory species that congregate at a limited number of staging sites, such as waterfowl and shorebirds (Newton 2006). Negative density dependence at staging sites could in such cases be strong, as bird densities are often high, and resources become heavily depleted (Newton 2006). Annual survival of White Storks *Ciconia ciconia* was strongly correlated with primary production indexed by the normalized difference vegetation index (NDVI) at a major staging area (Schaub, Kania & Koppen 2005). The absence of density dependence in adult survival in early winter indicates that – at least during southward migration – resource availability at staging sites is not (yet) limiting for spoonbills.

Instead of, or in addition to, food limitation at staging areas, food may be limiting on the wintering grounds. This may either be due to lower per capita food availability or to higher energetic demands in winter, for example due to higher energetic costs of thermoregulation (Wiersma & Piersma 1994; Doherty *et al.* 2001). This may have led to increased mortality at the wintering grounds or, via carry-over effects, to increased mortality during spring migration. Many studies found a relationship between food conditions on the wintering grounds and annual survival (Peach, Baillie & Underhill 1991; Gill *et al.* 2001), timing of arrival at breeding grounds and/or reproductive output (reviewed in Harrison *et al.* 2011). The fact that annual survival of the subadult birds that generally remain on the wintering grounds year-round also decreased with population size (though in early rather than late winter, perhaps because subadult birds face different constraints than adult birds), suggests that at least part of the observed decline in adult survival in late winter is mediated by conditions at the wintering grounds rather than at stopover sites during northward migration. Two adult spoonbills equipped with GPS satellite transmitters died shortly after northward departure from their West-African wintering grounds. Unfortunately, these birds could not be retrieved and therefore the potential role of starvation in causing death could not be assessed.

Seasonal variation in survival

Most mortality occurred away from the breeding grounds, although the exact timing (early or late winter) differed among age classes. That survival in summer is highest, as compared to other seasons, is in agreement with the few other studies that investigated seasonal survival. Sillett and Holmes (2002) found that most (over 85% of the) mortality occurred during the migratory seasons in a migratory passerine, the Black-throated Blue Warbler *Dendroica caerulescens*, although they compared different populations to get estimates of winter and summer survival. In the migratory Blue Petrel *Halobaena caerulea*, around 70% of the annual mortality of adult birds occurred during the non-breeding period (Barbraud & Weimerskirch 2003). Leyrer *et al.* (2013) found that in Red Knots *Canutus canutus canutus* using the same flyway and wintering areas as the Eurasian Spoonbills studied here, virtually all mortality occurred on the wintering grounds in West Africa. Gauthier *et al.* (2001) could not find seasonal differences in survival in Greater Snow Geese *Chen caerulescens atlantica*, but as they used a different categorization of seasons the results are difficult to compare.

Towards a general ecology of seasonal demography

Generally, it can be concluded that the shape and strength of density dependence in survival varies with season and age. Determining the seasons in which survival is density dependent can now be the basis for more detailed studies on the density-dependent processes occurring in those seasons. Revealing whether density-dependent survival in any season is mediated by intraspecific competition for food and space is important to predict the effect of habitat loss in any season on migratory populations (Sutherland 1996).

Another line of investigation could focus on comparisons of demographic patterns in different species using the same flyway (e.g. the Red Knots discussed above, Leyrer *et al.* 2013) or distinct populations of the same species using different flyways (Piersma 2007). Such demographic comparisons among populations and species will increase our understanding about the generalities and specificities of the limitation and regulation of migratory bird populations.

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APPENDIX II

Table II.1 Number of different spoonbills ringed, resighted and recovered per year of birth (on the left) and number of different spoonbills resighted per year, period and age class (on the right).

Per cohort (year of birth)			
Year of birth	Ringed	Resighted	Recovered
1988	108	96	4
1989	130	104	3
1990	152	104	6
1991	177	144	5
1992	279	219	12
1993	271	221	8
1994	298	270	4
1995	1	1	0
1996	233	202	8
1997	220	205	11
1998	214	197	7
1999	330	292	5
2000	195	177	8
2001	265	240	1
2002	182	156	4
2003	301	272	9
2004	393	318	18
2005	393	346	4
2006	460	388	5
2007	483	412	6
2008	590	432	15
2009	508	396	9
2010	299	-	-

Per year							
	Different birds resighted						
	Capture occasions (at *i*)			Interval (between *i* and *i*+1)			
Year *i*	1 yr	2 yr	≥3 yr	1st yr	2nd yr	3rd yr	≥ 4th yr
1988	-	-	-	82	-	-	-
1989	0	-	-	94	5	-	-
1990	1	6	-	82	11	14	-
1991	0	3	15	118	7	10	18
1992	0	3	31	160	26	11	39
1993	5	3	46	164	27	12	64
1994	7	11	83	232	31	36	109
1995	2	16	128	0	37	49	162
1996	0	22	185	186	1	79	280
1997	8	0	293	198	68	0	351
1998	17	30	264	170	77	64	304
1999	14	12	241	259	60	57	294
2000	4	4	185	149	75	44	362
2001	7	37	211	201	48	55	304
2002	11	16	253	134	54	47	379
2003	7	43	259	253	41	78	387
2004	14	24	276	288	64	42	419
2005	10	18	222	297	71	53	410
2006	8	26	348	337	80	75	406
2007	39	34	376	379	145	107	530
2008	14	48	343	398	122	114	494
2009	17	41	423	391	104	104	589
2010	16	65	449	-	-	-	-

Table II.2 Model selection results to investigate whether fidelity (F), resighting (p, R and R') and recovery (r) probabilities are more parsimoniously modelled with between-year variation (t), as a linear function of population size (N_{lin}, only for fidelity) or as constant (.). Survival is modelled as S_0(t) S_1(t) S_2(t) $S_{\geq 3}$(t).

Parameterization					K	ΔQDev	ΔQAIC$_c$
F_{012}(t) F_{ad}(t)	p_1(t) p_2(t) $p_{\geq 3}$(t)	r(.)	R(t)	R'(t)	223	0.00*	4.26
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	p_1(t) p_2(t) $p_{\geq 3}$(t)	r(t)	R(t)	R'(t)	209	36.25	11.95
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	p_1(t) p_2(t) $p_{\geq 3}$(t)	r(t)	R(t)	R'(.)	188	101.96	34.88
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	p_1(t) p_2(t) $p_{\geq 3}$(t)	r(t)	R(.)	R'(t)	188	337.64	270.56
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	p_1(t) p_2(t) $p_{\geq 3}$(t)	r(t)	R(.)	R'(.)	167	408.53	298.76
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	p_1(t) p_2(t) $p_{\geq 3}$(t)	**r(.)**	**R(t)**	**R'(t)**	**188**	**67.08**	**0.00****
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	p_1(t) p_2(t) $p_{\geq 3}$(t)	r(.)	R(t)	R'(.)	167	135.49	25.72
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	p_1(t) p_2(t) $p_{\geq 3}$(t)	r(.)	R(.)	R'(t)	167	367.99	258.22
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	p_1(t) p_2(t) $p_{\geq 3}$(t)	r(.)	R(.)	R'(.)	146	442.06	289.67
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	(p_1, p_2, $p_{\geq 3}$(t)	r(t)	R(t)	R'(t)	172	150.32	50.71
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	(p_1, p_2, $p_{\geq 3}$(t)	r(t)	R(t)	R'(.)	151	208.61	66.37
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	(p_1, p_2, $p_{\geq 3}$(t)	r(t)	R(.)	R'(t)	151	450.45	308.20
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	(p_1, p_2, $p_{\geq 3}$(t)	r(t)	R(.)	R'(.)	130	514.94	330.14
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	(p_1, p_2, $p_{\geq 3}$(t)	r(.)	R(t)	R'(t)	151	182.22	39.98
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	(p_1, p_2, $p_{\geq 3}$(t)	r(.)	R(t)	R'(.)	130	247.12	62.33
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	(p_1, p_2, $p_{\geq 3}$(t)	r(.)	R(.)	R'(t)	130	489.80	305.00
$F_{012}(N_{lin})$ $F_{ad}(N_{lin})$	(p_1, p_2, $p_{\geq 3}$(t)	r(.)	R(.)	R'(.)	109	554.44	327.18

K = number of parameters. The best-supported (full) model is shown in bold. Results are adjusted for overdispersion (c = 1.16, see Methods). Note that the fully time-dependent model (the first model in the list) was run using the simulated annealing optimization routine.

*QDeviance = 24479.92

**QAIC$_c$ = 56977.74

Table II.3 Model selection results for reduced fixed and random effects models of age-specific survival and fidelity, starting from the full model.

Parameterization	K	ΔQDev	$\Delta QAIC_c$
S_0(t) S_1(t) S_2(t) $S_{\geq 3}$(t) **F_{012}(N_{lin}) $F_{\geq 3}$(N_{lin})**	186	0.00*	0.00**
Reduced parameterizations of:			
1st year survival (S_0)			
μ	166	181.57	140.91
N_{lin}	167	170.74	132.12
N_{quad}	168	59.11	22.51
μ, σ^2	184.00	0.49	-3.57
N_{lin}, σ^2	184.10	0.46	-3.40
N_{quad}, σ^2	**181.96**	**1.45**	**-6.77**
2nd year survival (S_1)			
μ	167	56.43	17.80
Nlin	168	41.96	5.36
Nquad	169	40.18	5.62
μ, σ^2	181.96	1.48	-6.73
N_{lin}, σ^2	**180.88**	**2.35**	**-8.07**
N_{quad}, σ^2	181.20	2.21	-7.54
3rd year survival (S_2)			
μ	168	37.04	0.45
Nlin	169	28.81	-5.75
Nquad	170	28.53	-4.00
μ, σ^2	180.95	2.49	-7.78
N_{lin}, σ^2	**179.89**	**3.21**	**-9.22**
N_{quad}, σ^2	180.39	2.89	-8.53
Adult survival ($S_{\geq 3}$)			
μ	168	29.18	-7.41
Nlin	**169**	**18.84**	**-15.72**
Nquad	170	18.54	-13.99
μ, σ^2	182.35	0.60	-6.83
N_{lin}, σ^2	180.95	2.02	-8.25
N_{quad}, σ^2	180.82	2.99	-7.54
Immature fidelity (F_{012})			
μ	185	8.86	6.82
Adult fidelity ($F_{\geq 3}$)			
μ	185	15.61	13.57

Nuisance parameters are modelled as p_1(t) p_2(t) $p_{\geq 3}$(t) r(.) R(t) R'(t). $\mu = \beta_0$, $N_{lin} = \beta_0+\beta_1 \cdot N$ and $N_{quad} = \beta_0+\beta_1 \cdot N+\beta_2 \cdot N^2$, with or without random between-year variation (σ^2 or σ^2_{res}). In bold, the best-supported parameterization for each age-specific survival and fidelity parameter. Results are adjusted for overdispersion (c = 1.16, see Methods).

*QDeviance = 24547.00

**$QAIC_c$ = 56973.67

Table II.4 Shrunken estimates (mean ± SE) for age-specific survival from the best-supported random effects parameterization per age class (N_{quad}, σ^2 for S_0 and N_{lin}, σ^2 for S_1, S_2 and $S_{\geq 3}$, see Table II.3). For fidelity, the maximum likelihood estimates of the full Barker model are shown which were modelled as a linear function of population size.

Year	Population size	S_0	S_1	S_2	$S_{\geq 3}$	F_{012}	$F_{\geq 3}$
1988	415	0.46 ± 0.04	n.a.	n.a.	n.a.	0.94 ± 0.008	n.a.
1989	492	0.43 ± 0.04	1.00 ± 0.00	n.a.	n.a.	0.94 ± 0.007	n.a.
1990	438	0.39 ± 0.04	0.96 ± 0.04	0.96 ± 0.05	n.a.	0.94 ± 0.007	n.a.
1991	527	0.52 ± 0.04	0.95 ± 0.03	0.99 ± 0.03	1.00 ± 0.00	0.93 ± 0.007	0.99 ± 0.004
1992	560	0.52 ± 0.03	0.91 ± 0.05	1.00 ± 0.00	0.88 ± 0.06	0.93 ± 0.007	0.99 ± 0.004
1993	593	0.57 ± 0.03	0.97 ± 0.02	1.00 ± 0.00	0.91 ± 0.02	0.93 ± 0.007	0.99 ± 0.004
1994	661	0.68 ± 0.03	0.99 ± 0.02	0.98 ± 0.02	0.91 ± 0.02	0.93 ± 0.007	0.99 ± 0.004
1995	810	n.a.	0.97 ± 0.02	0.97 ± 0.02	0.90 ± 0.02	0.92 ± 0.006	0.99 ± 0.004
1996	847	0.65 ± 0.03	n.a.	0.96 ± 0.02	0.89 ± 0.02	0.92 ± 0.006	0.99 ± 0.004
1997	1122	0.63 ± 0.03	0.88 ± 0.03	n.a.	0.88 ± 0.02	0.91 ± 0.005	0.98 ± 0.003
1998	1270	0.69 ± 0.03	0.87 ± 0.04	0.93 ± 0.02	0.85 ± 0.02	0.90 ± 0.005	0.98 ± 0.003
1999	1038	0.69 ± 0.03	0.86 ± 0.04	0.95 ± 0.02	0.90 ± 0.02	0.92 ± 0.005	0.98 ± 0.003
2000	1043	0.66 ± 0.03	0.90 ± 0.02	0.90 ± 0.05	0.88 ± 0.02	0.92 ± 0.005	0.98 ± 0.003
2001	1165	0.67 ± 0.03	0.89 ± 0.03	0.98 ± 0.02	0.90 ± 0.02	0.91 ± 0.005	0.98 ± 0.003
2002	1534	0.56 ± 0.03	0.95 ± 0.02	0.93 ± 0.02	0.87 ± 0.02	0.89 ± 0.007	0.97 ± 0.004
2003	1293	0.62 ± 0.03	0.96 ± 0.03	0.95 ± 0.02	0.88 ± 0.02	0.90 ± 0.005	0.98 ± 0.003
2004	1699	0.51 ± 0.03	0.84 ± 0.03	0.90 ± 0.03	0.84 ± 0.02	0.88 ± 0.009	0.96 ± 0.006
2005	1443	0.58 ± 0.03	0.85 ± 0.03	1.00 ± 0.00	0.88 ± 0.01	0.90 ± 0.006	0.97 ± 0.003
2006	1778	0.57 ± 0.03	0.93 ± 0.03	0.90 ± 0.03	0.86 ± 0.02	0.88 ± 0.010	0.96 ± 0.007
2007	1838	0.46 ± 0.03	0.85 ± 0.03	0.87 ± 0.04	0.84 ± 0.02	0.87 ± 0.011	0.96 ± 0.008
2008	1904	0.29 ± 0.03	0.84 ± 0.04	0.93 ± 0.03	0.85 ± 0.02	0.87 ± 0.012	0.95 ± 0.010

The standard errors associated with the age-specific survival estimates represent the RMSE estimates reported by program MARK, which give the unconditional sampling standard errors. Results are adjusted for overdispersion (c = 1.16, see Methods).

Table II.5 Estimates (and 95% confidence intervals) of resighting probabilities during capture occasions (*p*) and intervals (*R* and *R*′) and recovery probability (*r*) of the full model: $S_0(\mathrm{t})\ S_1(\mathrm{t})\ S_2(\mathrm{t})\ S_{\geq 3}(\mathrm{t})\ F_{012}(\mathrm{N_{lin}})\ F_{\geq 3}(\mathrm{N_{lin}})\ p_1(\mathrm{t})\ p_2(\mathrm{t})\ p_{\geq 3}(\mathrm{t})\ r(.)\ R(\mathrm{t})\ R'(\mathrm{t})$.

	Resighting probability during capture occasions (*p*)			Resighting probability during interval of	
Year	Age 1	Age 2	Age ≥ 3	survivors (*R*)	non-survivors (*R*')
1988	n.a.	n.a.	n.a.	0.71 (0.56-0.83)	0.78 (0.64-0.88)
1989	0.00 (0.00-1.00)	n.a.	n.a.	0.45 (0.35-0.55)	0.67 (0.54-0.77)
1990	0.02 (0.00-0.15)	0.13 (0.06-0.28)	n.a.	0.36 (0.29-0.45)	0.49 (0.39-0.60)
1991	0.00 (0.00-0.00)	0.07 (0.02-0.20)	0.38 (0.23-0.55)	0.40 (0.33-0.46)	0.64 (0.51-0.75)
1992	0.00 (0.00-0.00)	0.06 (0.02-0.19)	0.38 (0.27-0.51)	0.40 (0.35-0.46)	0.55 (0.46-0.64)
1993	0.04 (0.01-0.09)	0.04 (0.01-0.13)	0.40 (0.31-0.50)	0.38 (0.34-0.43)	0.57 (0.47-0.66)
1994	0.05 (0.02-0.10)	0.09 (0.05-0.16)	0.48 (0.40-0.57)	0.48 (0.44-0.52)	0.70 (0.58-0.80)
1995	0.01 (0.00-0.05)	0.12 (0.07-0.19)	0.48 (0.41-0.54)	0.36 (0.32-0.40)	0.43 (0.21-0.68)
1996	0.00 (0.00-0.00)	0.13 (0.08-0.19)	0.50 (0.45-0.56)	0.63 (0.59-0.66)	0.57 (0.46-0.68)
1997	0.06 (0.03-0.12)	0.00 (0.00-0.00)	0.61 (0.56-0.66)	0.63 (0.59-0.67)	0.70 (0.59-0.79)
1998	0.14 (0.08-0.22)	0.28 (0.20-0.39)	0.62 (0.57-0.67)	0.61 (0.57-0.64)	0.65 (0.54-0.74)
1999	0.11 (0.06-0.18)	0.13 (0.07-0.23)	0.55 (0.50-0.60)	0.58 (0.54-0.61)	0.62 (0.52-0.71)
2000	0.02 (0.01-0.05)	0.04 (0.01-0.11)	0.40 (0.35-0.45)	0.52 (0.48-0.55)	0.70 (0.57-0.80)
2001	0.06 (0.03-0.13)	0.22 (0.16-0.30)	0.44 (0.39-0.49)	0.47 (0.43-0.50)	0.66 (0.55-0.76)
2002	0.07 (0.04-0.12)	0.17 (0.10-0.27)	0.43 (0.39-0.48)	0.46 (0.43-0.49)	0.64 (0.54-0.74)
2003	0.08 (0.03-0.16)	0.31 (0.23-0.40)	0.45 (0.40-0.50)	0.54 (0.50-0.57)	0.67 (0.57-0.76)
2004	0.08 (0.05-0.14)	0.29 (0.20-0.41)	0.45 (0.40-0.49)	0.52 (0.49-0.55)	0.56 (0.48-0.63)
2005	0.06 (0.03-0.11)	0.14 (0.09-0.22)	0.39 (0.35-0.44)	0.51 (0.48-0.54)	0.65 (0.57-0.72)
2006	0.04 (0.02-0.08)	0.20 (0.13-0.28)	0.57 (0.53-0.62)	0.51 (0.48-0.54)	0.58 (0.51-0.65)
2007	0.17 (0.12-0.23)	0.20 (0.14-0.28)	0.61 (0.57-0.66)	0.61 (0.58-0.63)	0.68 (0.62-0.74)
2008	0.07 (0.04-0.12)	0.28 (0.21-0.37)	0.55 (0.51-0.60)	0.56 (0.53-0.59)	0.61 (0.56-0.66)
2009	0.12 (0.07-0.20)	0.28 (0.21-0.37)	0.64 (0.60-0.69)	0.56 (0.52-0.60)	0.88 (0.51-0.98)

Recovery probability (*r*) was estimated at 0.03 (0.03-0.04). Confidence intervals are adjusted for overdispersion (c = 1.16, see Methods).

Table II.6 Model selection results for reduced parameterizations of resighting probability (p) and apparent survival (Φ).

Parameterization	K	ΔQDev	$\Delta QAIC_c$
1. $\Phi_{0,s}(t)\ \Phi_{0,w1}(t)\ \Phi_{0,w2}(t)\ \Phi_{12,s}(t)\ \Phi_{12,w1}(t)\ \Phi_{12,w2}(t)\ \Phi_{\geq 3,s}(t)\ \Phi_{\geq 3,w1}(t)\ \Phi_{\geq 3,w2}(t)\ (p_{0,s2}\ p_{\geq 3,s2})(t)\ p_{12,s1}(t)\ p_{\geq 3,s1}(t)\ p_{12,s2}(t)\ p_{w}(t)$	296	0.00*	202.77
Step 1. Reduced parameterizations of Φ with other parameterizations as in model 1			
2. $\Phi_{0,s}(N_{quad})$	277	17.48	181.28
3. $\Phi_{0,w1}(N_{quad})$	277	23.25	187.05
4. $\Phi_{0,w2}(N_{quad})$	277	14.00	177.79
5. $\Phi_{12,s}(N_{lin})$	276	3.05	164.80
6. $\Phi_{12,w1}(N_{lin})$	276	8.94	170.69
7. $\Phi_{12,w2}(N_{lin})$	276	11.81	173.55
8. $\Phi_{\geq 3,s}(N_{lin})$	278	1.80	167.64
9. $\Phi_{\geq 3,w1}(N_{lin})$	278	15.55	181.39
10. $\Phi_{\geq 3,w2}(N_{lin})$	277	17.77	181.57
11. $\Phi_{0,s}(N_{quad})\ \Phi_{0,w1}(N_{quad})\ \Phi_{0,w2}(N_{quad})\ \Phi_{12,s}(N_{lin})\ \Phi_{12,w1}(N_{lin})\ \Phi_{12,w2}(N_{lin})\ \Phi_{\geq 3,s}(N_{lin})\ \Phi_{\geq 3,w1}(N_{lin})\ \Phi_{\geq 3,w2}(N_{lin})$	**134**	**127.48**	**0.00****
Step 2. Reduced parameterizations of *p* with other parameterizations as in model 11			
12. $p_{12,s1}(.)$	113	234.34	64.40
13. $p_{\geq 3,s1}(.)$	115	243.46	77.56
14. $p_{12,s2}(.)$	113	294.14	124.20
15. $(p_{0,s2}\ p_{\geq 3,s2})(.)$	112	460.64	288.68
16. $p_{w}(.)$	113	420.74	250.80
Step 3. Reduced parameterizations of Φ with other parameterizations as in model 11			
17. $\Phi_{0,s}(N_{lin})$	133	127.48	0.26
18. $\Phi_{0,s}(.)$	132	129.76	28.49
19. $\Phi_{0,w1}(N_{lin})$	133	160.02	3.47
20. $\Phi_{0,w1}(.)$	132	132.98	4.86
21. $\Phi_{0,w2}(N_{lin})$	133	136.39	-0.63
22. $\Phi_{0,w2}(.)$	132	128.87	0.65
23. $\Phi_{12,s}(.)$	133	132.18	2.41
24. $\Phi_{12,w1}(.)$	133	131.91	4.02
25. $\Phi_{12,w2}(.)$	133	133.53	-1.81
26. $\Phi_{\geq 3,s}(.)$	133	127.69	-2.02
27. $\Phi_{\geq 3,w1}(.)$	133	127.48	-1.73
28. $\Phi_{\geq 3,w2}(.)$	133	127.77	13.29
Step 4. Combinations of supported parameterizations from step 3 (*p* as in model 1)			
29. $\Phi_{0,s}(N_{quad})\ \Phi_{0,w1}(N_{quad})\ \Phi_{0,w2}(N_{lin})\ \Phi_{12,s}(N_{lin})\ \Phi_{12,w1}(N_{lin})\ \Phi_{12,w2}(.)\ \Phi_{\geq 3,s}(.)\ \Phi_{\geq 3,w1}(.)\ \Phi_{\geq 3,w2}(N_{lin})$	130	129.55	-6.02
30. $\Phi_{0,s}(N_{lin})\ \Phi_{0,w1}(N_{quad})\ \Phi_{0,w2}(N_{lin})\ \Phi_{12,s}(N_{lin})\ \Phi_{12,w1}(N_{lin})\ \Phi_{12,w2}(.)\ \Phi_{\geq 3,s}(.)\ \Phi_{\geq 3,w1}(.)\ \Phi_{\geq 3,w2}(N_{lin})$	129	131.81	-5.79
31. $\Phi_{0,s}(N_{quad})\ \Phi_{0,w1}(N_{quad})\ \Phi_{0,w2}(.)\ \Phi_{12,s}(N_{lin})\ \Phi_{12,w1}(N_{lin})\ \Phi_{12,w2}(.)\ \Phi_{\geq 3,s}(.)\ \Phi_{\geq 3,w1}(.)\ \Phi_{\geq 3,w2}(N_{lin})$	129	132.76	-4.84
32. $\Phi_{0,s}(N_{lin})\ \Phi_{0,w1}(N_{quad})\ \Phi_{0,w2}(.)\ \Phi_{12,s}(N_{lin})\ \Phi_{12,w1}(N_{lin})\ \Phi_{12,w2}(.)\ \Phi_{\geq 3,s}(.)\ \Phi_{\geq 3,w1}(.)\ \Phi_{\geq 3,w2}(N_{lin})$	128	134.93	-4.69

Φ_0 = 1st year survival, Φ_{12} = 2nd and 3rd year survival, and $\Phi_{\geq 3}$ = survival of older birds. Survival is modelled as a linear ($N_{lin} = \beta_0+\beta_1 \cdot N$) or quadratic ($N_{quad} = \beta_0+\beta_1 \cdot N+\beta_2 \cdot N^2$) function of population size, or as constant (.). Definition of resighting periods: s1= start summer, s2 = end summer, w = winter. Definition of survival seasons: s = summer, w1 = early winter, w2 = late winter. K = number of parameters. The starting model to investigate the support for density dependence in age- and season-specific survival (step 3 and 4) is shown in bold. Overdispersion was assessed for this model (c = 1.61, see Methods) and results have been adjusted accordingly.

*QDeviance = 20862.13

**$QAIC_c$ = 45145.08

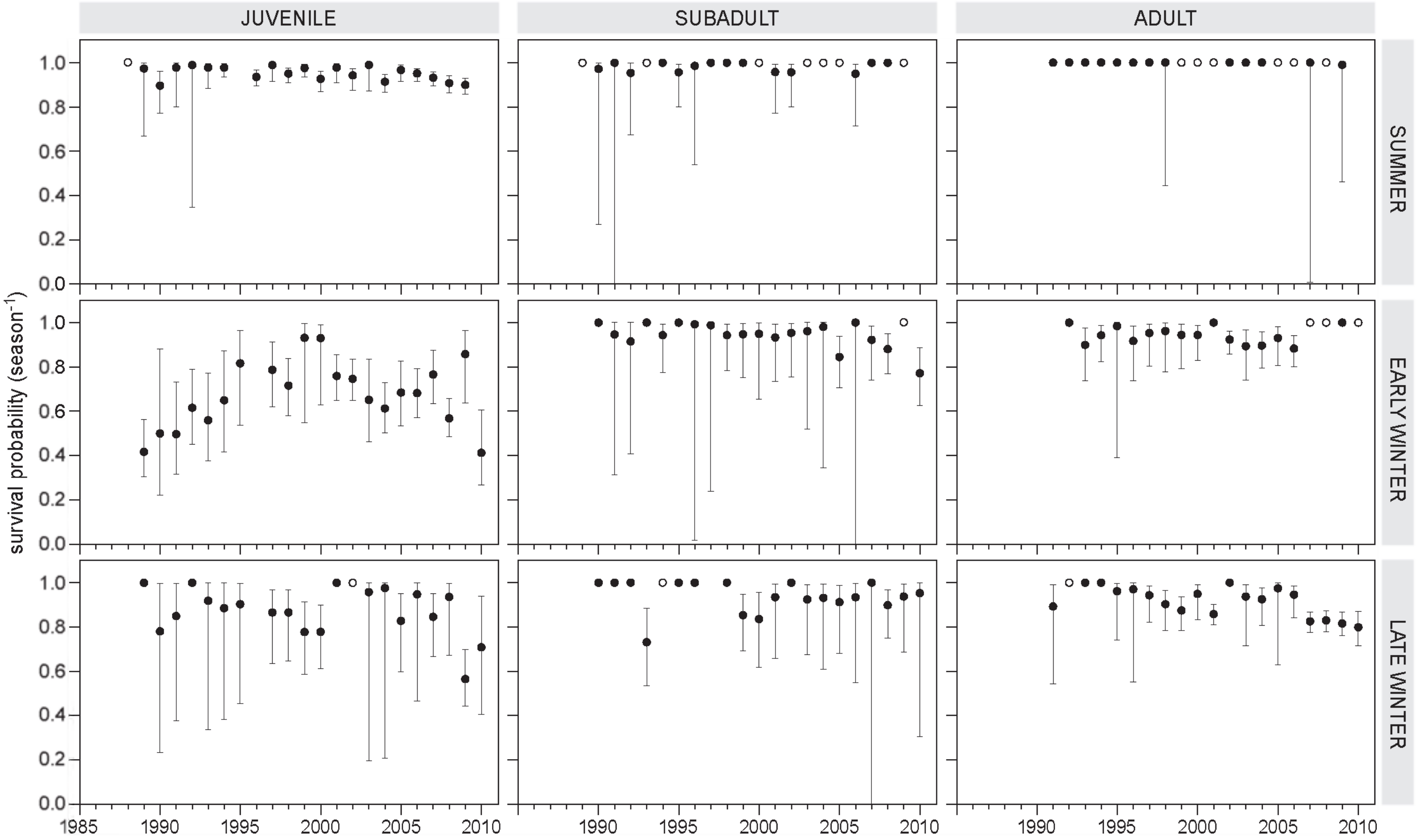


Figure II.1 Estimates of between-year variation in seasonal survival rates of juvenile, subadult (2nd and 3rd year) and adult spoonbills from model 1 in Table II.6. 95% confidence intervals, as indicated by the error bars, are adjusted for overdispersion ($\hat{c}$ = 1.61, see Methods). Inestimable parameters (as indicated by negative variances of the associated beta (logit link) parameters) are shown as open circles.

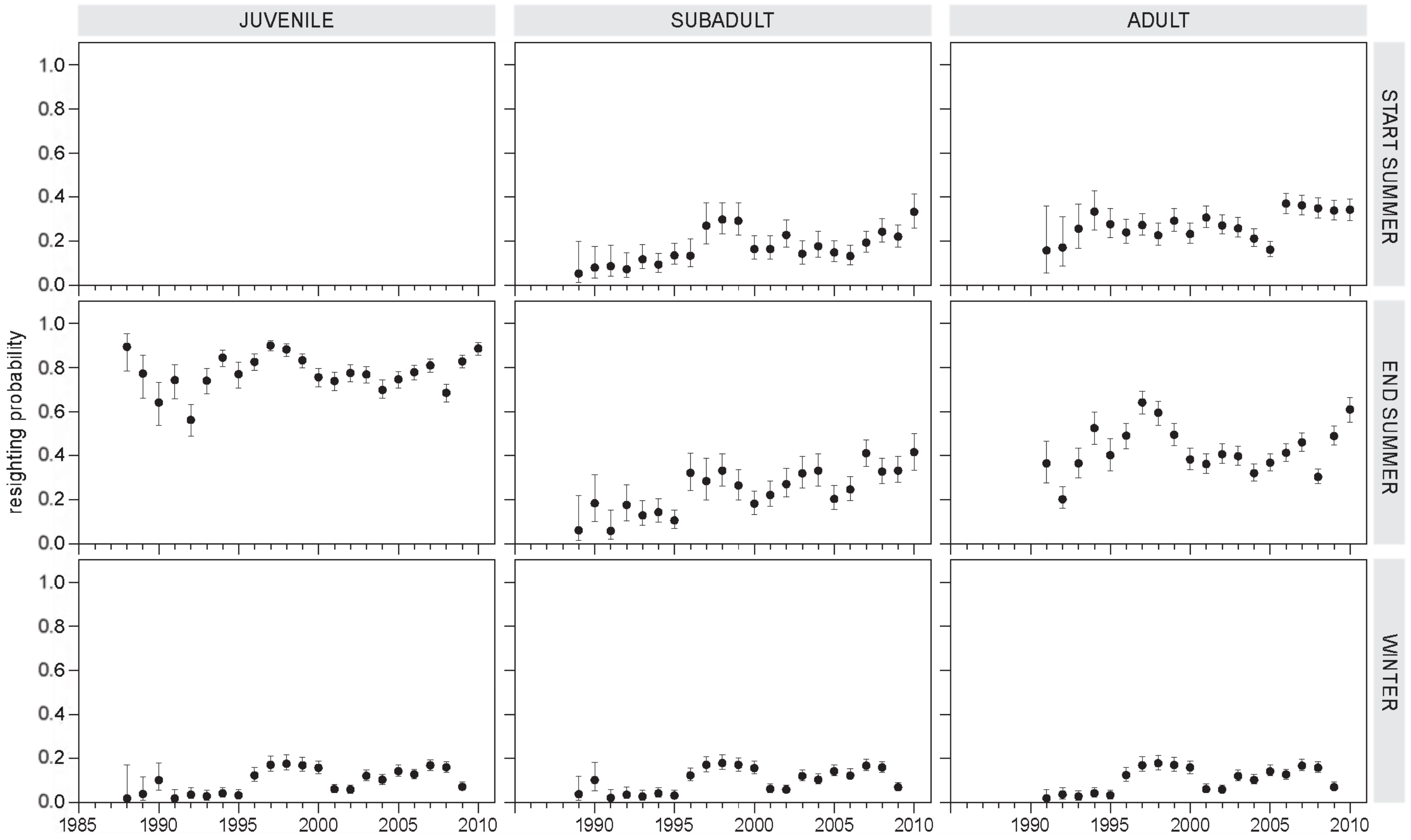


Figure II.2 Estimates of age- and season-specific resighting probabilities of the best-supported model (Table II.6, model 29). 95% confidence intervals, as indicated by the error bars, are adjusted for overdispersion ($\hat{c}$ = 1.61, see Methods).

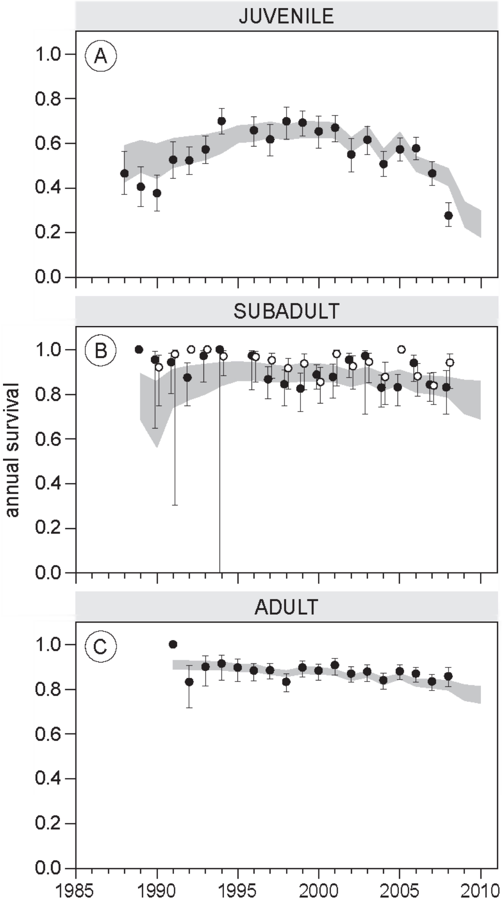
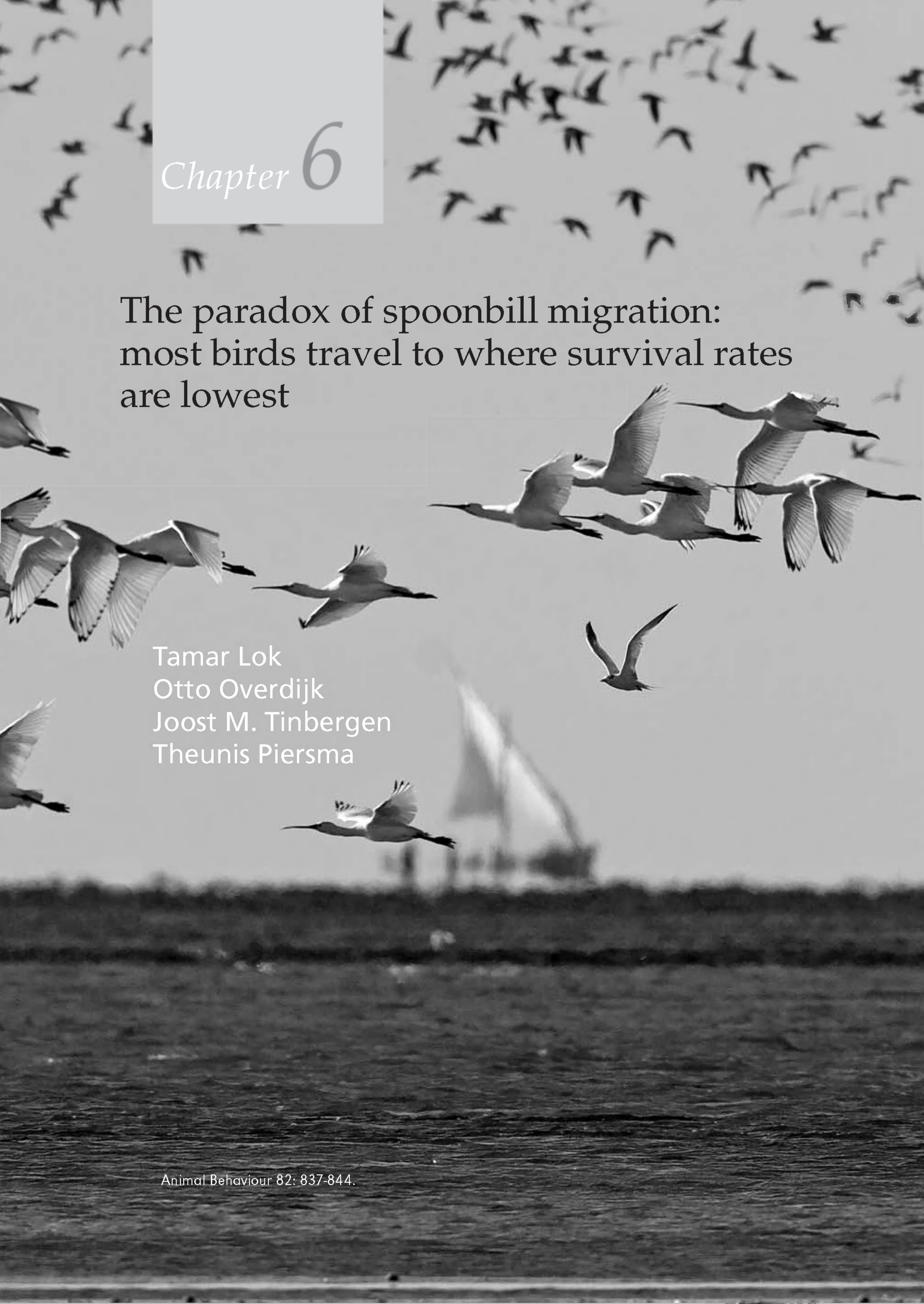


Figure II.3 Comparison of estimates of annual survival of (A) juvenile, (B) subadult and (C) adult birds. The black and white dots are the maximum likelihood estimates of annual true survival of the full Barker model and the shaded grey area is the 95% confidence interval of annual survival when calculated from the seasonal survival estimates of the best-supported CJS model, calculated using the delta method. The closed and open dots in (b) represent 2nd and 3rd year annual true survival.



Chapter 6

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

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Animal Behaviour 82: 837-844.

ABSTRACT

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. Here we compare 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 (52%) migrated to the southernmost wintering region (Mauritania and Senegal). Other birds were likely to move there from the 1st to the 2nd winter, whereas hardly any birds moved to a more northerly wintering area. For the rest of the life spoonbills remained highly site faithful. This resulted in most birds ending up wintering in Mauritania and Senegal (66% by the 2nd winter, against 7% in France and 27% in 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 maximisation 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.

INTRODUCTION

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, Hobson & Holmes 1998; Saino *et al.* 2004), reproductive output (Sedinger *et al.* 2006) and survival (Peach *et al.* 1991; Schaub, Kania & Koppen 2005). These wintering conditions, in combination with the route and distance to be migrated, 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 where 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). Nonetheless, the widespread occurrence of age-differential migration, i.e. different geographical wintering distributions of juvenile and adult birds (reviewed in Cristol, Baker & Carbone 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 ~82% to ~95% between the 1st and 4th 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 three years of life, after which between-winter displacement distances strongly decreased (Marques, Sowter & Jorge 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 birds are forced to winter at suboptimal sites but that they gradually move to more suitable sites (with higher fitness prospects) when getting 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 immediately 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 where 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, i.e. that 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 dataset 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 ~4000 km, were collected on 1256 birds that were individually marked as nestlings between 1992 and 2009.

Applying a multi-state mark-recapture approach, we investigate whether and how wintering site choice and fidelity changes 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 predict that (1) under the *dominance hypothesis* individuals switch to more suitable areas with age; (2) under the *arrival time hypothesis* individuals 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, Horn & Overdijk 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 predict that (3) the levels of wintering site fidelity are 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 at 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 (Chapter 5, this thesis). Our study population shows weak migratory connectivity (Webster *et al.* 2002), with birds from different wintering areas breeding together in the same colony (Chapter 9, this thesis).

Between 1992 and 2009, 5627 spoonbills have been ringed as pre-fledged chicks in 19 different colonies (Table III.1). The colour-ring combinations usually consist of a metal ring and a unique combination of either 2 inscribed PVC plastic colour-rings or 5 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 ≈ 1000 km) along the east-Atlantic coast southward to Senegal (migration distance ≈ 5000 km). We divided the study area into four regions (Fig. 6.1),

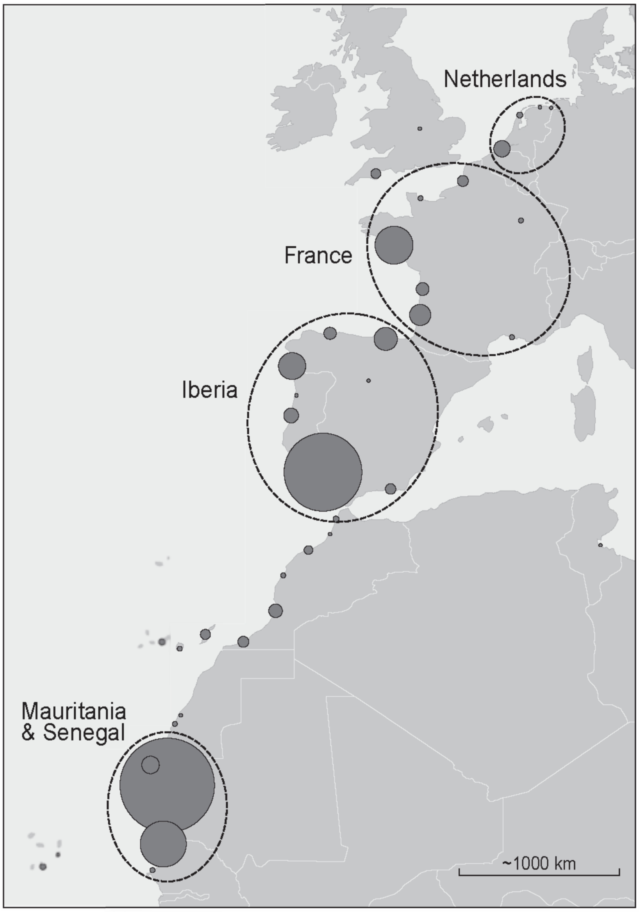

Figure 6.1 Defined borders of the four regions (dashed circles) and the distribution of winter resightings (dots), where the size of the dots represents the number of different colour-ringed birds observed at each wintering site.

comprising the breeding region, The Netherlands, where the birds are ringed, and three main wintering regions which are France, Iberia (comprising Spain and Portugal) and Mauritania and Senegal in West Africa. The vast majority (~96%) of all resightings made during winter originates from these regions (N = 4230) and excludes 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.

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 pre-fledged chick in The Netherlands. To select birds at their likely terminal wintering areas, we used resightings between October and February for Mauritania and Senegal, but only the months December and January in France and Iberia, as these sites are known to be used as stop-over 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 were 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 dataset consists of 1256 spoonbills observed in 2179 bird-winters (Table III.1).

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: multi-state mark-recapture modelling

We used a multi-site (being a specific case of multi-state) mark-recapture modelling approach (Arnason 1973; Brownie *et al.* 1993; Schwarz, Schweigert & Arnason 1993).

This approach is based on individual encounter histories. All individuals start their encounter history when they are marked as fledgling 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, multi-site models can estimate site-specific survival probabilities (ϕ_s), i.e., the probability to survive 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, i.e., survival within the study area. If there is permanent emigration away from the study area, local survival will be lower than true survival. Moreover, multi-site 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 and 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.

In order 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: juveniles (survival from 1st to 2nd winter) and older birds (≥2nd winter). 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, i.e. the transition probabilities ($\psi_{s \cdot d}$, see above). Therefore, the general model did not yet 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 ± 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 1st winter and less than 8% after their 6th 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 1st and >1st winter birds, to a4, distinguishing 1st, 2nd, 3rd and >3rd winter birds as well as a linear effect of age. Furthermore, we assessed whether fidelity differed between wintering regions, either as 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 1st winter (juv) and older birds (older), or was only present in one of these age classes. This resulted in 7 survival functions: $\phi_{s \cdot a2}$, $\phi_{juv+s.older}$, $\phi_{s.juv+older}$, ϕ_{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 to each wintering region during the 1st winter were different by testing a model where these probabilities differed among the three wintering regions against a model where these probabilities were constrained to be the same ($\mu_{NL \rightarrow F} = \mu_{NL \rightarrow IM} = \mu_{NL \rightarrow WA} = 1/3$), 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 where subsequent movement probabilities differed between the two remaining regions and a model where 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, Rouan & Pradel 2009) to obtain maximum likelihood estimates of the parameters and to perform model selection. Because multi-site 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 multi-site 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. It should be noted however, that the estimated fidelity ratios using this method are sensitive to spatial variation in survival and resighting probabilities. We will calculate these fidelity ratios for a range of scales (from fidelity within 0 km to fidelity within 1000 km) and compare these with the values of true wintering site fidelity on a regional level (Fig. 6.1) to assess the spatial scale-dependence of wintering site fidelity of spoonbills.

RESULTS

Models that did not include an age-by-region interaction in the fidelity function had $\Delta QAIC_c$ values of 30.95–44.14 and were not competitive. The model with two age classes (1st and >1st 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 $\Delta QAIC_c > 2$ (Table 6.1). Wintering site fidelity was lower for juvenile birds (fidelity from 1st to 2nd winter) than for older birds, but only in European wintering regions (Fig. 6.2A). In Mauritania and Senegal, birds showed high levels of site fidelity throughout life. Adult birds show high levels of site fidelity in all wintering regions. Resighting probabilities were considerable 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.

The best supported survival model included an additive effect of age and region (Table 6.2, Fig. 6.2B). Survival of juveniles (from 1st to 2nd winter) was significantly

Table 6.1 Model results of site fidelity (*f*) as different functions of site of origin (s) and age.

Fidelity function	K	Deviance	$\Delta QAIC_c$	Akaike weight
s·a2	21	12075.26	0.00*	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 = 1st winter and >1st winter, a3 = 1st winter, 2nd winter and >2nd winter, a4 = 1st winter, 2nd winter, 3rd winter and >3rd winter. Other parameters are modelled as in the general model ($\phi_{s.a2}\, \mu_{s \cdot d}\, p_{s \cdot e}$).
Only models with an Akaike weight of ≥ 0.01 are shown.
*$QAIC_c = 7636.77$

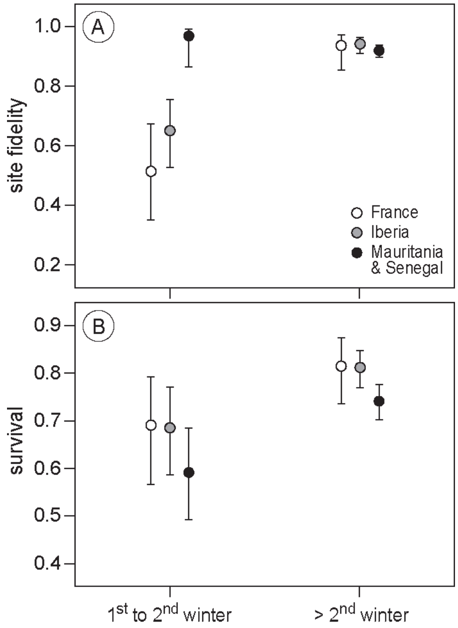

Figure 6.2 (A) Estimates of winter site fidelity to France, Iberia and Mauritania & Senegal as a function of age. (B) Estimates of annual survival probabilities in France, Iberia and Mauritania & Senegal as a function of age. Estimates are based on the best supported model (model 3, Table 6.3). Vertical lines indicate 95% confidence intervals.

lower than of older birds. Moreover, the region effect on survival was significant and seemed similar for juvenile and older birds (model 4 vs. model 5), rather than to be different for juveniles and adults (model 1), or to be only present in juveniles (model 3, Table 6.2). However, the model where 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, though not very strong. This may be due to the small sample size, as the estimates of juvenile survival are based on only 1st winter birds. Survival was lower in Mauritania and Senegal than in France and Iberia.

First-winter movement probabilities differed significantly between wintering regions (model 1 vs. model 2, Table 6.3) and increased towards the south. Juveniles had the highest probability to migrate 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 directed towards the southernmost remaining region, being significant for Iberia (model 4 vs. model 1, Table 6.3) and Mauritania and Senegal (model 5 vs. model 1, Table 6.3), but not for France (model 3 vs. 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 6.2). The combined processes of age-

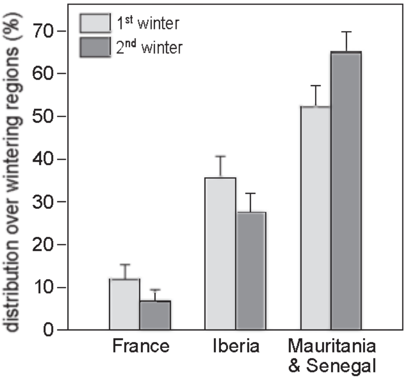

Figure 6.3 Predicted distribution of 1st winter and 2nd winter birds over the three wintering regions. Predictions are based on the estimated probabilities of movement and site fidelity from the best supported model (model 3, Table 6.3) by assuming constant juvenile survival. Vertical lines indicate 95% confidence intervals calculated using the Delta method (Cox 1998).

Table 6.2 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	0.00*	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 = 1st winter birds, older = >1st 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 6.1).
*QAIC$_c$ = 7632.86

Table 6.3 Model results of movement (μ).

Model	K	Deviance	ΔQAIC$_c$	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 regions. 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 (≠ 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 & 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 6.2).
*QAIC$_c$ = 7631.19

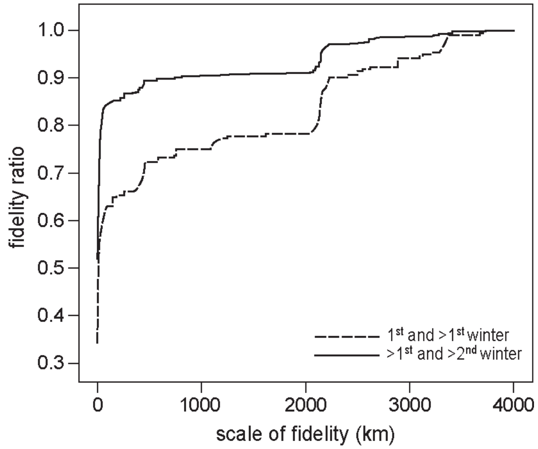

Figure 6.4 Fidelity ratios for site fidelity within 0 km up until fidelity within 4000 km between 1st and >1st winter (dashed line) and >1st and >2nd winter (solid line). Multiple between-winter movement distances of the same individuals are included in the calculations.

specific site fidelity and movement probabilities resulted in a geographical range shift between the 1st and 2nd winter towards more southern wintering regions (Fig. 6.3).

Fidelity ratios depended on the spatial scale examined and strongly increased up to a displacement distance of 100 km (Fig. 6.4). Between 500 and 2000 km, comparable to the spatial scale of our study, fidelity ratios approximate our estimated values of true wintering site fidelity, at least for adult birds (0.92–0.94, Fig. 6.4).

DISCUSSION

During their first southward migration, most spoonbills (52%) migrated to the southernmost wintering region (Mauritania and Senegal) while others moved there from the 1st to the 2nd winter, due to a combination of low site fidelity of 1st 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 2nd winter, against 7% in France and 27% in Iberia, Fig. 6.3). Surprisingly, survival probability was estimated to be lowest of birds wintering in this seemingly preferred area.

Wintering site fidelity was significantly lower in 1st winter birds compared with 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 cannot hold for spoonbills because they do not form pairs for life (unpublished data).

Our finding that spoonbills move southward between their 1st and 2nd winter and stay faithful afterwards results in adult birds wintering further away from the breeding grounds than juveniles (Fig. 6.3). This is opposite to most age-differential migrants (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, i.e. areas with better survival prospects. The pattern observed is precisely the opposite. Most movements between the 1st and 2nd winter are away from Europe to the wintering region with the lowest survival probability (Mauritania and Senegal). By the 2nd winter, most birds have ended up wintering in Mauritania and Senegal (66%, Fig. 6.3) and remain faithful to this wintering region. Therefore, also the prediction from the *dominance hypothesis* is 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 wintering site suitability but ignored the possible effect of wintering site on reproductive output. Although spoonbills wintering in Mauritania and Senegal could in practice compensate for lower survival by higher reproductive rates, we are not aware of any studies that 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 a 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 can be due to 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 stays in France and Iberia in their first winter but moves 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 1st and 2nd winter are predicted to have a lower survival probability compared to 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 due to 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. The southward movement of birds from the 1st to 2nd winter could in this case be due to deteriorating conditions in Europe during the course of the first winter or subsequent autumn, causing birds that are unable to handle these harsher wintering conditions to decide to winter further south in the 2nd 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 where 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 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 part of the immature spoonbills remain at the wintering grounds for one or two years (they only start breeding when 3-years old), birds will face the supposedly harsh spring migration conditions only after some years. This late experience may prevent birds to switch to more favourable wintering sites as they may have lost behavioural flexibility by then, as indicated by the strong site fidelity shown from the 2nd 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 started wintering in European wintering regions over the last decades (Chapter 7, this thesis). Moreover, climate change has been predicted to cause a northward shift of the wintering distribution of the black-faced spoonbill *Platalea minor* (Hu, Hu & Jiang 2010). This suggests that wintering sites in the northern part of the wintering range may have become relatively 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 part of them is 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 towards more southern wintering sites than where they had spent their first winter, which could explain the southward movement of spoonbills between the 1st and 2nd 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 the 1st and 2nd 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. 6.3) 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.

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APPENDIX III

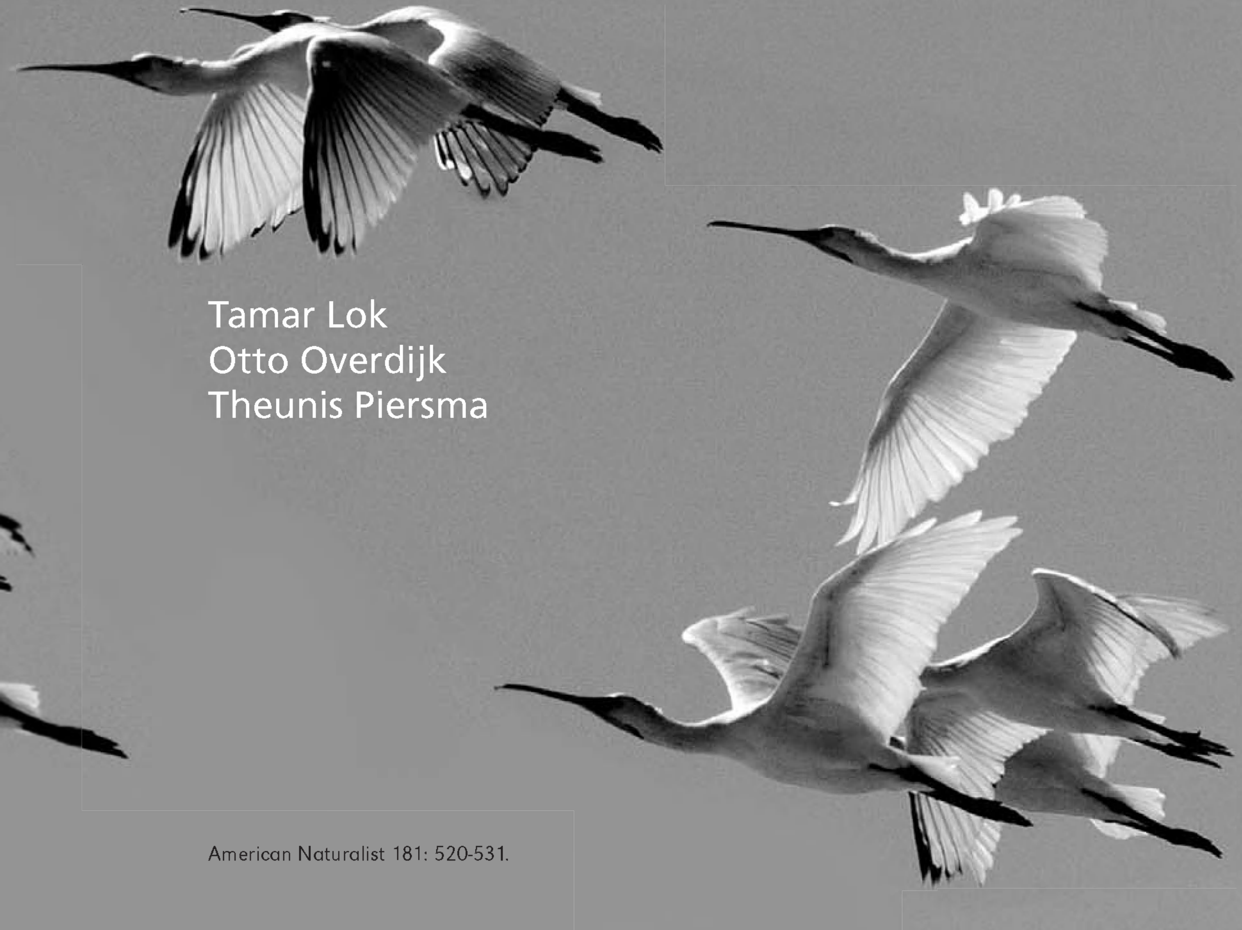
Table III.1 The number of spoonbills ringed, resighted in winter and resighted per wintering region, specified per year of birth, and the number of different birds resighted per winter.

Year of birth	Ringed	Resighted in winter	Resighted per wintering region			Winter	Number of different birds resighted per winter		
			France	Iberia	Mauritania & Senegal		France	Iberia	Mauritania & 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.

Chapter 7

Migration tendency delays distributional response to differential survival prospects along a flyway



Tamar Lok
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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 2095 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. Whilst 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.

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 animals utilize available sites in a preemptive manner and distribute according to the ideal preemptive distribution (Fig. 7.1; Kluyver & Tinbergen 1953; Brown 1969; Pulliam and Danielson 1991). This hypothesis assumes that sites differ in suitability for survival and/or reproduction (Fig. 7.1A), 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. 7.1B). The interference hypothesis predicts that all individuals have equal fitness and distribute according to the ideal free distribution (Fig. 7.1; 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. 7.1A, 7.1C), or (2) because interference mechanisms reduced the suitability of the higher quality habitat to the level of the lower (interference; Fig. 7.1B, 7.1D). 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. 7.1E). The interference hypothesis predicts changes in vital rates within individuals (hence within sites) and similar vital rates among sites at any one moment (i.e. at any specific total population size; Fig. 7.1F).

The two hypotheses have been widely tested with respect to small-scale habitat use in territorial animals during either the breeding or non-breeding 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; Morris 1991; Ferrer & Donazar 1996; Rodenhouse *et al.* 2003; Gunnarsson *et al.* 2005b; Nevoux *et al.* 2011) and survival (Holbrook & Schmitt 2002; Latta & Faaborg 2002; Studds & Marra 2005; Nevoux *et al.* 2011). While interference mecha-

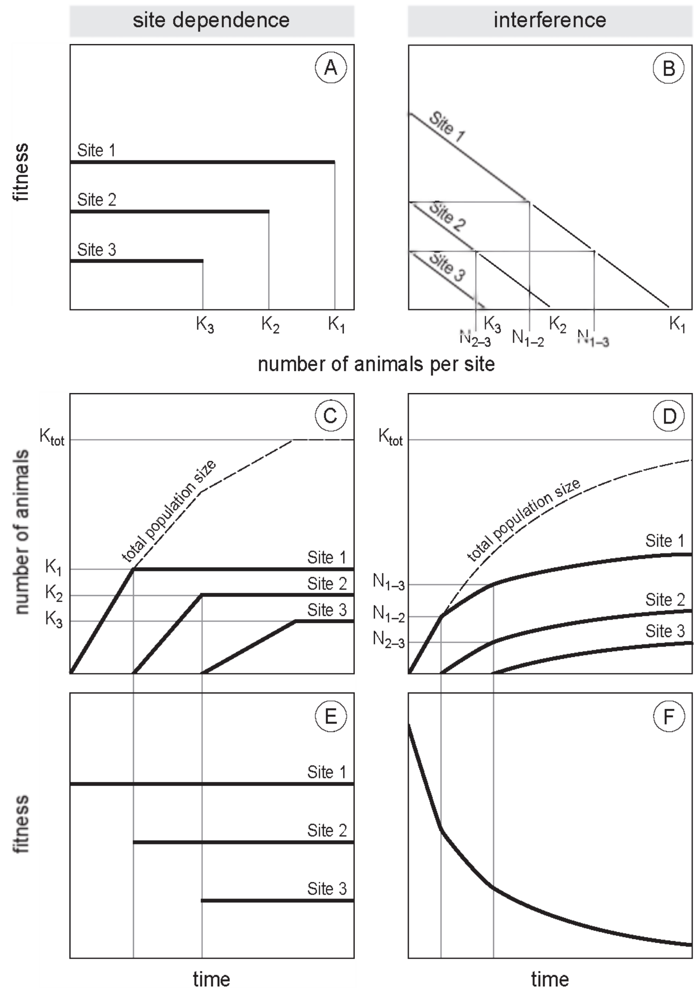

Figure 7.1 Assumptions and predictions of the site dependence and interference hypothesis (left versus right column). In (A, B), hypothetical relationships between the number of animals and individual fitness are shown for three sites that differ in quality (i.e. in maximum fitness). For graphical clarity, the carrying capacities, i.e. the maximum number of individuals that each site can harbour (K_1, K_2, K_3) differ between panel A and B, but the total maximum number of individuals over all sites (K_{tot}, see panel 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 harbours at least $N_{1\text{-}2}$ individuals, and site 3 when site 1 harbours at least $N_{1\text{-}3}$ and site 2 $N_{2\text{-}3}$ individuals. In (C, D), the predicted distribution of animals over the different sites and in (E, F) individual fitness within each site over time, i.e. during population growth, are shown.

nisms, 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 non-breeding 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 inter-site 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 (inter-site distances up to 1000 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 4000 km (Lok *et al.* 2011). During the 16-year study period from 1994 to 2010, the number of breeding pairs has increased almost 4-fold to approximately 2300; 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 northward migration (Lok *et al.* in press, Chapter 5), suggesting that, similar to the Icelandic godwits (Gill *et al.* 2001), density-dependent effects on survival occurred during the non-breeding 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 or interference hypothesis can explain the hemispheric winter distribution of adult spoonbills along the East Atlantic flyway. Applying the recently developed multievent mark-recapture modelling technique (Pradel 2005; Choquet, Rouan & Pradel 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. 7.1C, 7.1D; 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. 7.1E; prediction 2), or survival is the same in all occupied regions and decreases at equal rates within regions (interference: Fig. 7.1F; 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. 7.2). 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, 5092 spoonbills were colour-ringed before fledging. The recorded observations of these colour-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 only come to light when birds migrate, our analysis was restricted to adult birds. Immature birds generally remain in the wintering areas and only return to the Netherlands in their 3rd year to begin breeding (Lok *et al.* 2011). We considered individuals as adult from their 3rd winter, i.e. just prior to their first northward migration to the breeding grounds, and onward. For this study, we selected data of spoonbills that had been colour-ringed as chicks in the Netherlands between 1988 and 2007, and who were then resighted as adult between 1994 and 2010 (N = 2095), either in summer in the Netherlands (n=1931) 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 Appendix IV, Table IV.1). Data prior to 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 over-parameterization 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 Appendix IV, Fig. IV.1).

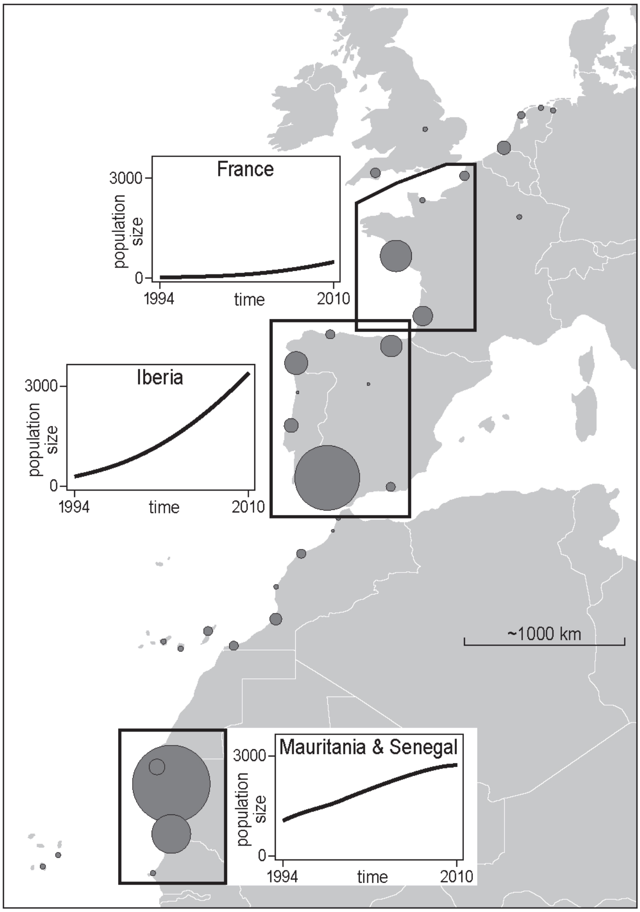

Figure 7.2 Map of the three wintering regions. The dots represent the sites where birds have been resighted and the size of the dots reflects the number of different colour-ringed birds observed in winter. The graphs show the estimated number of wintering Dutch spoonbills (for assumptions and calculations, see Appendix IV, Section IV.1) in each region over time and have the same scales on the axes.

Multievent mark-recapture modelling

Multievent mark-recapture models are a special type of multistate models, where observations ('events') and states are decoupled, resulting in a flexible modelling framework that allows the implementation of state uncertainty (Pradel 2005; Pradel 2009). In our case, the state of an individual is related to its wintering area. We defined 4 states: 'wintering in France' (F), 'wintering in Iberia' (I), 'wintering in Mauritania or Senegal' (MS) and 'dead' (D); and 5 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 only observed 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 parameters: 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:

$$\mathbf{\Pi_t} = \begin{array}{ccc} F & I & MS \\ [\ \pi_F & \pi_I & 1 - \pi_F - \pi_I\ ]. \end{array}$$

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, i.e. during population growth, we modelled 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:

$$\mathbf{\Phi_t} = \begin{array}{c} \\ F \\ I \\ MS \\ D \end{array} \begin{array}{c} \begin{array}{cccc} F & I & MS & D \end{array} \\ \left[\begin{array}{cccc} \Phi_F & 0 & 0 & 1 - \Phi_F \\ 0 & \Phi_I & 0 & 1 - \Phi_I \\ 0 & 0 & \Phi_{MS} & 1 - \Phi_{MS} \\ 0 & 0 & 0 & 1 \end{array}\right] \end{array}.$$

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 (Lok *et al.* in press, Chapter 5), we assumed survival in the summer-winter interval ($\Phi_{\text{s-w}}$) to be constant (c) and survival in the winter-summer interval ($\Phi_{\text{w-s}}$) to be density dependent. The metapopulation of spoonbills (Western European and Mauritanian breeding populations mix in winter) has increased over time (Lok *et al.* in press, Chapter 5), 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 modelled $\Phi_{w\text{-}s}$ 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 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 to 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:

$$\boldsymbol{B_t} = \begin{array}{c} \\ F \\ I \\ MS \\ D \end{array} \begin{array}{ccccc} \text{'0'} & \text{'1'} & \text{'2'} & \text{'3'} & \text{'4'} \\ \end{array}$$

$$\boldsymbol{B_t} = \begin{array}{c|ccccc} & \text{'0'} & \text{'1'} & \text{'2'} & \text{'3'} & \text{'4'} \\ \hline F & 1-p_{s,FI}-p_{w,F} & p_{s,FI} & p_{w,F} & 0 & 0 \\ I & 1-p_{s,FI}-p_{w,I} & p_{s,FI} & 0 & p_{w,I} & 0 \\ MS & 1-p_{s,MS}-p_{w,MS} & p_{s,MS} & 0 & 0 & p_{w,MS} \\ D & 1 & 0 & 0 & 0 & 0 \end{array}$$

Resighting probabilities in winter (p_W) were modelled as a function of year (t) and wintering state. Resighting probabilities in summer (p_S) were modelled 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 modelled 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) $\Phi_{s\text{-}w}$(c,c,c) $\Phi_{w\text{-}s}$(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 yet available for multievent models. To get an estimate of the level of overdispersion in our dataset, 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) $\Phi_{s\text{-}w}(g)$ $\Phi_{w\text{-}s}(g \cdot T)$ $p(g \cdot t)$ using the median c-hat approach in program MARK (White & Burnham 1999). In this model the winter resighting probability of group 4 was fixed to zero. The level of overdispersion, caused by extra-binomial variation, was estimated at $\hat{c} = 1.16 \pm 0.01$ S.E.

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 modelled by first testing reduced parameterizations for initial state probabilities and then for survival probabilities. When multiple models were supported at step 1 ($\Delta QAIC_c <2$), 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 modelled 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 8 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 modelling an additive linear 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 overdisperson ($QAIC_c$, Burnham & 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 & 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 summer-winter survival (Table 7.1), 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. 7.3A). 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 Appendix IV, Fig. IV.2). This was demonstrated by the fact that removing the effect of state for summer-winter survival from model 1 (Table 7.1, using model 2 gave similar results) substantially reduced the model fit ($\Delta QAIC_c = 9.68$), whereas removing the state effect for winter-summer survival did not ($\Delta QAIC_c = -0.44$). When testing for each wintering state separately, there was substantial evidence for a decrease in winter-summer survival (model 2, Table 7.1) for Iberia and West Africa (Iberia: model 2 vs.

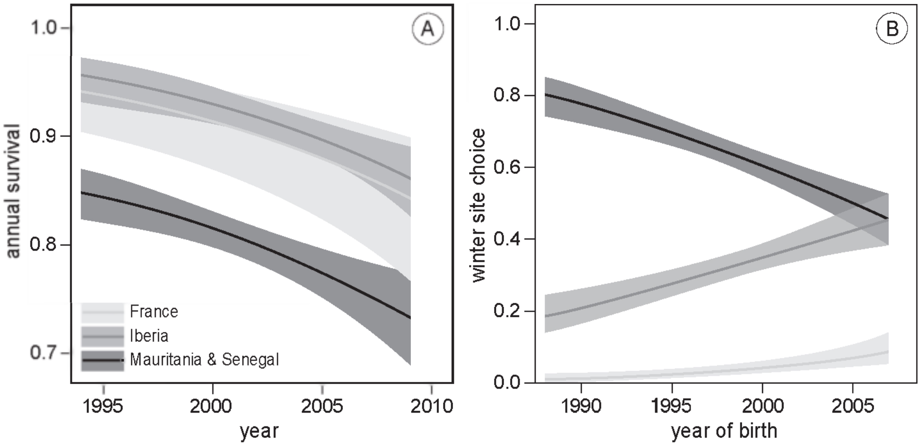

Figure 7.3 (A) Annual survival and (B) initial state probabilities, the probabilities to choose to winter in France, Iberia or Mauritania and Senegal, as a function of year and year of birth, estimated from the best-supported model (model 1, Table 7.1). Lines and shaded areas represent means and 95% 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).

Table 7.1 Model selection results for initial state probabilities (p) modelled constant (c) or as a function of year of birth (yb) and survival from winter to summer ($\Phi_{W\text{-}S}$), 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 modelled as in the full model ($\Phi_{S\text{-}W}$ (c,c,c) p_{NL} (t1,t1,t2) p_W (c,t,t)). Results are adjusted for overdispersion ($\hat{c}$ = 1.16, see Methods).

Model	Description		K	ΔDeviance	$\Delta QAIC_c$	Model weight
1	μ(yb, yb, yb)	$\Phi_{W\text{-}S}$ (T+,T+,T+)	76	0.73	0.00*	0.75
2	μ (yb, yb, yb)	$\Phi_{W\text{-}S}$ (T,T,T)	78	0.00**	3.46	0.13
3	μ (yb, yb, yb)	$\Phi_{W\text{-}S}$ (c,T,T)	77	3.40	4.34	0.09
4	μ (yb, yb, yb)	$\Phi_{W\text{-}S}$ (T,T,c)	77	6.95	7.41	0.02
5	μ (yb, yb, yb)	$\Phi_{W\text{-}S}$ (c,T,c)	76	10.96	8.82	0.01
6	μ (yb, yb, yb)	$\Phi_{W\text{-}S}$ (T,c,T)	77	13.13	12.73	0.00
7	μ (yb, yb, yb)	$\Phi_{W\text{-}S}$ (c,c,T)	76	16.21	13.34	0.00
8	μ (yb, yb, yb)	$\Phi_{W\text{-}S}$ (T,c,c)	76	23.56	19.68	0.00
9	μ (yb, yb, yb)	$\Phi_{W\text{-}S}$ (c,c,c)	75	26.87	20.48	0.00
10	μ (c,c,c)	$\Phi_{W\text{-}S}$ (T,T,T)	76	47.73	40.51	0.00

* $QAIC_c$ = 16198.04
** Deviance = 18610.75

model 6, $\Delta QAIC_c$ = -9.27; Mauritania and Senegal: model 2 vs. model 4, $\Delta QAIC_c$ = -3.95, Table 7.1), but not for France (model 2 vs. model 3, $\Delta QAIC_c$ = -0.88, Table 7.1).

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 versus model 10, $\Delta QAIC_c$ = -37.06, Table 7.1, Fig. 7.3B).

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 (Chapter 9), 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 poorer 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 non-territorial 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. IV.2). 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. 7.3B), 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 prior to 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 & 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, Hu & Jiang 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 & 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 7.2; for assumptions and calculations, see Appendix IV, Section IV.1) 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. 7.4; Appendix IV, Section IV.2). 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 & 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 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. 7.4).

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 & 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 & Simmons 1977). While the two European breeding populations are migratory, with their main wintering areas located in Mauritania and Senegal (de le Court & Aguilera 1997; Lok *et al.* 2011), the breeding population in Mauritania is resident (Cramp & 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 populations.

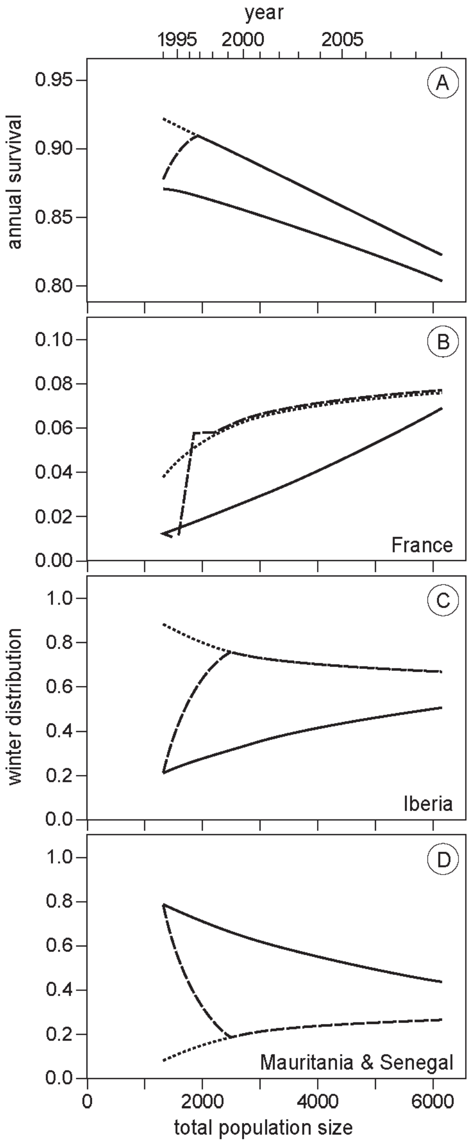

Figure 7.4 Adult survival and winter distribution over time and during population growth. The solid lines represent the estimated actual (A) population-level annual survival and proportion of adult birds wintering in (B) France, (C) Iberia and (D) Mauritania and Senegal (for assumptions and calculations, see Appendix IV, Section IV.1). The dotted lines represent survival and distribution if birds had been ideal free distributed over the three wintering regions (see Appendix IV, Section IV.2). 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, i.e. 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.

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 & 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 as a cue for the suitability of a site for wintering, rather than just using it for staging in preparation for onward movements. 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 prospects 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 programme 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).

Acknowledgements

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APPENDIX IV

Table IV.1 The number of spoonbills ringed and resighted as adult in summer and/or winter, specified per year of birth, and the number of different adult spoonbills resighted per summer and/or winter, where the winter of '94-'95 is, for example, referred to as winter 1994.

Year of birth	Ringed	Resighted				
		Total	Summer	Winter		
				France	Iberia	Mauritania & Senegal
1988	109	28	28	1	5	3
1989	130	34	34	0	5	6
1990	152	44	44	0	4	15
1991	177	70	66	2	4	16
1992	279	126	120	2	11	27
1993	271	139	136	4	12	31
1994	300	180	171	1	22	34
1995	0					
1996	233	112	97	2	13	40
1997	221	96	85	4	10	42
1998	214	91	81	0	13	24
1999	330	167	155	6	26	21
2000	195	90	84	1	19	12
2001	265	138	128	10	30	18
2002	184	74	72	1	14	10
2003	301	128	121	4	21	21
2004	393	125	110	3	17	23
2005	395	160	128	3	11	50
2006	460	172	157	10	21	15
2007	483	121	114	2	6	4

Year	Number of different birds resighted			
	Summer	Winter		
		France	Iberia	Mauritania & Senegal
1994	92	3	5	6
1995	156	4	7	8
1996	245	4	22	43
1997	359	6	11	53
1998	318	2	20	59
1999	283	7	10	69
2000	279	7	12	86
2001	289	9	22	1
2002	375	7	22	9
2003	344	14	58	17
2004	362	7	54	8
2005	323	7	64	27
2006	425	14	38	40
2007	474	21	70	96
2008	409	17	51	61
2009	537	8	39	17
2010	615			

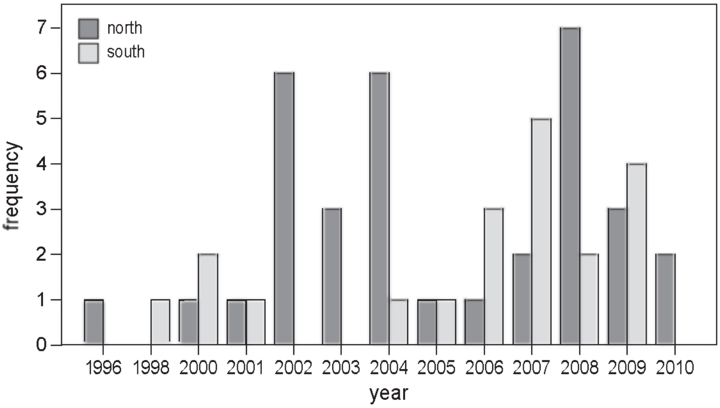

Figure IV.1 The number of within-individual changes in wintering region (N = 54) against the year when the change was observed, grouped by changes northward (dark grey, from Mauritania and Senegal to France or Iberia and from Iberia to France) or southward (light grey, from France to Iberia or Mauritania and Senegal and from Iberia to Mauritania and Senegal). 49 individuals changed wintering region (out of total of 832 individuals, thus comprising 6.2 % of the population), of which 5 changed back again to their previous wintering region. 45 cases concerned movement between Mauritania and Senegal and Iberia. Overall, more individuals moved north (N = 34) than south (N = 20). Especially in 2002, 2004 and 2008, many individuals changed from wintering in Mauritania and Senegal to wintering in Europe (i.e., they moved north). However, between 2000 and 2005, winter resighting probabilities in Europe (France and Iberia) were much higher than in Mauritania and Senegal (Fig. IV.2F), so the probability to observe a northward change was much higher than to observe a southward change in these years. Interpretation of the absolute numbers of changes should thus be done carefully, by taking into account differences in region-specific resighting probabilities.

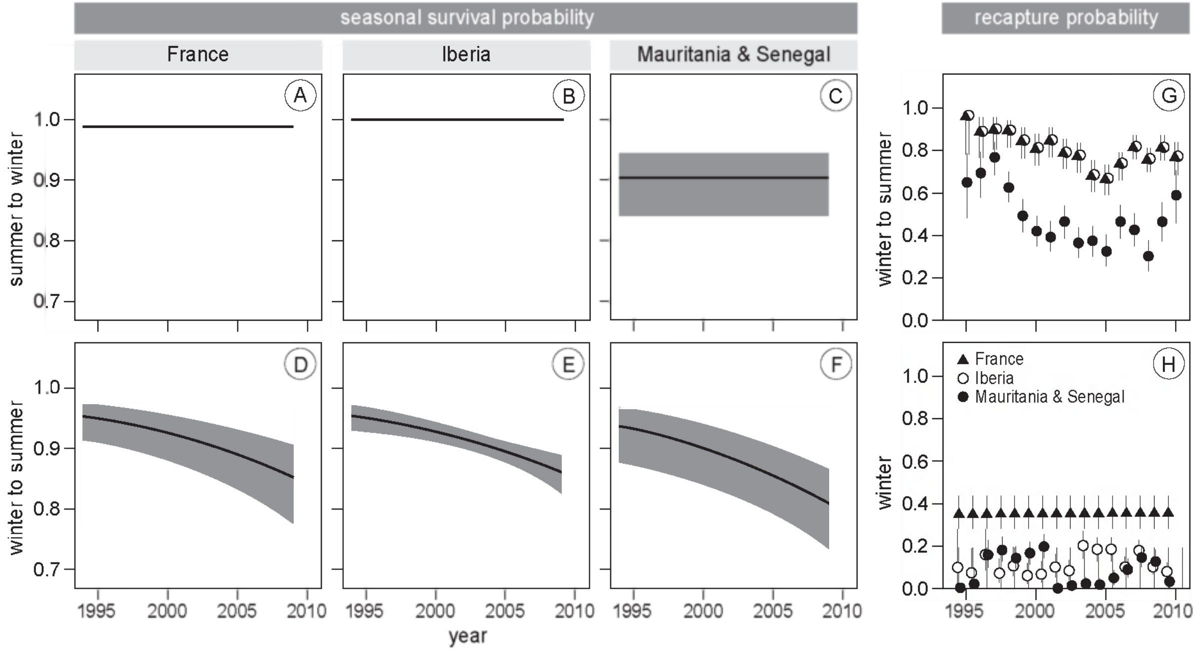

Figure IV.2 Survival (A-C) from summer to winter and (D-F) from winter to summer and recapture probability in (G) summer and (H) winter. Estimates shown are of the best-supported model (model 1, Table 7.1).

Section IV.1. Actual wintering distribution and population-level annual survival

To get from the estimated changes in initial state and annual survival probabilities (see Fig. 7.3) to the number of adult Dutch spoonbills wintering in each region, we assumed constant reproductive output ($f = 0.65$, the number of female offspring produced per adult female). This value of f gave a good fit between predicted and observed development of the number of breeding pairs in the Netherlands (Lok *et al.* in press, Chapter 5). We used immature survival parameters from Lok *et al.* (in press, Chapter 5), estimated separately for age 0 to age 1 ($S_1 = 0.56$), age 1 to age 2 ($S_2 = 0.91$) and age 2 to age 3 ($S_3 = 0.95$). We applied a pre-breeding census stage-structured population matrix model (Caswell 2001), which is compactly written as: $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$.
The stage vector $\mathbf{n}(t)$ is defined as:

$$\mathbf{n}(t) = \begin{bmatrix} N_1 \\ N_2 \\ N_{ad,F} \\ N_{ad,I} \\ N_{ad,MS} \end{bmatrix}_t$$

where N_i represents the number of females in each age class (N_1, N_2, N_{ad}) with the adult age class divided into three wintering region classes ($N_{ad,F}$, $N_{ad,I}$, $N_{ad,MS}$). Assuming no annual movements between wintering regions, the stage-structured projection matrix $\mathbf{A}$ becomes:

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & fS_1 & fS_1 & fS_1 \\ S_2 & 0 & 0 & 0 & 0 \\ 0 & S_3\pi_{F(yb)} & S_{F(T)} & 0 & 0 \\ 0 & S_3\pi_{I(yb)} & 0 & S_{I(T)} & 0 \\ 0 & S_3\pi_{MS(yb)} & 0 & 0 & S_{MS(T)} \end{bmatrix}_t$$

We assumed that the total number of adult females at the start of the study ($N_{ad,t0}$, with $t_0 = 1994$) was 661 (equal to the number of breeding pairs in the Netherlands in 1994, Lok *et al.* 2009) and that numbers of adult females in each wintering region ($N_{ad,F}$, $N_{ad,I}$, $N_{ad,MS}$) were proportional to the initial state probabilities. As Π was a function of year of birth and birds that are adult in 1994 were born in 1991 or earlier, we used the estimated initial state probabilities averaged over the years of birth 1988 to 1991 (Fig. 7.3B). Numbers of birds in the immature age classes in 1994 were estimated as: $N_{1,t0} = N_{ad,t0}S_1f$ and $N_{2,t0} = N_{1,t0}S_2$.

Demonstration of effects of some assumptions on population size estimates

In the above matrix, we assumed constant immature survival and no annual movement between wintering areas. However, Lok *et al.* (in press, Chapter 5) found substantial evidence for an effect of population size on age-specific survival between 1988 and 2010: a quadratic effect on S_1 (= $0.67 - 0.031N_z - 0.161N_z^2$) and linear effects on S_2 (= $0.91 - 0.044N_z$) and S_3 (= $0.95 - 0.032N_z$) where $N_z = \frac{N-\bar{N}}{\sigma}$, $\bar{N} = 1175$ and $\sigma = 585$. Moreover, despite the high fidelity (92-94%) of adult spoonbills to their chosen wintering region (Lok *et al.* 2011), there is still some probability of movement between wintering regions. To test the effects of density-dependent effects on immature survival and movement between wintering regions, we extended the matrix, where fid_i = fidelity to region *i* and $\mu_{i\text{-}j}$ = movement probability (when not faithful) from region *i* to *j*:

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & fS_{1(N)} & fS_{1(N)} & fS_{1(N)} \\ S_{2(N)} & 0 & 0 & 0 & 0 \\ 0 & S_{3(N)}\pi_{F(yb)} & S_{F(T)}fid_F & S_{I(T)}(1-fid_I)\mu_{I\text{-}F} & S_{MS(T)}(1-fid_{MS})\mu_{MS\text{-}F} \\ 0 & S_{3(N)}\pi_{I(yb)} & S_{F(T)}(1-fid_F)\mu_{F\text{-}I} & S_{I(T)}fid_I & S_{MS(T)}(1-fid_{MS})\mu_{MS\text{-}I} \\ 0 & S_{3(N)}\pi_{MS(yb)} & S_{F(T)}(1-fid_F)\mu_{F\text{-}MS} & S_{I(T)}(1-fid_I)\mu_{I\text{-}MS} & S_{MS(T)}fid_{MS} \end{bmatrix}_t$$

We used the values estimated by Lok *et al.* 2011: $fid_F = 0.94$, $fid_I = 0.94$, $fid_A = 0.92$, $\mu_{F\text{-}I} = \mu_{F\text{-}MS} = 0.5$, $\mu_{I\text{-}F} = 0.06$, $\mu_{I\text{-}MS} = 0.94$, $\mu_{MS\text{-}F} = 0.10$, $\mu_{MS\text{-}I} = 0.90$). The estimated population sizes using constant or density-dependent immature survival and no or some movement between wintering regions are shown in Appendix IV, Fig. IV.3. As can be seen, the estimated population sizes do not differ that much. Because the estimated initial state probabilities and survival came from a multi-event mark-recapture model that assumed no movement and for graphical clarity, we decided to use the matrix model with constant immature survival and no between winter movements for estimating population sizes (Fig. 7.2) and ideal free and observed distribution patterns (Fig. 7.4). Using the estimated number of adult birds wintering in each region (Fig. 7.2), we calculated the population-level decrease in adult annual survival (Fig. 7.4A) from the proportions of birds wintering in each region (Fig. 7.4B-D) and the region-specific annual survival estimates (Fig. 7.3A):

$$\Phi_{pop} = \frac{N_{ad,F}}{N_{ad,tot}}\,\Phi_F + \frac{N_{ad,I}}{N_{ad,tot}}\,\Phi_I + \frac{N_{ad,MS}}{N_{ad,tot}}\,\Phi_{MS}$$

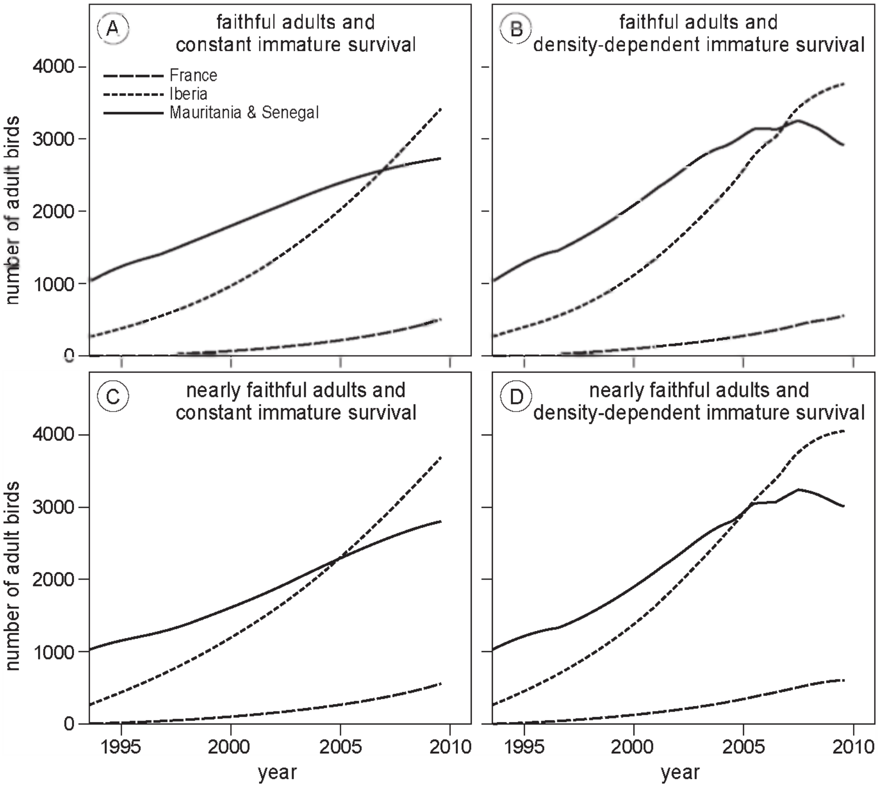

Figure IV.3 The estimated number of adults from the Netherlands in each wintering region under different assumptions (A-D).

Section IV.2. Annual survival with an ideal free wintering distribution

To calculate the ideal free wintering distribution, we assumed (1) that all individuals are equal and (2) that the decrease in survival as observed in each wintering region was caused by local density dependence. To estimate the strength of density dependence in each wintering region, we assumed linear relationships between local wintering population size (estimated number of adult Dutch spoonbills, see Fig. 7.2 and Appendix IV, Section IV.1) and region-specific annual survival (Fig. 7.3A). These relationships are shown in Appendix IV, Fig. IV.4.
The region-specific equations are:

$$\Phi_F = \alpha_F + \beta_F N_F$$
$$\Phi_I = \alpha_I + \beta_I N_I$$
$$\Phi_{MS} = \alpha_{MS} + \beta_{MS} N_{MS}$$

with the following estimates: $\alpha_F = 0.935$, $\alpha_I = 0.967$, $\alpha_{MS} = 0.922$, $\beta_F = -2.67 \cdot 10^{-4}$, $\beta_I = -3.86 \cdot 10^{-5}$ and $\beta_{MS} = -7.23 \cdot 10^{-5}$.
From Fig. IV.4 it can be seen that at low population sizes, all animals should winter in Iberia, where they can achieve the highest survival, until

$$\Phi_{F(N=0)} = \Phi_I$$

which happens when Iberia reaches size:

$$\alpha_F + \beta_F \cdot 0 = \alpha_I + \beta_I N_{I\rightarrow F}$$

$$N_{I\rightarrow F} = \frac{\alpha_F - \alpha_I}{\beta_I}$$

For $N_{tot} > N_{I\rightarrow F}$, animals should also start to occupy France, until France has the size:

$$\Phi_F = \Phi_{MS(N=0)}$$
$$\alpha_F + \beta_F \cdot N_{F\rightarrow MS} = \alpha_{MS} + \beta_{MS} \cdot 0$$
$$N_{I\rightarrow MS} = \frac{\alpha_{MS} - \alpha_F}{\beta_F}$$

and Iberia the size:

$$N_{I\rightarrow MS} = \frac{\alpha_{MS} - \alpha_I}{\beta_I}$$

When only France and Iberia are being occupied ($N_{I\rightarrow F} > N_{tot} > N_{I\rightarrow MS} + N_{F\rightarrow MS}$), birds should distribute over both Iberia and France so that survival is equal in both sites:

$$
\begin{aligned}
\Phi_F &= \Phi_I \\
\alpha_F + \beta_F \cdot N_F &= \alpha_I + \beta_I N_I \\
\alpha_F + \beta_F \cdot N_F &= \alpha_I + \beta_I\,(N_{tot} - N_F) \\
(\beta_F + \beta_I) \cdot N_F &= \alpha_I - \alpha_F + \beta_I N_{tot} \\
N_F &= \frac{\alpha_I - \alpha_F + \beta_I N_{tot}}{\beta_F + \beta_I}
\end{aligned}
$$

and

$$N_I = \frac{\alpha_F - \alpha_I + \beta_F N_{tot}}{\beta_I + \beta_F} \quad (= N_{tot} - N_F)$$

For $N_{tot} > N_{I \rightarrow MS} + N_{F \rightarrow MS}$, (i.e. $N_I > \frac{\alpha_{MS} - \alpha_I}{\beta_I}$, $N_I > \frac{\alpha_{MS} - \alpha_F}{\beta_I}$ and $N_{MS} > 0$) birds should distribute over all three wintering regions, with equal survival in all three regions:

$$\Phi_F = \Phi_I = \Phi_{MS}$$

Using the equations $\Phi_I = \Phi_F$ and $\Phi_{MS} = \Phi_F$ we can calculate N_I for a given N_{tot} ($= N_F + N_I + N_{MS}$) as follows:

(1) $\Phi_I = \Phi_F$

$$
\begin{aligned}
\alpha_I + \beta_I N_I &= \alpha_F + \beta_F N_F = \alpha_F + \beta_F (N_{tot} - N_I - N_{MS}) \\
(\beta_I + \beta_F) N_I &= \alpha_F - \alpha_I + \beta_F\,(N_{tot} - N_{MS})
\end{aligned}
$$

(2) $\Phi_{MS} = \Phi_F$

$$
\begin{aligned}
\alpha_{MS} + \beta_{MS} N_{MS} &= \alpha_F + \beta_F N_F = \alpha_F + \beta_F (N_{tot} - N_I - N_{MS}) \\
(\beta_{MS} + \beta_F) N_{MS} &= \alpha_F - \alpha_{MS} + \beta_F\,(N_{tot} - N_I) \\
N_I &= \frac{\alpha_F - \alpha_{MS} + \beta_F\,(N_{tot} - N_I)}{\beta_{MS} + \beta_F}
\end{aligned}
$$

Substituting equation 2 into equation 1 gives

$$(\beta_I + \beta_F) N_I = \alpha_F - \alpha_I + \beta_F\, N_{tot} - \beta_F \frac{\alpha_F - \alpha_{MS} + \beta_F\,(N_{tot} - N_I)}{\beta_{MS} + \beta_F}$$

$$((\beta_I + \beta_F)(\beta_{MS} + \beta_F) - \beta_F{}^2) N_I = (\alpha_F - \alpha_I + \beta_F N_{tot})(\beta_{MS} + \beta_F) - \beta_F(\alpha_F - \alpha_{MS} + \beta_F N_{tot})$$

$$N_I = \frac{(\alpha_F - \alpha_I + \beta_F N_{tot})(\beta_{MS} + \beta_F) - \beta_F\,(\alpha_F - \alpha_{MS} + \beta_F N_{tot})}{(\beta_F + \beta_I)(\beta_F + \beta_I) - \beta_F{}^2}$$

With some rewriting this becomes:

$$N_I = \frac{\beta_{MS}\,(\alpha_F - \alpha_I + \beta_F N_{tot}) - \beta_F\,(\alpha_I - \alpha_{MS})}{\beta_{MS}\,(\beta_F + \beta_I) + \beta_F \beta_I}$$

Similarly, N_F and N_{MS} ($= N_{tot}$ - N_F - N_I) can be calculated. The population-level annual survival was calculated as $\Phi_I = \alpha_I + \beta_I N_I$ in combination with the relationship between

N_I and N_{tot}. The calculated ideal free wintering distribution as a function of total population size, and the population-level annual survival that could have been achieved by distributing as such, are shown in Fig. 7.4.

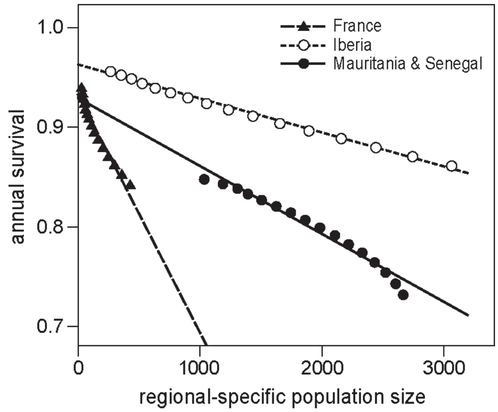

Figure IV.4 Estimated relationships between region-specific annual survival and wintering population sizes (number of adult birds from the Netherlands). Population sizes are estimated from the matrix that assumed constant immature survival and no movements between winter regions (Fig. IV.3). Note that survival is plotted against population size, not population density. To determine population density (i.e., population size per unit suitable winter habitat surface) is very hard, if not impossible, due to the variability and dynamical nature of feeding habitats used by spoonbills. Consequently, the intercept of the lines with the y-axis should not be interpreted as a measure of winter site quality.

Part III

A demographic cost-benefit analysis of differential migration

Chapter 8

Migration sometimes takes a toll: spoonbills suffer higher mortality during longer northward migrations

Tamar Lok
Otto Overdijk
Theunis Piersma

ABSTRACT

The wide variety of migration patterns throughout the animal kingdom has intrigued many biologists and led to the development of numerous theories to explain this variation. These theories all assume that migration is costly and that this cost increases with migration distance. Although some studies investigated the relationship between migration distance and breeding success or annual survival, none have investigated whether mortality during the actual migration (or potentially in the next season, through a carry-over effect) increases with migration distance. Here we estimated such seasonal survival of Eurasian spoonbills that breed in the Netherlands and have different migration strategies (i.e. different migration distances and wintering areas). Resighting periods at the start and end of the summer and at the start and end of the winter in different wintering regions (France, Iberia and Mauritania), allowed us to distinguish among survival during summer, autumn migration, winter and spring migration. We show that summer, autumn and winter survival were very high (near unity) and independent of migration strategy, whereas mortality during spring migration was much higher (21%) for the birds that winter in Mauritania, compared to those flying only as far as France (2%) or Iberia (5%). To conclude, this study showed, for the first time, that migrating far is associated with increased mortality during migration, suggesting a mortality cost of migration.

INTRODUCTION

Migration – the regular seasonal movement of individuals, often from a breeding location to a non-breeding location and back – is a common and taxonomically widespread phenomenon throughout the animal kingdom (Dingle 1980). Migration is considered as an adaptation to exploit seasonal peaks in resource abundance for reproduction, and to avoid seasonal resource depression during the non-breeding period by migrating to more benign, lower latitude, areas, while paying some cost for travelling between breeding and non-breeding area. There is much variation in migration patterns, between species, within species and even within (breeding or wintering) populations of the same species (Alerstam 1990; Newton 2008).

Many theories have been developed to explain the enormous variation in migration patterns (Ketterson & Nolan 1976; Greenberg 1980; Myers 1981; Gauthreaux 1982; Alerstam, Hedenstrom & Akesson 2003). These theories all assume that migration is costly, and that this cost increases with migration distance. This cost may be direct, causing reduced survival during migration, or it may carry over to the next season, reducing subsequent survival or reproductive output. Several studies on migratory birds (mainly geese) have estimated survival during different seasons of the year (Clausen *et al.* 2001; Gauthier *et al.* 2001; Madsen, Frederiksen & Ganter 2002; Juillet *et al.* 2011), but only three were able to separate mortality during migration from that during the stationary periods. Sillett & Holmes (2002) estimated mortality during migration from survival during breeding and wintering survival based on two (potentially unlinked) populations of black-throated blue warblers *Dendroica caerulescens* and showed that 85% of the mortality occurred during migration. In contrast, survival of trumpeter swans *Cygnus buccinator*, was high and similar during stationary and migratory seasons (Varner & Eichholz 2012). Although Leyrer *et al.* (2013) were not able to separate the migratory seasons from the breeding seasons, they showed that virtually all mortality of the long-distance migrating red knots *Calidris canutus canutus* occurred at the wintering grounds, but shortly after arrival, suggesting that this mortality could have been a carryover cost of the migratory journey.

Studies that investigated whether the cost of migration increased with the distance migrated mainly focussed on its correlation with timing of arrival and breeding, with contrasting results (Hötker 2002; Gunnarsson *et al.* 2006). But whether direct or delayed mortality increases with migration distance has never been investigated. The only evidence is indirect, by comparing annual survival of closely related species, populations or individuals with varying migration distances. Some studies indeed found a negative relationship between migration distance and annual survival (Pienkowski & Evans 1985; Harrington, Hagen & Leddy 1988; Nichols & Johnson 1990). However, other studies found no relationship (Sandercock & Jaramillo 2002), or a positive relationship (Hestbeck, Nichols & Hines 1992; Sanz-Aguilar *et al.* 2012). Interpreting the results from these comparisons is difficult, because different species or populations (that do not share a breeding or wintering area) vary in many more aspects than just their migration distance, making it difficult to interpret the results of such a comparison. Even when the comparison is among individuals from the same breeding (e.g., Sanz-Aguilar *et al.* 2012) or wintering population, estimating annual survival is not appropriate for measuring the cost of migration, as animals may balance the mortality cost of migration with the survival benefit of wintering further away from the breeding grounds (i.e. in more tropical areas) (Greenberg 1980). What is needed is a comparison of survival during migratory and stationary periods of individuals with varying migration distances, while preferably keeping at least one of the seasons similar for all individuals (that is, comparing individuals with varying migration distances that either share their breeding or wintering area).

We appear the first to here make such a comparison of seasonal survival by comparing individuals that share their breeding area, and show considerable variation in migration distances and wintering areas (hereafter called 'migration strategies'). Our study population is the Eurasian spoonbill *Platalea leucorodia leucorodia* that breeds in the Netherlands and winters along the Atlantic coast between France and Senegal. Spoonbills are very faithful to their wintering area (Lok *et al.* 2011), allowing the comparison of seasonal survival rates among individuals with different migration strategies. We predict that (1) mortality during migration increases with migration distance (delayed cost of migration), (2) mortality during the breeding season increases with migration distance (indirect cost of migration), and (3) mortality during winter decreases with migration distance (benefit of wintering in tropical areas).

METHODS

Spoonbills have been colour-ringed as pre-fledged chicks in the Netherlands for more than 25 years. For this study, we relied on a large network of dedicated voluntary and professional ornithologists that read their rings throughout the European part of their geographical range. To allow the separation of the winter season from the migratory seasons for spoonbills wintering in West Africa, additional expeditions were organized to the Banc d'Arguin (Mauritania) in early winter (Dec 2005, Oct-Nov 2006, 2007, 2008) and late winter (Jan 2006, 2008, 2009, 2011, 2012) with the specific aim to read spoonbill colour-rings. In addition, we benefited from expeditions in December 2006-2011 by other researchers that performed ring-reading of spoonbills aside their main research activities (see Leyrer *et al.* 2012; van Gils *et al.* 2012). Due to lack of seasonal resightings in Senegal, we excluded birds wintering there.

We used resightings between October 2005 and September 2012. Four resighting periods and areas were defined: start of summer (April – June in the Netherlands), end of summer (July – September in the Netherlands), start of winter (October – December in an individual's wintering area) and end of the winter (January – March in an individual's wintering area). This allowed the estimation of survival during four seasons of 3 months: summer (mid-May – mid-August), autumn migration (mid-August – mid

November), winter (mid-November – mid-February) and spring migration (mid-February – mid-May). Although the resighting periods are long relative to the intervals over which survival is being estimated, the bias incurred from this has been shown to be relatively small, especially when mortality and resighting probabilities are lower than 50% (Hargrove & Borland 1994), and may even increase precision of the estimates (O'Brien, Robert & Tiandry 2005).

To be sure that we modelled seasonal survival for birds that migrate, we restricted the survival analysis to birds that were observed at least once as adult bird (3 years or older) in the Netherlands prior to the start of their encounter history. Although we cannot be sure that these individuals complete their migratory journeys and breed each year, the probability of skipping breeding is relatively low (Chapter 9). The wintering area of an individual was defined as the area where it was observed in its 2nd or later winter in December or January in France or Iberia (to minimize the probability that an individual was observed at a stopover rather than its wintering site), or between October and February in Mauritania (not used as a stopover). Although most spoonbills remain faithful to a single wintering area (Lok *et al.* 2011), some switched sites between winters, either prior or during the study period (N = 27), and were excluded from the analysis. Only birds of which their wintering area was known were included in the analysis. To avoid this selection to influence the survival estimates, the individual encounter histories were started at the first winter observation when this was at the age of 3 years or older, or at the first observation in any season when 3 years or older, when the first winter observation was before 3 years. This selection resulted in encounter histories of 345 birds, of which 40 wintered in France, 197 in Iberia and 108 in the Banc d'Arguin (Mauritania).

Based on previous results (Lok, Overdijk & Piersma 2013), we included annual variation in resighting probability during the summer periods in the Netherlands and during the winter periods in Iberia and Mauritania. Due to limited data, we modelled constant resightings probabilities for the winter periods in France. We tested for, but did not find, an effect of migration strategy on resighting probabilities during the summer periods in the Netherlands. We therefore assumed that resighting probabilities during the resighting periods in the Netherlands were independent of migration strategy.

To estimate seasonal survival, we used Cormack-Jolly-Seber (CJS) models (Lebreton *et al.* 1992). Our starting model was $\Phi^{\text{summer}}_{m}\ \Phi^{\text{autumn}}_{m}\ \Phi^{\text{winter}}_{m}\ \Phi^{\text{spring}}_{m}\ p^{s1}_{t}\ p^{s2}_{t}\ p^{w1,F}_{c}\ p^{w1,I}_{t}\ p^{w1,A}_{t}\ p^{w2,F}_{c}\ p^{w2,I}_{t}\ p^{w2,A}_{t}$, for which we tested goodness-of-fit using the median-$\hat{c}$ procedure implemented in program MARK (White & Burnham 1999). Median-$\hat{c}$ was estimated at $\hat{c} = 1.25 \pm 0.01$. Some survival parameters in the full model, but also in reduced models, were estimated at the boundary. We used the profile likelihood function to estimate confidence intervals around these boundary estimates. There may be several reasons for the occurrence of a boundary parameter: (1) it is not uniquely identifiable (intrinsic identifiability), (2) it is not estimable due to lack of data (extrinsic identifiability), or (3) this parameter is truly at the boundary (see

Leyrer *et al.* 2013 who reported similar analytical problems). Given the structural simplicity of our models (single state, no temporal variation in survival) all parameters were identifiable. To test whether the parameter was estimated at the boundary due to lack of data, we applied data cloning (see the manual of program MARK for a description, Cooch & White 2011). Survival estimates are reported as mean with 95% confidence interval.

Models were built in R (version 2.13.0, R Development Core Team 2011) using package RMark (Laake 2011) and then run using program MARK (White & Burnham 1999).

RESULTS

As assessed from cloning the data 100 times and checking whether the profile likelihood based 95% confidence intervals were reduced, the full model was unable to estimate winter survival of the birds wintering in France (model 8, Table 8.1, for cloning results, see Appendix V, Table V.1), the best-supported model was unable to estimate summer survival of birds wintering in France (model 1, Table 8.1, for cloning results, see Appendix V, Table V.2), but all survival parameters were estimable in the most parsimonious model (model 2, Table 8.1, for cloning results, see Appendix V, Table V.3). We found strong support for an effect of migration strategy on survival during spring migration (Table 8.1). Survival of trans-Sahara migrants during spring migration was 0.79 (0.73–0.85), compared to 0.98 (0.93–1.00) and 0.95 (0.91–0.99) for birds wintering in France and Iberia. We found some evidence for an effect of migration strategy on summer survival, being somewhat lower for Iberian winterers (0.97, 0.92-0.99, model 1, Table 8.1) than for French (1.00, 1.00–1.00) and Mauritanian winterers (1.00, 0.82–1.00), but there were indications that the summer survival of French winterers was inestimable (Table V.2). Moreover, this difference was rather small and confidence intervals were overlapping. In fact, the most parsimonious model, i.e. the model within 2 $QAIC_C$-points of the best-supported model that has the least parameters, does not include the effect of migration strategy on summer survival (model 2, Table 8.1). That summer survival was not lower in Mauritanian winterers leads to the rejection of prediction 2 of a delayed mortality cost of migration. Survival rates during autumn (0.99, 0.96-1.00) and winter (1.00, 0.96-1.00) were high and independent of an individual's migration strategy (Table 8.1) and leads to the rejection of prediction 3, that winter survival would be higher further south. Resighting probabilities of the best-supported model are shown in Appendix V, Fig. V.1.

We multiplied the seasonal survival estimates to derive annual survival estimates and applied the delta method based on the variance-covariance matrix on the probability (not logit) scale to derive the profile likelihood confidence intervals. This resulted in annual survival of 0.95 (0.88-0.98) for the birds wintering in France, 0.92 (0.89-0.94) for Iberian winterers and 0.77 (0.67-0.84) for birds wintering in Mauritania.

DISCUSSION

The main result from this study is that mortality during migration was higher in the longest-distance (trans-Sahara) migrating spoonbills that wintered in Mauritania, compared to those staying in Europe. This supports the main assumption of theories of the evolution of migration patterns that the cost of migration increases with the distance migrated. However, our results also showed that the increased mortality is not simply a function of the distance migrated, because (1) birds wintering in Iberia did not have increased mortality compared to the birds wintering in France, and (2) the increased mortality of trans-Sahara migrants was only manifested during spring migration, not during autumn migration.

Table 8.1 Model selection results for survival (Φ) during summer, autumn, winter and spring. Survival is modelled either as constant (c) or as a function of migration strategy (m). In all models, resighting probability was modelled as $p^{s1}_{t}\ p^{s2}_{t}\ p^{w1,F}_{c}\ p^{w1,I}_{t}\ p^{w1,A}_{t}\ p^{w2,F}_{c}\ p^{w2,I}_{t}\ p^{w2,A}_{t}$. Results have been adjusted for overdisperion ($\hat{c} = 1.25$). Competing models (within 2 $QAIC_c$ of the best-supported model, without uninformative parameters (Arnold 2010)) are shown in bold.

Model		K	Qdeviance	$\Delta QAIC_c$	Akaike weight
(1)	**$\Phi^{summer}_{m}\ \Phi^{autumn}_{c}\ \Phi^{winter}_{c}\ \Phi^{spring}_{m}$**	**50**	**2.79**	**0.00***	**0.28**
(2)	**$\Phi^{summer}_{c}\ \Phi^{autumn}_{c}\ \Phi^{winter}_{c}\ \Phi^{spring}_{m}$**	**48**	**7.13**	**0.13**	**0.26**
(3)	$\Phi^{summer}_{c}\ \Phi^{autumn}_{m}\ \Phi^{winter}_{c}\ \Phi^{spring}_{m}$	50	4.15	1.36	0.14
(4)	$\Phi^{summer}_{c}\ \Phi^{autumn}_{c}\ \Phi^{winter}_{m}\ \Phi^{spring}_{m}$	50	4.84	2.05	0.10
(5)	$\Phi^{summer}_{m}\ \Phi^{autumn}_{c}\ \Phi^{winter}_{m}\ \Phi^{spring}_{m}$	52	0.75	2.18	0.09
(6)	$\Phi^{summer}_{m}\ \Phi^{autumn}_{m}\ \Phi^{winter}_{c}\ \Phi^{spring}_{m}$	52	1.35	2.78	0.07
(7)	$\Phi^{summer}_{c}\ \Phi^{autumn}_{m}\ \Phi^{winter}_{m}\ \Phi^{spring}_{m}$	52	2.88	4.32	0.03
(8)	$\Phi^{summer}_{m}\ \Phi^{autumn}_{m}\ \Phi^{winter}_{m}\ \Phi^{spring}_{m}$	54	0.00**	5.66	0.02
(9)	$\Phi^{summer,autumn,winter,spring}_{m}$	45	20.24	6.94	0.01
(10)	$\Phi^{summer,winter}_{m}\ \Phi^{autumn,spring}_{m}$	48	14.41	7.42	0.01
(11)	$\Phi^{summer}_{c}\ \Phi^{autumn}_{c}\ \Phi^{winter}_{m}\ \Phi^{spring}_{c}$	48	21.06	14.06	0.00
(12)	$\Phi^{summer}_{m}\ \Phi^{autumn}_{c}\ \Phi^{winter}_{m}\ \Phi^{spring}_{c}$	50	18.06	15.27	0.00
(13)	$\Phi^{summer}_{c}\ \Phi^{autumn}_{m}\ \Phi^{winter}_{m}\ \Phi^{spring}_{c}$	50	19.32	16.53	0.00
(14)	$\Phi^{summer}_{m}\ \Phi^{autumn}_{m}\ \Phi^{winter}_{m}\ \Phi^{spring}_{c}$	52	17.33	18.76	0.00
(15)	$\Phi^{summer}_{m}\ \Phi^{autumn}_{c}\ \Phi^{winter}_{c}\ \Phi^{spring}_{c}$	48	29.33	22.33	0.00
(16)	$\Phi^{summer}_{m}\ \Phi^{autumn}_{m}\ \Phi^{winter}_{c}\ \Phi^{spring}_{c}$	50	28.06	25.27	0.00
(17)	$\Phi^{summer}_{c}\ \Phi^{autumn}_{m}\ \Phi^{winter}_{c}\ \Phi^{spring}_{c}$	48	33.35	26.35	0.00
(18)	$\Phi^{summer}_{c}\ \Phi^{autumn}_{c}\ \Phi^{winter}_{c}\ \Phi^{spring}_{c}$	46	41.09	29.89	0.00
(19)	$\Phi^{summer,winter}_{c}\ \Phi^{autumn,spring}_{c}$	44	51.64	36.24	0.00

* $QAIC_c = 4779.87$
** QDeviance = 3398.46

The very high survival during spring migration of birds wintering in Europe (France or Iberia) suggests that the main spring migration mortality of the birds wintering in Mauritania occurred during the crossing of the Sahara, or shortly after, when attempting to refuel in southern Spain. When crossing the Sahara during northward migration, trade winds cause a high incidence of headwinds at lower altitudes of flight, up to c. 2 km height (Piersma & van de Sant 1992; Shamoun-Baranes *et al.* 2010), which could reduce their migration speed and increase the necessary time in the air. Conversely, these trade winds result in a high incidence of tailwinds during autumn migration, which could also explain the absence of increased mortality during autumn migration. Rather than being caused by a direct effect during migration, the increased mortality could reflect a carry-over effect from poor fuelling conditions in the wintering areas in Mauritania and Senegal, or from poor refuelling conditions at stopover sites in southern Spain (Odiel marshes and Coto Doñana), that these birds use after having crossed the Sahara. Yet little is known about (poor) feeding conditions at wintering sites in West Africa or at stopover sites.

We found no support for the hypothesis that winter survival increases towards the tropics (Greenberg 1980) as winter survival was similar, and near unity, in all wintering areas. High winter survival was also found in black-throated blue warblers (Sillett & Holmes 2002), but not in red knots (Leyrer *et al.* 2013). However, the low winter survival of red knots may well have been a carryover effect from migration. Whether mortality is manifested during migration could depend on the type of migration. For example, the spoonbills wintering in Mauritania use many refuelling sites during their 4,500 km migration, whereas red knots migrate 9,000 km using a single stopover in the Wadden Sea (Leyrer *et al.* 2013), and only when necessary, a second in France (Shamoun-Baranes *et al.* 2010). Perhaps the morphology and physiology of red knots enabled them to fly these bouts of 4,500 km, even when conditions are not optimal and that costs will be paid only after arrival, whereas spoonbills are simply not able to fly such large distances at once, and may therefore also be more vulnerable to adverse conditions during their relatively short bouts of migration.

To enable generalization of our results, we now need to examine the causes of mortality during migration. For example, longer migrations are more likely to include a bottleneck, such as the crossing of a desert. Moreover, birds that migrate longer distances are more likely to encounter adverse weather conditions during migration, simply because they spend a longer time in the air (Newton 2007). In addition, studies on other species with varying body size, morphology and physiology are wanted, to better understand the generality of migration-associated mortality causes and patterns and the role of species-specific traits in determining the relationship between migration distance and direct or delayed mortality.

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APPENDIX V

Table V.1 Data cloning results for seasonal apparent survival parameters in year^{-1} of the full model. 95% confidence intervals (CI) were estimated using the profile likelihood function. In bold the parameters of which the 95% CI did not reduce after data-cloning, and were therefore considered as being inestimable.

Season	Wintering area	Original			Cloned (100x)			$SE_{original}$/ SE_{cloned}	$95\%CI_{original}$/ $95\%CI_{cloned}$	95% CI reduced?
		Mean	S.E.	95% CI	Mean	S.E.	95% CI			
Summer	France	1.00	0.00	0.87-1.00	1.00	0.00	1.00-1.00	256.83	19964.55	Y
Summer	Iberia	0.89	0.06	0.76-1.00	0.89	0.01	0.88-0.90	10.00	9.65	Y
Summer	Mauritania	1.00	0.00	0.82-1.00	1.00	0.00	1.00-1.00	n.a.	n.a.	Y
Autumn	France	0.99	0.04	0.84-1.00	0.99	0.00	0.98-1.00	10.00	8.90	Y
Autumn	Iberia	0.93	0.07	0.78-1.00	0.93	0.01	0.92-0.94	10.00	7.44	Y
Autumn	Mauritania	1.00	0.00	0.79-1.00	1.00	0.00	1.00-1.00	n.a.	n.a.	Y
Winter	**France**	**1.00**	**0.00**	**1.00-1.00**	**1.00**	**0.00**	**1.00-1.00**	**0.00**	**0.00**	**N**
Winter	Iberia	0.90	0.07	0.76-1.00	0.90	0.01	0.89-0.92	10.00	8.01	Y
Winter	Mauritania	1.00	0.00	0.68-1.00	1.00	0.00	1.00-1.00	7.43	850.57	Y
Spring	France	0.87	0.07	0.69-0.98	0.87	0.01	0.85-0.88	10.00	9.22	Y
Spring	Iberia	0.92	0.07	0.76-1.00	0.92	0.01	0.90-0.93	10.00	8.06	Y
Spring	Mauritania	0.36	0.05	0.26-0.48	0.36	0.01	0.36-0.37	10.00	11.04	Y

Table V.2 Data cloning results on seasonal apparent survival parameters in year^{-1} of the best-supported model (model 1, Table 8.1). For further details, see Table V.1.

Season	Wintering area	Original			Cloned (100x)			$SE_{original}$/ SE_{cloned}	$95\%CI_{original}$/ $95\%CI_{cloned}$	95% CI reduced?
		Mean	S.E.	95% CI	Mean	S.E.	95% CI			
Summer	**France**	**1.00**	**0.00**	**1.00-1.00**	**1.00**	**0.00**	**1.00-1.00**	**0.56**	**0.09**	**N**
Summer	Iberia	0.87	0.05	0.74-0.98	0.87	0.01	0.86-0.88	10.00	9.98	Y
Summer	Mauritania	1.00	0.00	0.82-1.00	1.00	0.00	1.00-1.00	65.88	728.28	Y
Autumn	All	0.97	0.04	0.87-1.00	0.97	0.00	0.96-0.98	10.00	6.89	Y
Winter	All	0.98	0.06	0.85-1.00	0.98	0.01	0.97-1.00	10.00	5.53	Y
Spring	France	0.89	0.07	0.70-1.00	0.89	0.01	0.87-0.90	10.00	9.36	Y
Spring	Iberia	0.84	0.07	0.71-1.00	0.84	0.01	0.82-0.86	10.00	9.14	Y
Spring	Mauritania	0.37	0.05	0.27-0.50	0.37	0.01	0.36-0.39	10.00	9.92	Y

Table V.3 Data cloning results on seasonal apparent survival parameters year^{-1} of the most parsimonious model (model 2, Table 8.1). For further details, see Table V.1.

Season	Wintering area	Original			Cloned (100x)			$SE_{original}$/ SE_{cloned}	$95\%CI_{original}$/ $95\%CI_{cloned}$	95% CI reduced?
		Mean	S.E.	95% CI	Mean	S.E.	95% CI			
Summer	All	0.94	0.04	0.84-1.00	0.94	0.00	0.93-0.95	10.00	8.37	Y
Autumn	All	0.95	0.05	0.84-1.00	0.95	0.00	0.94-0.96	10.00	7.56	Y
Winter	All	0.99	0.06	0.85-1.00	0.99	0.01	0.97-1.00	9.99	5.74	Y
Spring	France	0.92	0.08	0.73-1.00	0.92	0.01	0.90-0.94	10.00	8.12	Y
Spring	Iberia	0.80	0.07	0.68-0.94	0.80	0.01	0.79-0.82	10.00	8.98	Y
Spring	Mauritania	0.39	0.06	0.28-0.53	0.39	0.01	0.38-0.40	10.00	9.91	Y

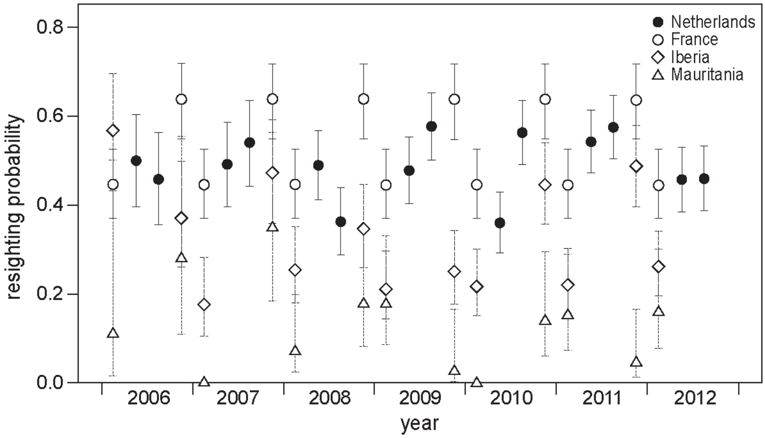

Figure V.1 Resighting probabilities (p) over time. Estimates are from the best-supported model in Table 8.1. Error bars represent 95% confidence intervals corrected for overdispersion ($\hat{c} = 1.25$, see Methods).

Chapter 9

A cross-seasonal fitness cost of migration: trans-Sahara wintering spoonbills breed later and skip more often than birds from Europe

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ABSTRACT

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 ecological trade-offs and constraints moulding migration systems from assessments of the fitness costs and benefits associated with migration and wintering in different areas. Here, we compare the reproductive performance of spoonbills that breed in the same colony in the Netherlands, but have contrasting migration strategies. We show that long-distance migrating birds that cross the Sahara for wintering, and migrate 8,000–10,000 km each year, breed later and seem to skip breeding more often compared to short-distance migrating birds that remain in Europe in winter and migrate only 2,000–4,000 km each year. As the recruitment probability into the breeding population of a chick is negatively correlated with date of birth (either direct or via its negative correlation with chick body condition), long-distance migrating birds probably have lower reproductive performance than short-distance migrants. Assuming that the long-distance migrating birds are not the poorer quality birds, which we consider a reasonable assumption because these birds occupy the traditional wintering areas, our results suggests that long-distance migration may be costly in terms of reduced reproductive performance.

INTRODUCTION

Migration is a widespread phenomenon in the animal kingdom (Dingle 1980; Chapman *et al.* 2011). Considerable variation in migration patterns exists between species, within species, and even within breeding populations of the same species (Alerstam 1990; Newton 2008). The latter is often referred to as differential migration (Ketterson & Nolan 1983), with as a special case, (non-breeding) partial migration when populations consist of both migratory and resident individuals (Chapman *et al.* 2011). Several hypotheses have been proposed to explain variation in migration patterns and make assumptions about migration-distance related trade-offs between survival and reproduction (Greenberg 1980), individual differences in the costs and benefits associated with different migration strategies, and about the role of competition for breeding and non-breeding resources (Ketterson & Nolan 1976; Gauthreaux 1982; Alerstam, Hedenstrom & Akesson 2003; Bell 2005). All theories have in common that they assume that migration incurs a fitness cost, and that this cost increases with the distance migrated. This cost may be direct, causing reduced survival during migration, but may also carry over to the next season, reducing subsequent survival or reproductive output via effects on arrival time or body condition (Harrison *et al.* 2011). Later arrival at the breeding grounds may result in the occupation of poorer quality breeding sites/territories (Ketterson & Nolan 1976; Myers 1981; Kokko 1999), causing reduced breeding success (Daan *et al.* 1989).

Only few studies, all on birds, were able to investigate (indicators of) breeding success in relation to migration distance. This is probably due to the difficulty to follow individuals during both breeding season (to collect breeding data) and non-breeding season (to determine an individual's wintering area). Migration distance was negatively correlated with arrival time at the breeding grounds in pied avocets *Recuvirostra avosetta* (Hötker 2002) and great cormorants *Phalacrocorax carbo sinensis* (Bregnballe, Frederiksen & Gregersen 2006), but not in Icelandic Black-tailed godwits *Limosa limosa islandica* (Gunnarsson *et al.* 2006; Alves *et al.* 2012). Only two studies directly investigated breeding success in relation to individual migration distance of great cormorants (Bregnballe, Frederiksen & Gregersen 2006) or between resident and migrant white storks *Ciconia ciconia* (Massemin-Challet *et al.* 2006), but found no effects. Here, we investigate timing of breeding and breeding success of a differentially (rather than partially) migrating animal, the Eurasian spoonbill *Platalea leucorodia leucorodia*.

Eurasian spoonbills that breed in the Netherlands winter along the Atlantic coast between France and Senegal. This wide 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 coastal Sahara. We test the hypothesis that there may be a cross-seasonal fitness cost of migrating far in terms of reduced reproductive output. To do so, we compare the breeding performance of long-distance migrants, that travel over 4,000 km each way, and short-distance migrants, commuting over only 1,000–2,000 km. We investigate several mechanisms that could reduce the reproductive output of long-distance migrants by testing whether they (1) more often skip breeding, (2) breed later and/or (3) have lower breeding success.

MATERIAL AND METHODS

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 – 2009. A total of 208, 232, 217 and 223 nests were counted during these years (including some re-nesting attempts), spread over 11 or 12 colonies (with inter-colony distances of 100 m to 3 km), varying in size from one to 60 nests. The study population bred on the ground in saltmarsh habitat, with a preference for areas where the vegetation was dominated by *Elytrigia atherica* and *Atriplex prostrata*. This vegetation is typical of middle to high saltmarshes (ca. 50–70 cm above mean high tide sea level) that are only flooded during stormfloods (van de Pol *et al.* 2010).

The breeding season of spoonbills on Schiermonnikoog is long, with egg-laying occurring between late March and early July. Spoonbills usually lay an egg every 2nd day and clutch sizes varied 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 hours of colony observations (see below). Incubation usually starts after the first egg has been laid, takes 25 to 26 d (Lok, unpublished data) and causes asynchronous hatching. Spoonbill chicks are altricial and fledge when ca. 35 d old, after which they are still fed by their parents for at least another month (Cramps & Simmons 1977).

Colony observations

During the incubation period, between April and July, the entire breeding area was searched on foot for new colonies every two weeks. When a group of spoonbills was detected, we slowly approached to assess from the birds' vigilance whether the colony was still in the settling phase (when birds are very vigilant, flying up already when still at ca. 200 m distance) or already in the incubation phase (birds could be approached without flying up to a distance of ca. 50 m without a hide). When a colony appeared to be in the settling phase it was left undisturbed for another two weeks. When a colony appeared to be in the incubation phase, it was visited again within a couple of days, using a mobile hide. From ca. 100 m distance, the observer entered the hide, and approached the colony slowly up to 10 m hidden by the hide.

This first visit from the mobile hide was used to check from which positions the colony could be well observed (so that nests and parents were not hidden behind vegetation), to determine where to place marks – that should be visible from the mobile hide – to facilitate identification of the nests. To facilitate identification of the nests during the subsequent observations from the mobile hide, marks (uniquely labelled wooden sticks) were placed the next day near (groups of) nests, the number of eggs (or small young) in each nest was determined and a map was drawn of the position of the nests within the colony. Colonies were subsequently observed every 1–3 d, with the aim to determine, for each nest, parents (either or not colour-ringed) and hatching date (i.e., the date when a chick was observed in the nest for the first time). A bird was considered as the parent of a specific nest, when it was observed breeding, feeding, or guarding a nest with chicks. Incubation shifts generally take place in the early morning (male takes over female) and in the evening (female takes over male). Observations during these periods of incubation shifts allow the fastest assignment of both parents to each nest (and allow the assessment whether both parents are unringed). Regular observations of a colony were continued until all nests had hatched and all parents were identified.

Temporary and permanent ringing of chicks

Within two weeks after hatching, i.e. when still attached to their own nest, all chicks within the monitored colonies received a temporary individual label (an individually numbered cotton band knitted around the tibia), and head-bill length was measured to accurately estimate age (Chapter 3). The labelling allowed us to identify the original nest of each chick when it was colour-ringed at the age of 3 to 5 weeks, i.e. when they were no longer attached to their own nest but gathered in crèches. The temporary label was then replaced by a unique colour-ring combination, and head-bill, head, 8th primary length and body mass were measured. 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).

Visits to the breeding colonies without a hide, for nest marking or chick ringing, were restricted to days with favourable weather conditions (avoiding very cold, very warm or rainy days). Moreover, most spoonbills, as well as the herring gulls *Larus argentatus* and lesser black-backed gulls *Larus fuscus* that breed in the vicinity of the spoonbill colonies, forage during low tide and roost in the colony at high tide. Therefore, to minimize the number of birds that is disturbed by our visits, we avoided visits during high tide as much as possible. In addition, chicks are mostly fed during incoming tide (pers. obs), and when they were being handled just after they had been fed, they sometimes regurgitated their food. To avoid this, colour-ringing of chicks (regurgitation did not occur during nest marking or temporary ringing) was preferably timed within 4 hours prior to low tide.

2006: a pilot year

The first breeding season, 2006, was a pilot to fine-tune the methods to estimate timing of breeding and breeding success and to assess any observable disturbing effects of our research activities on the breeding spoonbills. The distance between the colonies was such that visiting one colony did not disturb other colonies. To ensure that some colonies remained relatively undisturbed, we did not mark nests and perform daily observations in all colonies during this pilot year. However, conforming to the protocol of earlier years, we did visit all colonies once or twice do identify colour-ringed parents. The method of temporarily ringing chicks was developed during this pilot year, and only applied in very late colonies. The visits for nest marking and temporary ringing of chicks did not result in any direct nest desertion. Moreover, concerning the observations from a mobile hide, the birds were only shortly alert when the hide arrived at the colony, but they quickly resumed their normal breeding activities. Given the absence of any observable immediate negative effects of our research activities on breeding output, we did monitor all later colonies in 2006. Because all unmonitored colonies were early colonies, and because the methods to estimate timing of breeding and breeding success were still in development, data from this pilot year were excluded from the analyses on timing of breeding and breeding success.

Age and wintering area (migration strategy) of colour-ringed parents

With the exception of the single breeding bird that was caught as an unringed adult on the nest and provided with a satellite-transmitter, the exact age of all adult colour-ringed spoonbills is known because they were ringed as pre-fledged chicks. Spoonbills have been shown to be highly faithful to their wintering area from their 2nd winter onward (Lok *et al.* 2011), and therefore, a single winter resighting of a bird was sufficient to determine its migration strategy. We divided the wintering range into three regions (France, Iberia and Mauritania & Senegal, Lok *et al.* 2011) and defined a bird's wintering area as the most southern area where a bird was observed within a winter (defined as December–January for France and Iberia, and October–February for Mauritania and Senegal, Lok *et al.* 2011) as a 2nd winter or older bird. Because the sample size for birds wintering in France was very low (N = 7), we defined two migration strategies: short-distance migrants (< 2,400 km one-way, wintering in either France or Iberia) and long-distance migrants (> 4,000 km one-way, i.e. the trans-Sahara migrants, wintering in Mauritania or Senegal), in addition to a category of unknown migration strategy. Although the majority of birds remain faithful to their wintering areas (Lok *et al.* 2011), 15 birds were short-distance migrant in one winter, and long-distance migrant in another. Some of these cases may have been due to ring reading errors, or a very late (autumn) or early (spring) stopover observation, and hence, we selected the migration strategy that was observed in most winters. For those birds that were observed the same number of winters in Europe and West Africa, migration strategy was set as unknown (N = 6). This resulted in 180 different colour-ringed breeding birds during the study period 2006–2010, of which 61 were short-distance migrants, 38 were long-distance migrants and 81 were colour-ringed birds with unknown migration strategy. Of the birds of which the sex was determined (either from visual observations of breeding pairs, or from molecular assays), 14 females and 6 males were long-distance migrants, and 17 females and 23 males were short-distance migrants. This shows there is considerable overlap in the winter distribution of males and females, but a tendency towards more females among the long-distance migrants and more males among the short-distance migrants ($\chi^2 = 3.01$, df = 1, $p = 0.08$). Sample sizes for sexes were too small to incorporate into the analyses.

Breeding propensity

Lok *et al.* (2013) found that resighting probabilities in the Netherlands were much lower for birds wintering in West Africa than for birds wintering in Europe. This may be caused by the fact that birds wintering in West Africa less often return to The Netherlands for breeding than birds wintering in Europe, in other words, that breeding propensity is lower for long-distance migrants. To estimate breeding propensity, we created encounter histories for the period 2006–2010, where '1' represents 'observed as breeding bird' and '0' represents 'not observed as breeding bird'. Individuals that were observed, but not breeding, were excluded from this analysis. Because resighting effort was similar in 2007–2009 (all colonies were observed daily during the incubation period), but much lower in 2010 (not all colonies were observed, and only biweekly), we modelled resighting probability separately for 2007–2009 and for 2010. When a bird is breeding, its true resighting probability is very high and independent of an individual's migration strategy. Therefore, any effect of migration strategy on apparent resighting probabilities (which is the product of true resighting probability and temporary emigration) will reflect differences in breeding propensity. Failure during the early egg phase could affect true resighting probabilities, yet this was rarely observed in our study population.

Timing of breeding

To determine hatching dates of individual nests, we preferably used the estimated age from the head-bill length of the largest chick in the nest during temporarily labelling (i.e. when younger than two weeks old), using $\mathrm{age}(t) = -\ln(-\ln(y_t/y_\infty))/k+T_i$, where $y_\infty = 184$, $k = 0.052$ and $T_i = 7.9$ (see Table 3.1). When the head-bills of the chicks in a nest were not measured during temporary labelling but some survived to ringing, the 8th primary length of the largest chicks was used to estimate age using the above formula and $y_\infty = 254$, $k = 0.093$ and $T_i = 19.7$ (see Table 3.3), which could then be used to estimate hatching date. In other cases, we used the observed hatching date, but only for the nests that were checked daily. Other nests were not included in this analysis, as timing of breeding could not be accurately determined. This included nests that failed before hatching or never hatched (very few), were found empty (unknown whether these nests failed or never had eggs) or nests of which hatching date was not accurately observed and that failed before the chicks were temporarily labelled. Therefore, the data on timing of breeding are biased towards nests that hatched and survived until temporary banding.

Breeding success and chick body condition

Breeding success was defined as the number of chicks that were colour-ringed per nest. Because the number of chicks hatched per nest is unknown, we cannot calculate the proportion of chicks that survived until colour-ringing. 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. All chicks in the colony were colour-ringed. For small and synchronized colonies, this could be achieved with a single colour-ringing event, whereas for large, less synchronized colonies two or sometimes three colour-ringing events were necessary to ring all chicks.

As a result of the minimization of the number of visits per colony for colour-ringing chicks, there was considerable variation in the age at which chicks were colour-ringed, which varied between 16 days and 39 days (75% was ringed between day 21 and 32). Consequently, estimates of breeding success of nests of which chicks were ringed at a young age may have been biased high compared to nests of which chicks were ringed very close to fledging. However, correcting for this variation in age at ringing turned out to be problematic. Although we know the age of the nests at ringing for successful nests, because the date when the chicks were ringed is known, this is not the case for unsuccessful nests. There was a trade-off between minimizing the number of visits to the colony and the duration of the ringing sessions (which should not be longer than ca. 1,5 hours), which was an issue especially in large colonies. For unsuccessful nests in such large colonies, it is uncertain before which ringing session (i.e. at which date and age) all chicks had died. We nevertheless tested for the effect of age at ringing on breeding success, whilst assuming that all unsuccessful nests were evaluated 27 days after hatching (mean age at ringing). As we found no statistical support for an effect of age at ringing, and as there was also no correlation between age at ringing and hatching day or year, the variation in age at ringing was considered as random noise.

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 growth curves for body mass estimated in Chapter 3 (females: $y_\infty = 1485$, $k = 0.141$ and $T_i = 8.4$ and males: $y_\infty = 1741$, $k = 0.127$ and $T_i = 9.7$; Table 3.3). To calculate the predicted body mass, age was estimated from head-bill length at labelling, or otherwise 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 at labelling relative to that of its siblings that survived to ringing, or, when not measured, from 8th primary length relative to that of its siblings at ringing.

Post-fledging survival and winter site choice

Post-fledging and subsequent survival was estimated for all chicks colour-ringed in 2006–2010, and resighted during post-fledging (August-September) in The Netherlands, anywhere in winter (November – February) or anywhere in summer (April–September) in the years thereafter. This allowed us to estimate survival during post-fledging (ca. during the 3 month period after colour-ringing), first autumn migration (September – January), first 'winter' (January – July, as first-year bird), and of older birds. Due to limited data, we did not distinguish between survival of subadult and adult birds and did not model annual variation in survival. We accounted for the effect of age at ringing on post-fledging survival and for annual variation in resighting probabilities during the post-fledging, winter and summer periods. Resighting probability in summer was modelled separately for subadult (age 1 – 2) and adult birds (age 3 – 6).

Statistical analysis

Analyses of timing of breeding, breeding success (number of chicks colour-ringed per nest) and body condition were performed on several selections of the data. The first analysis included all nests and all chicks for the years when all nests were monitored (2007–2009), independent of whether the parents were colour-ringed or their migration strategy was known, to test for annual variation in the above breeding parameters. For the nests of which timing of breeding was accurately determined, its effect on breeding success, chick body condition and winter site choice of the young was investigated. We further tested whether a chick's body condition was influenced by the number of siblings in the nest and age relative to that of its siblings and whether a chick's body condition influenced its winter site choice.

In the second analysis, only nests with at least one colour-ringed parent were included to test the effect of age and migration strategy (long, short or unknown) of the parent(s) on timing of breeding, breeding success and chick condition. Because age-related changes have now been established in a variety of birds (Reid *et al.* 2003; McCleery *et al.* 2008), with an initial increase in breeding performance followed by a decrease at old ages, we considered both a linear and a quadratic effect of age. Moreover, we tested whether any age-related pattern in reproductive parameters differed between short- and long-distance migrants by considering interactions between migration strategy and age. In this second analysis, birds with an unknown migration strategy are included because their exact age is known. However, they consist of a mixture of long- and short-distance migrants, and may blur any existing effects of migration strategy. Therefore, to specifically test for the effect of migration strategy, we also did a third analysis where we excluded these unknown migrants.

To investigate performance of the young after they have been colour-ringed, we estimated their survival and migration strategy in relation to body condition and time of the season (hatching day). Because in some birds, migration strategy is socially (Harrison *et al.* 2010) or genetically (Pulido & Berthold 2010) inherited from their parents, we also tested for an effect of the migration strategy of the parent(s) on the migration strategy of the chick.

When testing an effect of timing of breeding, we both considered a linear and a quadratic effect of hatching day, because breeding success may peak for birds that breed in the middle of the season. Linear decreases in breeding performance over the season suggest the existence of differential selection on earlier breeding. Furthermore, we only considered biologically plausible interactions. The performance of long-distance migrants may depend on the conditions experienced during migration, which are variable between years. Consequently, we may expect an interaction between year and migration strategy on breeding performance. Furthermore, the optimal timing of breeding may vary between years, as a consequence of for example the mildness of the preceding winter affecting spring phenology, and hence we may expect an interaction between year and timing of breeding on breeding performance.

The analyses involved data of the same individuals in different breeding seasons. However, because we cannot discriminate among individuals when they are unringed, we could not account for this pseudoreplication in the first analysis. We did account for pseudoreplication in the chick condition index analysis by modelling random variation in chick condition among nests. Accounting for pseudoreplication in the second analysis where we tested for the effect of age and migration distance of the parent(s) on breeding parameters was somewhat tedious. Spoonbills are not monogamous for life and therefore, the same individual often had different partners in different years. This was statistically problematic because we had to use 'individual' instead of 'pair' as the random level. However, because there were many cases (N = 46) where two colour-ringed individuals shared the same nest, this would yield another type of pseudoreplication that could not be statistically accounted for. Therefore, we selected one colour-ringed adult 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. We included random individual (adult) variation in the models explaining variation in timing of breeding, breeding success and condition of their chicks. For the analyses of chick condition, we additionally modelled random variation among nests within individuals. Breeding success was log-transformed and modelled with Poisson errors. Winter site choice was analysed using logistic regression with migration strategy of the chick as a binomial response variable (short- or long-distance migrant). We checked for, but did not find, trends or heteroscedasticity in residuals.

To investigate the effect of migration strategy on breeding propensity, we modelled survival of breeding birds as a function of migration strategy (m2: long- versus short-distance migrants) (Lok *et al.* 2011; Lok, Overdijk & Piersma 2013), but due to limited data, we also considered a model with constant survival. Resighting probability was modelled as a function of resighting effort (2007–2009 versus 2010, referred to as 'effort') and with or without an effect of migration strategy. Because in this analysis, we were primarily interested in the difference between long- and short-distance migrants (and not in age effects), we excluded the unknown migrants.

In the post-fledging survival analysis, we first separately tested a linear effect of body condition and hatching day, as well as a quadratic effect of hatching day, 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 for breeding propensity, Φ(m2) p(m2+effort), and post-fledging survival, $\Phi_{pf}(t)$ $\Phi_{m1}(t)$ $\Phi_{w1}(t)$ $\Phi_{older}(t)$ $p_{pf}(t)$ $p_{w}(t)$ $p_{s,sub}(t)$ $p_{s,ad}(t)$, was assessed using the median c-hat test in program MARK. The level of overdispersion was estimated at $\hat{c} = 1.14 \pm 0.03$ S.E for the breeding propensity model, and $\hat{c} = 1.17 \pm 0.01$ S.E for the post-fledging survival model.

Breeding propensity and post-fledging survival were analysed using the package RMark (Laake 2011) in program R (version 2.13.0, R Development Core Team 2011) and program MARK (White & Burnham 1999). Timing of breeding, breeding success, chick body condition and body condition of the young were analysed with (generalized) linear (mixed) models using program R (R Development Core Team 2011) and the R packages nlme (Pinheiro *et al.* 2012) and lme4 (Bates, Maechler & Bolker 2011). Model selection results are based on Akaike Information Criterion adjusted for small sample size (AIC_c), and in case of the breeding propensity and post-fledging survival analysis for overdispersion ($QAIC_c$) (Akaike 1973; Burnham & Anderson 2002). When only one variable was tested, its marginal significance was assessed with the function anova (Pinheiro & Bates 2000). Unless stated otherwise, survival rates are presented as mean ± S.E.

RESULTS

Breeding propensity

Long- and short-distance migrants breeding on Schiermonnikoog had similar survival (0.84 ± 0.03), but there was some evidence that they had different resighting probabilities (Table 9.1, model 1 vs. model 2, $\Delta QAIC_c = -1.13$), with a trend towards lower apparent resightings probabilities of long-distance migrants (0.85 ± 0.06 in 2007–2009) than short-distance migrants (0.94 ± 0.03 in 2007–2009).

Table 9.1 Model selection results for the analysis of breeding propensity in relation to migration strategy. Migration strategy (m2) consists of two categories: short-distance migrants (N = 56) and long-distance migrants (N = 34). Resighting probability is modelled separately for 2007–2009 and for 2010 (effort). Results are adjusted for overdisperion ($\hat{c} = 1.14$). The most parsimonious model is shown in bold.

Breeding propensity		K	QDeviance	$\Delta QAIC_c$	Akaike weight
(1)	Φ(.) p(m2+effort)	4	47.35	0.00*	0.40
(2)	**Φ(.) p(effort)**	**3**	**50.55**	**1.13**	**0.23**
(3)	Φ(m2) p(effort)	4	48.81	1.46	0.19
(4)	Φ(m2) p(m2+effort)	5	46.90	1.64	0.18

$^*AIC_c = 276.72$

As they only comprise resightings of breeding birds, the apparent resighting probability is the product of true resighting probability and breeding propensity (i.e., 1 – the probability to skip breeding). Because true resighting probability can be expected to be the same for long- and short-distance migrants, long-distance migrants have a lower breeding propensity than short-distance migrants on the basis of the following argument: when short-distance migrants breed every year, i.e. when their breeding propensity is 1, and thus that 0.94 was the true resighting probability in 2007–2009, the breeding propensity of long-distance migrants is 0.85/0.94 = 0.90. When true resighting probability was in fact nearly 1 in 2007–2009, which we expect given the very thorough monitoring of the breeding colonies on Schiermonnikoog during these years, breeding propensity of short-distance migrants was 0.94 versus 0.85 for long-distance migrants.

Timing of breeding

95% of the 545 nests in 2007–2009 hatched between 22 April and 24 June, with 11 May as the average. There was no year to year variation in the timing of breeding ($F_{2,542}$ = 0.0042, p = 1.00), but there was substantial evidence for effects of age and migration strategy on the timing of breeding (Table 9.2). Short-distance migrants on average bred

Table 9.2 Model selection results for timing of breeding as a function of age (a), age squared (a^2) and migration strategy of the parents (m, consisting of 3 categories: short-distance migrants (N = 54), long-distance migrants (N = 30) and unknown migrants (N = 58)) and the two-way interactions between migration strategy and age, age squared and year (y). Models with only a main effect of year, but no interactions with year, were not considered because there was no statistical support for a main effect of year in the analysis on all nests (N = 545). The most parsimonious model is shown in bold. Of the 17 candidate models, only the models with Akaike weight ≥ 0.01 are shown.

Hatching day		K	-2logL	ΔAIC_c	Akaike weight
(1)	$a+a^2+m+m{:}a+m{:}a^2$	11	1935.21	0.00*	0.37
(2)	**$a+a^2+m$**	**7**	**1945.11**	**1.26**	**0.20**
(3)	$a+a^2+m+m{:}a$	9	1941.94	2.37	0.11
(4)	$a+m$	6	1949.05	3.09	0.08
(5)	$a+m+m{:}a$	8	1945.51	3.80	0.06
(6)	$a+a^2$	5	1952.08	4.02	0.05
(7)	$a+a^2+m+m{:}a^2$	9	1943.73	4.16	0.05
(8)	a	4	1955.13	4.98	0.03
(9)	$a+a^2+m+y+m{:}a+m{:}a^2+m{:}y$	17	1927.43	5.71	0.02
(10)	$a+a^2+m+y+m{:}y$	13	1937.04	6.25	0.02
(11)	$a+a^2+m+y+m{:}a+m{:}y$	15	1933.98	7.69	0.01
(12)	$a+m+y+m{:}y$	12	1941.37	8.36	0.01

*AIC_c = 1958.31

6.3 days earlier than long-distance migrants (Table 9.3). Moreover, there was some evidence for an interaction between age and migration strategy on timing of breeding. When the unknown migrants were included, this interaction included a quadratic age effect (Table 9.2, model 1 vs. model 2, $\Delta AIC_c = -1.26$), whereas excluding them resulted in similar and more substantial support for the interaction between migration strategy and either a linear or a quadratic age effect (Appendix VI, Table VI.1, model 1 vs. model 3, $\Delta AIC_c = -1.92$). Both long- and short-distance migrants strongly advanced breeding between their 3rd and 8th year and bred at similar times at these ages (Fig. 9.1). At an age of 9 years or older, there were suddenly many late-breeding long-distance migrants. Such delayed breeding by older birds was much less apparent in short-distance migrants and only in some very old age classes (14 and 15 years old). Neither a quadratic, nor a linear age effect was able to capture the peculiar relationship between age and timing of breeding of especially the long-distance migrants (Fig. 9.1), and may explain the marginal level of support for the interaction between migration strategy and age (Table VI.1).

Breeding success

Breeding success, i.e. the number of chicks colour-ringed per nest, was higher in 2008 (1.64; 95% C.I.: 1.47–1.83, N = 194) than in 2007 (0.98; 0.85–1.11, N = 215) and 2009 (1.02; 0.88–1.17, N = 187) and decreased over the season, with its slope varying between years (Appendix VI, Table VI.2, Fig. 9.2). Breeding success most steeply decreased over the season in 2008, which was also the year with the highest average breeding success. There was no support for any effects of migration strategy and age of the parents (Table 9.4). When the unknown migrants were excluded from the analysis, there was still no support for an effect of migration strategy on breeding success ($\Delta AIC_c = 1.96$).

Table 9.3 Parameter estimates and approximate 95% confidence intervals of the most parsimonious model for timing of breeding (Table 9.2, model 2).

		95% CI	
Hatching day	Estimate	Lower	Upper
Intercept	63.44	52.68	74.19
Age -3.27	-5.35	-1.20	
Age^2	0.10	0.00	0.20
Migration tendency[1]			
Short-distance	-6.34	-11.93	-0.75
Unknown	-1.21	-6.71	4.29
Random effects			
$\sigma^2_{individual}$	115.38	83.17	160.06
$\sigma^2_{residual}$	54.39	41.61	71.09

[1] Reference category: long-distance migrants

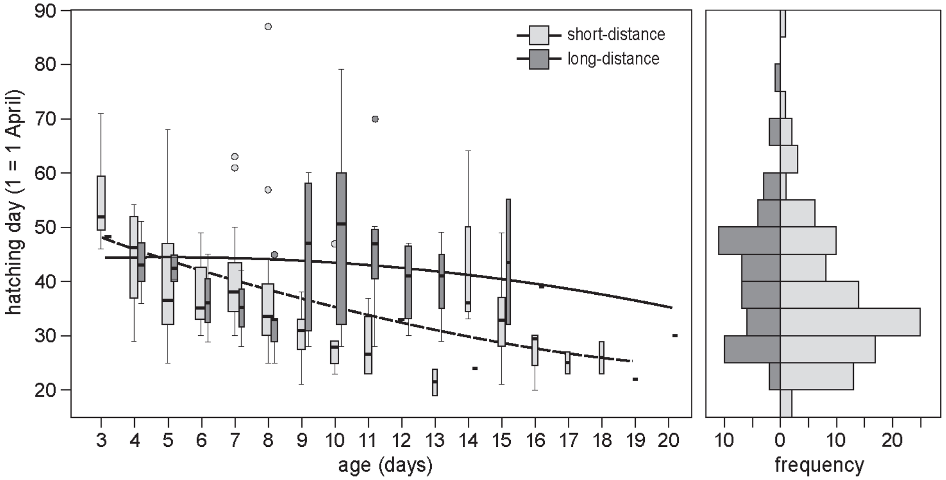

Figure 9.1 Hatching day as a function of age and migration strategy of parent spoonbills. One randomly chosen parent with known migration strategy per nest is shown in this plot. Trend lines represent model-averaged estimates of the two competitive models ($\Delta AIC_c < 2$) of Table VI.1. Box widths represent sample sizes. The histogram on the right shows the distribution of hatching days of short- and long-distance migrating spoonbills.

Table 9.4 Model selection results for breeding success in relation to age (a), age squared (a^2) and migration strategy (m) of the parents, and interactions between migrations strategy and year, age and age squared. All models include an effect of hatching day, year and the interaction between hatching day and year (as supported from the analysis of all nests, N = 505, Table VI.2). This analysis is based on 237 nests and 133 individuals (27 long-distance migrants, 45 short-distance migrants and 61 unknown migrants). The most parsimonious model is shown in bold. Of the 17 candidate models, only the models with Akaike weight ≥ 0.01 are shown.

Breeding success		K	-2logL	ΔAIC_c	Akaike weight
(1)	h+y+h:y	7	164.20	0.00*	0.36
(2)	h+y+h:y+a	8	162.17	0.12	0.34
(3)	h+y+h:y+a+a^2	9	161.40	1.51	0.17
(4)	h+y+h:y+m	9	163.80	3.90	0.05
(5)	h+y+h:y+a+m	10	161.85	4.14	0.05
(6)	h+y+h:y+a+a^2+m	11	161.19	5.67	0.02
(7)	h+y+h:y+a+m+m:a	12	160.18	6.88	0.01
(8)	h+y+h:y+m+m:y	13	159.30	8.25	0.01
(9)	h+y+h:y+a+a^2+m+m:a	13	159.51	8.46	0.01

*AIC_c = 178.69

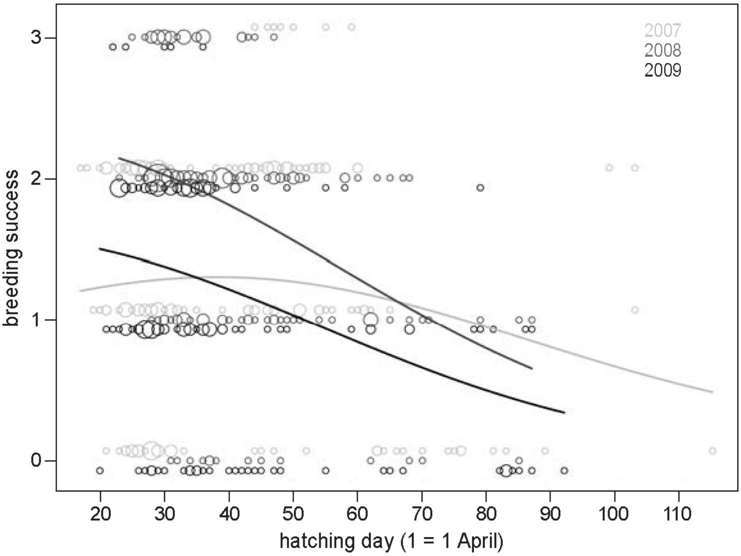

Figure 9.2 Breeding success as a function of hatching day and year. Size of the dots reflects sample size. Lines represent model-averaged estimates of the models in Table VI.2.

Chick condition, post-fledging survival and winter site choice

Chick condition differed between years, depended on relative age in the nest and was negatively correlated with hatching day (Table 9.6, Appendix VI, Table VI.3). Migration strategy or age of the parent(s) did not affect chick condition (Table 9.5). Chick condition was higher in 2009 than in 2007 and 2008 (Table 9.6). Relative age was more important in explaining variation in body condition than the number of siblings: third chicks in a nest had lower condition than first and second chicks in the nest (Table 9.6).

Post-fledging survival was strongly positively correlated with age at ringing and negatively correlated with chick body condition (Table 9.7, Fig. 9.3). Post-fledging survival decreased with hatching day for chicks born in April and May (92% of the chicks), but increased again for chicks born later in the season (Table 9.7, Fig. 9.3). The increased survival of late born chicks may be an artefact because those chicks had a much shorter post-fledging period (and hence, less time to die) than the early born chicks. Chick body condition was not correlated with survival during first autumn migration or first winter, but tended to be negatively correlated with survival after the first year ($\Delta QAIC_c = -1.50$, Table 9.7, Fig. 9.4). Parameter estimates of the most parsimonious model are shown in Table 9.8.

Winter site choice in the first winter was correlated with hatching date and differed between years (N = 106, Appendix VI, Table VI.7, Fig. VI.1). Spoonbill chicks born in 2006 and 2008 were much more likely to be observed in West Africa in their first winter than chicks born in 2007, 2009 and 2010. This could not obviously be explained by

Table 9.5 Model selection results for chick body condition index as a function of age (a), age squared (a^2) and migration strategy (m) of the parents, and the interaction between migration strategy and year (y), age and age squared. Based on the most parsimonious model based on all 714 colour-ringed chicks (Table VI.3), we included hatching day (h), relative age in the nest (a_{rel}) and year in all models. Results are based on 313 chicks from 191 nests. The most parsimonious model is shown in bold. Of the 17 candidate models, only the models with Akaike weight ≥ 0.01 are shown.

Chick condition		K	-2logL	ΔAIC_c	Akaike weight
(1)	$h+a_{rel}+y+a$	10	-693.06	0.00*	0.25
(2)	$h+a_{rel}+y+a+m$	12	-696.53	0.82	0.17
(3)	$h+a_{rel}+y+m$	11	-694.15	1.05	0.15
(4)	**$h+a_{rel}+y$**	**9**	**-689.78**	**1.15**	**0.14**
(5)	$h+a_{rel}+y+a+a^2$	11	-693.37	1.82	0.10
(6)	$h+a_{rel}+y+a+a^2+m$	13	-696.67	2.85	0.06
(7)	$h+a_{rel}+y+a+m+m:a$	14	-698.15	3.55	0.04
(8)	$h+a_{rel}+y+m+m:h$	13	-694.71	4.81	0.02
(9)	$h+a_{rel}+y+a+m+m:h$	14	-696.84	4.86	0.02
(10)	$h+a_{rel}+y+a+a^2+m+m:a$	15	-698.54	5.35	0.02
(11)	$h+a_{rel}+y+a+a^2+m+m:a^2$	15	-698.15	5.74	0.01
(12)	$h+a_{rel}+y+a+a^2+m+m:h$	15	-697.03	6.86	0.01

*AIC_c = –672.37

Table 9.6 Parameter estimates and approximate 95% confidence intervals of the most parsimonious model for chick body condition (Table VI.3). Results are based on 714 chicks from 416 nests.

		95% CI	
Chick body condition	Estimate	Lower	Upper
Intercept	0.0482	0.0241	0.0723
Hatch day	-0.0011	-0.0016	-0.0006
Relative age[1]			
Second	-0.0087	-0.0202	0.0028
Third	-0.1019	-0.1264	-0.0774
Year[2]			
2008	-0.0024	-0.0187	0.0140
2009	0.0199	0.0017	0.0381
Random effects			
σ^2_{nest}	0.0020	0.0013	0.0030
$\sigma^2_{residual}$	0.0050	0.0043	0.0059

Reference categories: [1] First, [2] 2007

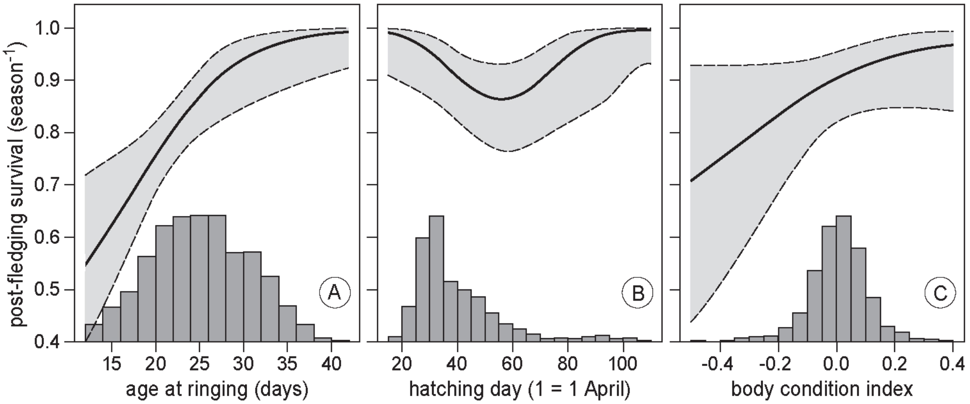

Figure 9.3 Post-fledging survival (over 3 months, from colour-ringing until the onset of autumn migration) as a function of (A) age at ringing, (B) hatching day and (C) body condition index. For the estimates in each panel, the mean covariate values for the other two explanatory individual covariates are used, i.e. mean ringing day is 27 days, mean hatching day 41 (11 May) and mean body condition index is 0. Mean (solid lines) and 95% confidence intervals (dashed lines) are model-averaged estimates based on the models in Table 9.7, adjusted for overdispersion ($\hat{c}$ = 1.17). Histograms represent the distribution of the individual covariates in the dataset.

Table 9.7 Model selection results of the effects of hatching day (h), hatching day squared (h^2) and chick body condition index (BCI) on survival. We only tested the covariate effects that were substantially supported in steps 1-3 (Appendix VI, Table VI.4 – VI.6), i.e. an effect of chick body condition on post-fledging (Φ_{pf}) and (sub)adult survival (Φ_{older}) and a quadratic effect of hatching day on post-fledging survival. In all models, an effect of age at ringing on post-fledging survival was included and survival was modelled constant during first autumn migration (Φ_{m1}) and first winter (Φ_{w1}). Results have been adjusted for overdispersion ($\hat{c}$ = 1.17). The most parsimonious model is shown in bold.

Post-fledging survival			K	-2logL	ΔAIC_c	Akaike weight
(1)	$\Phi_{pf}(a_{ring}+h+h^2+BCI)$	$\Phi_{older}(BCI)$	31	8227.49	0.00*	0.56
(2)	$\boldsymbol{\Phi_{pf}(a_{ring}+h+h^2+BCI)}$	$\boldsymbol{\Phi_{older}(.)}$	**30**	**8231.64**	**1.50**	**0.26**
(3)	$\Phi_{pf}(a_{ring}+h+h^2)$	$\Phi_{older}(BCI)$	30	8233.49	3.09	0.12
(4)	$\Phi_{pf}(a_{ring}+h+h^2)$	$\Phi_{older}(.)$	29	8238.66	5.47	0.04
(5)	$\Phi_{pf}(a_{ring}+BCI)$	$\Phi_{older}(BCI)$	29	8240.82	7.32	0.01
(6)	$\Phi_{pf}(a_{ring}+BCI)$	$\Phi_{older}(.)$	28	8244.98	8.83	0.01
(7)	$\Phi_{pf}(a_{ring})$	$\Phi_{older}(BCI)$	28	8245.93	9.65	0.00
(8)	$\Phi_{pf}(a_{ring})$	$\Phi_{older}(.)$	27	8251.18	12.10	0.00

*$QAIC_c$ = 7094.67

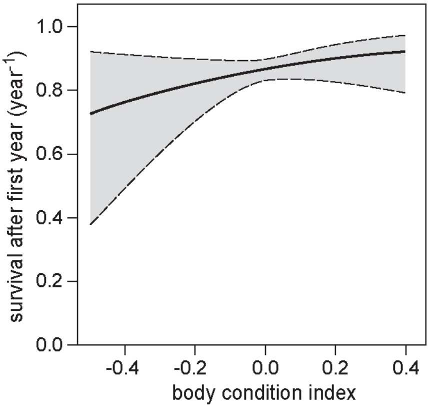

Figure 9.4 Survival probability after the first year as a function of chick body condition index. Mean (solid line) and 95% confidence intervals (dashed lines) shown are model-averaged estimates based on the models in Table 9.7, adjusted for overdispersion ($\hat{c} = 1.17$).

annual differences in resighting probabilities between Europe and West Africa (Lok, Overdijk & Piersma 2013). Ignoring differences among cohorts, the probability to be observed in West Africa in the first winter decreased from 0.43 for chicks born on 1 May to 0.12 for chicks born on 1 July. Because a considerable proportion of spoonbills have been shown to move further south between their first and second winter and only become faithful from their second winter onward (Lok *et al.* 2011), we also investigated the factors correlated with winter site choice after the first winter. This 'final' winter site choice no longer differed among cohorts and was not correlated with hatching date or body condition at fledging (N = 132, Appendix VI, Table VI.8). Of the 132 birds that were observed in their second or later winter, 44% was observed in West Africa compared to 56% in Europe.

Migration strategy of young was not related to that of their parents, neither in the first winter (N = 35, $\Delta AIC_c = 5.00$ when migration strategy of the parents (long- or short-distance) was added to the most parsimonious model of Table VI.7) nor later on (N = 30, $\Delta AIC_c = 2.30$ when migration strategy of the parents was added to the most parsimonious model of Table VI.8).

DISCUSSION

We showed that long-distance migrants breed later and that later breeding is correlated with fewer fledged chicks that are in poorer condition and (consequently) have lower post-fledging survival, and hence, recruitment probability (Fig. 9.5, 9.6). We further show that long-distance migrants more often skip breeding than short-distance migrants. This may be due to adverse weather conditions encountered when passing the Sahara, or to unfavourable refuelling conditions at southern stopover sites, during spring migration which may cause birds to abort their migration.

During the study period, the saltmarshes occasionally flooded, resulting in the failure of most nests with eggs and chicks younger than 4 weeks old. There were flood-

Table 9.8 Model-averaged parameter estimates and 95% confidence intervals based on the models in Table 9.7. Post-fledging and (sub)adult survival estimates are reported for mean ring age (27 days), hatching day (day 41) and chick body condition (BCI = 0). Survival estimates are shown on an annual basis (for comparison) and on a seasonal basis, being a period of 3 months for the post-fledging period, 4 months for first autumn migration, 6 months for the first winter and a year for (sub)adult survival. 95% confidence intervals have been adjusted for overdispersion ($\hat{c} = 1.17$).

	Estimate (95% C.I.)	
Apparent survival (Φ)	Annual	Seasonal
Post-fledging	0.67 (0.45-0.83)	0.90 (0.82-0.95)
First autumn migration	0.58 (0.39-0.75)	0.84 (0.73-0.91)
First winter	0.65 (0.49-0.78)	0.80 (0.70-0.88)
Subadult/Adult	0.87 (0.83-0.90)	0.87 (0.83-0.90)
Resighting probability (p)		
Post-fledging		
2006	0.81 (0.73-0.88)	
2007	0.22 (0.16-0.31)	
2008	0.47 (0.38-0.57)	
2009	0.21 (0.16-0.27)	
2010	0.33 (0.27-0.39)	
Winter		
2006/2007	0.23 (0.19-0.28)	
2007/2008	0.63 (0.52-0.73)	
2008/2009	0.11 (0.09-0.14)	
2009/2010	0.67 (0.60-0.74)	
2010/2011	0.13 (0.10-0.17)	
2011/2012	0.66 (0.59-0.73)	
2012/2013	0.16 (0.12-0.20)	
Subadult summer		
2007	0.49 (0.42-0.56)	
2008	0.03 (0.02-0.05)	
2009	0.73 (0.65-0.80)	
2010	0.30 (0.25-0.35)	
2011	0.55 (0.48-0.61)	
2012	0.36 (0.30-0.42)	
Adult summer		
2009	0.77 (0.69-0.83)	
2010	0.47 (0.37-0.57)	
2011	0.77 (0.57-0.89)	
2012	0.53 (0.27-0.77)	

ings in late March in 2006–2008 that may have biased the estimated decrease in breeding success over the season. In these years, we were informed, but not allowed to verify, that spoonbills had started incubating eggs already in mid March. These nests must have failed, given that incubation takes 25–26 d (Chapter 3) and the very first

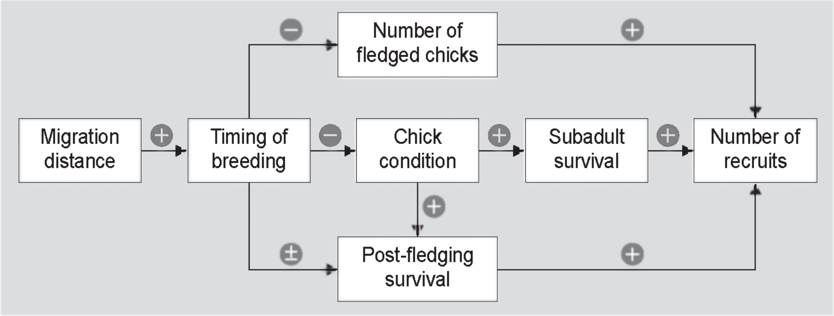

Figure 9.5 A diagram representing the estimated positive and negative relationships among migration distance and breeding parameters.

chicks hatched only on April 17. The breeding success of these very early breeders (numbers are unknown) was therefore 0, which, if we could have included these nests into the analyses, would have affected the estimated relationship between timing of breeding and breeding success. Moreover, it is possible that these very early breeders were mainly short-distance migrants, which could have even enlarged the difference in timing of breeding between long- and short-distance migrants, but this remains speculation. Despite the low success of these very early nests, these birds probably renested later in the season. Another disastrous storm flood occurred in late June 2007 and led to the failure of virtually all nests that had eggs or chicks younger than 4 weeks old at that time. Although the nests of which the chicks had been measured to estimate hatching date were included in the analysis and had a breeding success of 0, the nests that still had eggs or very small chicks that were not yet measured (at least 8 nests) were excluded which resulted in the underestimation of the number of failed nests with (expected) hatching dates in late June and July. Some of the individuals of which their nests were flooded renested (T. Lok, pers. obs.), resulting in some very late successful breeding attempts in 2007. This could have partly explained the shallower decrease in breeding success over the season in this year (Fig. 9.2).

Short-distance migrants bred earlier than long-distance migrants, the difference being more pronounced in older birds. The earlier breeding of short-distance migrants may have been mediated by earlier arrival at the breeding grounds, as was found in pied avocets (Hötker 2002). Alternatively, short-distance migrants may arrive in better condition because they only migrated half the distance compared to long-distance migrants. Body condition at arrival was shown to be an important determinant of the duration until egg laying in greater snow geese *Chen caerulescens atlantica* (Bêty, Gauthier & Giroux 2003). Assessing the timing of arrival at the breeding grounds using visual observations proved difficult in this spoonbill population, because the birds behave rather cryptically after their arrival and use a very large area for foraging. GPS- or satellite-tracking of birds from varying winter destinations are now a requirement before being able to advance these observations.

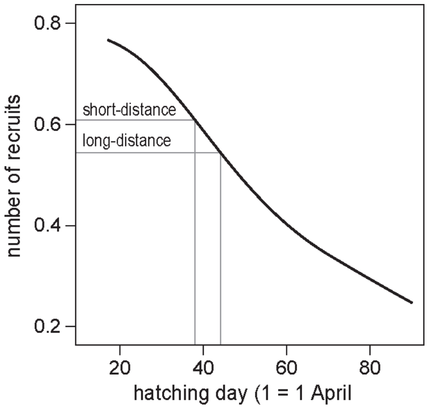

Figure 9.6 Number of recruits (number of chicks surviving until age 3) per breeding pair as a function of hatching day, calculated from the estimated relationships between timing of breeding, breeding success (using the estimates of Fig. 9.2, averaged over the three years), chick condition (Table 9.6) and post-fledging and subadult survival (using the estimates of the best-supported model in Table VI.6). Mean age of ringing (27 days) was used to calculate post-fledging survival. The mean timing of breeding and associated number of recruits per breeding pair for short- and long-distance migrants are shown with dotted lines.

We found a peculiar relationship between timing of breeding, age and migration strategy of the parents. Both long- and short-distance migrants strongly advanced breeding between their 3rd and 8th year and bred at similar times at these ages (Fig. 9.1). Unfortunately, our study period was too short relative to the lifespan of spoonbills to distinguish within- and between-individual effects on timing of breeding (cq. van de Pol & Verhulst 2006), so we cannot separate individual advancement of breeding from selective disappearance of late-breeding individuals. Individual advancement of breeding was shown in another colonial breeding bird, the mute swan *Cygnus olor*, and suggested to be caused by young individuals being more susceptible to social interference (McCleery *et al.* 2008). In migratory birds, the constraint on the timing of breeding may also be caused by later spring migration of young birds compared to older birds, as shown for a variety of passerines (Francis & Cooke 1986; Stewart, Francis & Massey 2002). Through improved competitive ability or experience, birds may advance their migration, and hence their breeding, with age. In contrast to the advancement of breeding up to 7 years, older birds bred later, which is especially apparent in long-distance migrants, where individuals of 9 years old or older breed much later than younger birds (Fig. 9.1). Late breeding of old short-distance migrants was much less apparent, and at a much later age (14–15 years old). Later breeding of very old birds has also been shown in some other birds (Goutte *et al.* 2010) and may have been caused by senescence (the late-life decline in organismal performance), as was shown in mute swans, where a delay in breeding was observed within individuals older than 12 years old (McCleery *et al.* 2008). Senescence in timing of breeding of migratory birds could be caused by reduced migration performance limiting the ability of old birds to arrive in time. Assuming that the observed pattern is caused by a within-individual delay in breeding when growing old, our results suggest earlier senescence in timing of breeding of long-distance migrants compared to short-distance migrants. A potential role of migration was also suggested to explain the contrasting pattern of senescence between two long-lived species of seabird (Berman, Gaillard & Weimerskirch 2009). Longer within-individual time series on timing of breeding are necessary to confirm this idea.

We did not find an effect of parental migration strategy on breeding success or chick condition. This could have been due to the fact that timing of breeding, an important determinant of breeding success and chick body condition, correlated with migration strategy. When the effect of hatching day was removed and unknown migrants were excluded from the analysis, chicks of short-distance migrants were in better condition (0.036 higher BCI, 95% C.I.: 0.004–0.069) than chicks of long-distance migrants ($\Delta AIC_c = -2.26$), but there was still no difference in breeding success ($\Delta AIC_c = 1.97$). The persisting absence of an effect of migration strategy on breeding success could be due to the large variation in breeding success, which may have been caused by methodological issues (variation in chick age at ringing, see Methods), or by environmental stochasticity. Chicks are very vulnerable to rainfall, especially when they are no longer able to shelter under their parents (after ca. 10 days) but not yet have a waterproof plumage. Moreover, sometimes both parents stay at the nest to provide shelter to the chicks during periods of heavy rain (O. Overdijk, pers. comm.) and consequently, the parents cannot feed and chicks may starve. In fact, 12% of the variation in breeding success turned out to be explained by the amount of rain that fell between 10 and 27 days (mean age at ringing, i.e. at which breeding success was evaluated) after hatching and was an important factor in explaining the annual variation in breeding success (2008 was a very dry year, compared to 2007 and 2009, Appendix VI, Fig. VI.2).

Overall, later breeding was associated with lower breeding success (Fig. 9.2), lower chick condition (Table 9.6), and lower post-fledging survival (assuming that the increase in survival of very late chicks was an artefact of their shorter post-fledging period, Fig. 9.3B). Moreover, chicks in poorer condition had less chance to survive the post-fledging period (Fig. 9.3C) and might even face a long-term reduction in survival probability (Fig. 9.4), suggesting long-term fitness consequences of rearing conditions (Metcalfe & Monaghan 2001).

To summarize, long-distance migrants breed later and (as a result) produce chicks of poorer condition, and seem to skip breeding more often. In combination with the general decrease in breeding success over the season, as well as the lower pre-breeding survival of late chicks and chicks in poor condition (Fig. 9.5), long-distance migrants will recruit less offspring into the breeding population than short-distance migrants (Fig. 9.6). Because their survival is also lower, this implies that the trans-Sahara migrants have lower fitness that the birds wintering in Europe. As our study is observational, it runs the risk of showing the effects of confounding variables, i.e. individual quality (Stearns 1992; Wilson & Nussey 2010). Although we cannot entirely exclude this possibility, we have strong indications that the long-distance migrating birds are unlikely to be poor quality birds. First, these birds occupy traditional wintering areas (Lok, Overdijk & Piersma 2013). In the Icelandic black-tailed godwits, the opposite pattern was found, with individuals wintering in the traditional, most distant, areas having higher survival (Gill *et al.* 2001), arriving earlier at the breeding grounds (Alves *et al.* 2012) and breeding in the higher quality habitats (Gunnarsson *et al.* 2005a), compared to individuals wintering in more recently occupied wintering areas. Unfortunately, measuring breeding success of Icelandic godwits is tricky because of the difficulty to find godwit nests and to follow chicks as they abandon their nest soon after hatching and remain very cryptic afterwards. In addition, we found that long-distance migrants had similar survival during summer and autumn migration as short-distance migrants (Chapter 8), when they can be expected to face similar (summer) or more intense environmental constraints (autumn migration).

To conclude, this study is the first to show that long-distance migrants have reduced reproductive performance compared to short-distance migrants. This suggests a cross-seasonal fitness cost of migration. The generality of these results, and the role of physiological and environmental constraints in mediating such a cost, will require further investigation, also among other migratory species. This may currently be limited by the fact that large birds are relatively easily traced in their wintering area, especially when only a limited number of areas is used, whereas monitoring reproductive output is generally easier in smaller animals, in particular nest-box breeding birds. Yet, in systems with strong gradients in isotopic signatures along the wintering range, stable isotope analysis may help in linking winter and summer events (Marra, Hobson & Holmes 1998), also of smaller animals. Moreover, the rapid development and miniaturization of tracking devices (e.g., geolocators, GPS loggers, satellite transmitters) allows the following of individuals throughout their migratory journey which will help to better understand the physiological and environmental constraints mediating such cross-seasonal costs of long-distance migration (e.g., Tøttrup *et al.* 2012). Ultimately, one would need to experimentally manipulate an individual's migration strategy to remove potentially confounding effects of individual quality, yet this appears a nearly impossible task, leaving us with the power of comparison while remaining cautious when it comes to the interpretation of the results.

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APPENDIX VI

Table VI.1 Model selection results for hatching day, when excluding the unknown migrants. The same models are considered as in Table 9.2. Results are based on 143 nests and 76 individuals (27 long- and 49 short-distance migrants). Of the 17 candidate models, only the models with Akaike weight ≥ 0.01 are shown. The most parsimonious model is shown in bold.

Hatching day		K	-2logL	ΔAIC_c	Akaike weight
(1)	$a+m2+m2:a$	6	1165.14	0.00*	0.29
(2)	$a+a^2+m2+m2:a+m2:a^2$	8	1160.75	0.03	0.28
(3)	$a+m2$	5	1169.22	1.92	0.11
(4)	$a+a^2+m2+m2:a$	7	1164.90	1.95	0.11
(5)	$a+a^2+m2+y+m2:a+m2:a^2+m2:y$	12	1154.52	3.00	0.06
(6)	$a+m2+y+m2:a+m2:y$	10	1159.35	3.16	0.06
(7)	$a+a^2+m2$	6	1168.81	3.67	0.05
(8)	$a+a^2+m2+m2:a^2$	7	1166.90	3.95	0.04
(9)	a	4	1173.90	4.47	0.03
(10)	$a+m2+y+m2:y$	9	1163.42	4.95	0.02
(11)	$a+a^2+m2+y+m2:a+m2:y$	11	1158.94	5.08	0.02
(12)	$a+a^2$	5	1173.77	6.47	0.01

*AIC_c = 1177.70

Table VI.2 Model selection results for breeding success in relation to hatching day (h), hatching day squared (h^2), year (y) and the interactions between hatching day (squared) and year. Results are based on 505 nests. The most parsimonious model is shown in bold.

Breeding success		K	-2logL	ΔAIC_c	Akaike weight
(1)	$h+h^2+y+h:y$	7	1332.21	0.00*	0.40
(2)	$h+h^2+y+h^2:y$	7	1333.46	1.24	0.22
(3)	**h+y+h:y**	**6**	**1335.80**	**1.53**	**0.19**
(4)	$h+h^2+y$	5	1339.49	3.17	0.08
(5)	$h+h^2+y+h:y+h^2:y$	9	1331.44	3.36	0.07
(6)	$h+y$	4	1342.99	4.63	0.04
(7)	$h+h^2$	3	1360.53	20.14	0.00
(8)	y	3	1362.44	22.05	0.00
(9)	h	2	1369.21	26.80	0.00
(10)	.	1	1387.06	42.63	0.00

*AIC_c = 1346.44

Table VI.3 Model selection results for chick body condition index as a function of hatching day (h), hatching day squared (h^2), year (y), number of siblings (n), relative age in the nest (a_{rel}) and interactions between hatching day (squared) and year. Results are based on 714 chicks from 416 nests. Of the 45 candidate models, only the models with Akaike weight ≥ 0.01 are shown. The most parsimonious model is shown in bold.

	Chick condition	K	-2logL	ΔAIC_c	Akaike weight
(1)	$a_{rel}+n+h+y+h{:}y$	11	-1557.87	0.00*	0.16
(2)	$a_{rel}+n+h+y$	9	-1553.48	0.27	0.14
(3)	$\mathbf{a_{rel}+h+y}$	**8**	**-1551.42**	**0.28**	**0.14**
(4)	$a_{rel}+h+y+h{:}y$	10	-1555.23	0.58	0.12
(5)	$a_{rel}+n+h+h^2+y+h^2{:}y$	12	-1558.11	1.83	0.06
(6)	$a_{rel}+n+h$	7	-1547.82	1.84	0.06
(7)	$a_{rel}+n+h+h^2+y+h{:}y$	12	-1558.05	1.89	0.06
(8)	$a_{rel}+n+h+h^2+y$	10	-1553.58	2.23	0.05
(9)	$a_{rel}+h+h^2+y$	9	-1551.51	2.25	0.05
(10)	$a_{rel}+h+h^2+y+h^2{:}y$	11	-1555.51	2.36	0.05
(11)	$a_{rel}+h+h^2+y+h{:}y$	11	-1555.35	2.52	0.04
(12)	$a_{rel}+h$	6	-1544.14	3.47	0.03
(13)	$a_{rel}+n+h+h^2$	8	-1547.82	3.88	0.02
(14)	$a_{rel}+h+h^2$	7	-1544.14	5.51	0.01

*$AIC_c = -1535.50$

Table VI.4 Model selection results for a linear effect of hatching day (h) on survival during post-fledging (Φ_{pf}), first autumn migration (Φ_{m1}), first winter (Φ_{w1}) and during subsequent years (Φ_{older}). In all models, post-fledging survival was modelled as a function of age of the chick at colour-ringing (a_{ring}). Resighting probability was modelled differently for the post-fledging, winter and summer period, and differently for subadult and adult birds in summer, with annual variation in each season. Results are adjusted for overdispersion ($\hat{c}$ = 1.17). Competing models are shown in bold.

Post-fledging survival – Hatching day					K	-2logL	ΔAIC_c	Akaike weight
(1)	**$\Phi_{pf}(a_{ring})$**	**$\Phi_{m1}(.)$**	**$\Phi_{w1}(.)$**	**$\Phi_{older}(.)$**	**28**	**8251.18**	**0.00***	**0.26**
(2)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(.)$	$\Phi_{older}(h)$	29	8250.49	1.44	0.12
(3)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(h)$	$\Phi_{w1}(.)$	$\Phi_{older}(.)$	29	8250.85	1.76	0.11
(4)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(h)$	$\Phi_{older}(.)$	29	8251.09	1.96	0.10
(5)	$\Phi_{pf}(a_{ring}+h)$	$\Phi_{m1}(.)$	$\Phi_{w1}(.)$	$\Phi_{older}(.)$	29	8251.17	2.03	0.09
(6)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(h)$	$\Phi_{w1}(.)$	$\Phi_{older}(h)$	30	8250.32	3.34	0.05
(7)	$\Phi_{pf}(a_{ring}+h)$	$\Phi_{m1}(.)$	$\Phi_{w1}(.)$	$\Phi_{older}(h)$	30	8250.46	3.46	0.05
(8)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(h)$	$\Phi_{older}(h)$	30	8250.48	3.48	0.04
(9)	$\Phi_{pf}(a_{ring}+h)$	$\Phi_{m1}(h)$	$\Phi_{w1}(.)$	$\Phi_{older}(.)$	30	8250.80	3.75	0.04
(10)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(h)$	$\Phi_{w1}(h)$	$\Phi_{older}(.)$	30	8250.84	3.79	0.04
(11)	$\Phi_{pf}(a_{ring}+h)$	$\Phi_{m1}(.)$	$\Phi_{w1}(h)$	$\Phi_{older}(.)$	30	8251.07	3.98	0.04
(12)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(h)$	$\Phi_{w1}(h)$	$\Phi_{older}(h)$	31	8250.26	5.33	0.02
(13)	$\Phi_{pf}(a_{ring}+h)$	$\Phi_{m1}(h)$	$\Phi_{w1}(.)$	$\Phi_{older}(h)$	31	8250.27	5.33	0.02
(14)	$\Phi_{pf}(a_{ring}+h)$	$\Phi_{m1}(.)$	$\Phi_{w1}(h)$	$\Phi_{older}(h)$	31	8250.45	5.49	0.02
(15)	$\Phi_{pf}(a_{ring}+h)$	$\Phi_{m1}(h)$	$\Phi_{w1}(h)$	$\Phi_{older}(.)$	31	8250.79	5.78	0.01
(16)	$\Phi_{pf}(a_{ring}+h)$	$\Phi_{m1}(h)$	$\Phi_{w1}(h)$	$\Phi_{older}(h)$	32	8250.21	7.33	0.01

*$QAIC_c$ = 7108.80

Table VI.5 Model selection results for a quadratic effect of hatching day ($h+h^2$) on survival during post-fledging, first autumn migration, first winter and during subsequent years. Resighting probability was modelled as in Table VI.4. Results have been adjusted for overdispersion ($\hat{c} = 1.17$). Competing models are shown in bold.

Post-fledging survival – Hatching day squared					K	-2logL	ΔAIC_c	Akaike weight
(1)	**$\Phi_{pf}(a_{ring}+h+h^2)$**	**$\Phi_{m1}(.)$**	**$\Phi_{w1}(.)$**	**$\Phi_{older}(.)$**	**29**	**8238.66**	**0.00***	**0.63**
(2)	$\Phi_{pf}(a_{ring}+h+h^2)$	$\Phi_{m1}(.)$	$\Phi_{w1}(.)$	$\Phi_{older}(h+h^2)$	31	8238.12	3.61	0.10
(3)	$\Phi_{pf}(a_{ring}+h+h^2)$	$\Phi_{m1}(h+h^2)$	$\Phi_{w1}(.)$	$\Phi_{older}(.)$	31	8238.30	3.76	0.10
(4)	$\Phi_{pf}(a_{ring}+h+h^2)$	$\Phi_{m1}(.)$	$\Phi_{w1}(h+h^2)$	$\Phi_{older}(.)$	31	8238.65	4.06	0.08
(5)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(.)$	$\Phi_{older}(.)$	27	8251.18	6.63	0.02
(6)	$\Phi_{pf}(a_{ring}+h+h^2)$	$\Phi_{m1}(h+h^2)$	$\Phi_{w1}(.)$	$\Phi_{older}(h+h^2)$	33	8237.72	7.35	0.02
(7)	$\Phi_{pf}(a_{ring}+h+h^2)$	$\Phi_{m1}(.)$	$\Phi_{w1}(h+h^2)$	$\Phi_{older}(h+h^2)$	33	8238.00	7.59	0.01
(8)	$\Phi_{pf}(a_{ring}+h+h^2)$	$\Phi_{m1}(h+h^2)$	$\Phi_{w1}(h+h^2)$	$\Phi_{older}(.)$	33	8238.05	7.63	0.01
(9)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(h+h^2)$	$\Phi_{w1}(.)$	$\Phi_{older}(.)$	29	8248.62	8.51	0.01
(10)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(h+h^2)$	$\Phi_{older}(.)$	29	8250.41	10.04	0.00
(11)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(.)$	$\Phi_{older}(h+h^2)$	29	8250.46	10.08	0.00
(12)	$\Phi_{pf}(a_{ring}+h+h^2)$	$\Phi_{m1}(h+h^2)$	$\Phi_{w1}(h+h^2)$	$\Phi_{older}(h+h^2)$	35	8237.40	11.17	0.00
(13)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(h+h^2)$	$\Phi_{w1}(.)$	$\Phi_{older}(h+h^2)$	31	8248.05	12.10	0.00
(14)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(h+h^2)$	$\Phi_{w1}(h+h^2)$	$\Phi_{older}(.)$	31	8248.47	12.45	0.00
(15)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(h+h^2)$	$\Phi_{older}(h+h^2)$	31	8249.79	13.58	0.00
(16)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(h+h^2)$	$\Phi_{w1}(h+h^2)$	$\Phi_{older}(h+h^2)$	33	8247.84	16.01	0.00

*$QAIC_c = 7100.14$

Table VI.6 Model selection results of the effect of chick body condition index (BCI) on survival during post-fledging, first autumn migration, first winter and during subsequent years. Resighting probability was modelled as in Table VI.4. Results have been adjusted for overdispersion ($\hat{c} = 1.17$). Competing models are shown in bold.

Post-fledging survival – BCI					K	-2logL	ΔAIC_c	Akaike weight
(1)	**$\Phi_{pf}(a_{ring}+BCI)$**	**$\Phi_{m1}(.)$**	**$\Phi_{w1}(.)$**	**$\Phi_{older}(BCI)$**	**30**	**8240.82**	**0.00***	**0.26**
(2)	**$\Phi_{pf}(a_{ring}+BCI)$**	**$\Phi_{m1}(.)$**	**$\Phi_{w1}(.)$**	**$\Phi_{older}(.)$**	**29**	**8244.98**	**1.52**	**0.12**
(3)	$\Phi_{pf}(a_{ring}+BCI)$	$\Phi_{m1}(BCI)$	$\Phi_{w1}(.)$	$\Phi_{older}(BCI)$	31	8240.27	1.56	0.12
(4)	$\Phi_{pf}(a_{ring}+BCI)$	$\Phi_{m1}(.)$	$\Phi_{w1}(BCI)$	$\Phi_{older}(BCI)$	31	8240.82	2.04	0.09
(5)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(.)$	$\Phi_{older}(BCI)$	29	8245.93	2.33	0.08
(6)	$\Phi_{pf}(a_{ring}+BCI)$	$\Phi_{m1}(BCI)$	$\Phi_{w1}(BCI)$	$\Phi_{older}(BCI)$	32	8239.47	2.92	0.06
(7)	$\Phi_{pf}(a_{ring}+BCI)$	$\Phi_{m1}(.)$	$\Phi_{w1}(BCI)$	$\Phi_{older}(.)$	30	8244.34	3.01	0.06
(8)	$\Phi_{pf}(a_{ring}+BCI)$	$\Phi_{m1}(BCI)$	$\Phi_{w1}(.)$	$\Phi_{older}(.)$	30	8244.98	3.55	0.04
(9)	$\Phi_{pf}(a_{ring}+BCI)$	$\Phi_{m1}(BCI)$	$\Phi_{w1}(BCI)$	$\Phi_{older}(.)$	31	8242.95	3.86	0.04
(10)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(BCI)$	$\Phi_{older}(BCI)$	30	8245.65	4.13	0.03
(11)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(BCI)$	$\Phi_{w1}(.)$	$\Phi_{older}(BCI)$	30	8245.93	4.37	0.03
(12)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(.)$	$\Phi_{older}(.)$	28	8251.18	4.78	0.02
(13)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(.)$	$\Phi_{w1}(BCI)$	$\Phi_{older}(.)$	29	8249.14	5.07	0.02
(14)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(BCI)$	$\Phi_{w1}(BCI)$	$\Phi_{older}(BCI)$	31	8245.06	5.66	0.02
(15)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(BCI)$	$\Phi_{w1}(.)$	$\Phi_{older}(.)$	29	8250.52	6.26	0.01
(16)	$\Phi_{pf}(a_{ring})$	$\Phi_{m1}(BCI)$	$\Phi_{w1}(BCI)$	$\Phi_{older}(.)$	30	8248.57	6.62	0.01

*$QAIC_c = 7103.98$

Table VI.7 Model selection results of first winter site choice of spoonbills (N = 106) in relation to hatching day, body condition and year. The most parsimonious model is shown in bold.

First winter site choice		K	-2logL	ΔAIC_c	Akaike weight
(1)	**h+y**	**6**	**112.60**	**0.00***	**0.60**
(2)	BCI+h+y	7	111.82	1.52	0.28
(3)	y	5	119.03	4.18	0.07
(4)	y	6	117.61	5.01	0.05
(5)	h+y	2	133.81	12.47	0.00
(6)	BCI+h	3	133.26	14.05	0.00
(7)	.	1	138.34	14.93	0.00
(8)	BCI	2	137.69	16.35	0.00

*AIC_c = 125.45

Table VI.8 Model selection results of final winter site choice of spoonbills (N = 130, 73 short-distance migrants and 57 long-distance migrants) in relation to hatching day, body condition and year. The most parsimonious model is shown in bold.

Final winter site choice		K	-2logL	ΔAIC_c	Akaike weight
(1)	**.**	**1**	**178.24**	**0.00***	**0.45**
(2)	BCI	2	177.69	1.51	0.21
(3)	h	2	177.87	1.68	0.19
(4)	BCI+h	3	177.42	3.34	0.08
(5)	y	5	175.27	5.47	0.03
(6)	BCI+y	6	174.77	7.18	0.01
(7)	h+y	6	174.78	7.19	0.01
(8)	BCI+h+y	7	174.42	9.07	0.00

*AIC_c=183.08

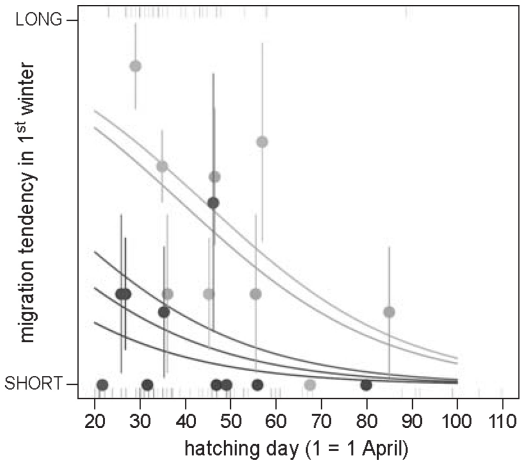


Figure VI.1 Migration strategy in the first winter as a function of hatch day and year. For 2006, data on very early chicks is missing. Winter resighting probabilities in Europe were similar in 2006–2009 and were high in West Africa in 2008 and 2009 and lowest in 2006 (Lok *et al.* 2013). Greytones represent year of birth: 2006, 2007, 2008, 2009 and 2010.

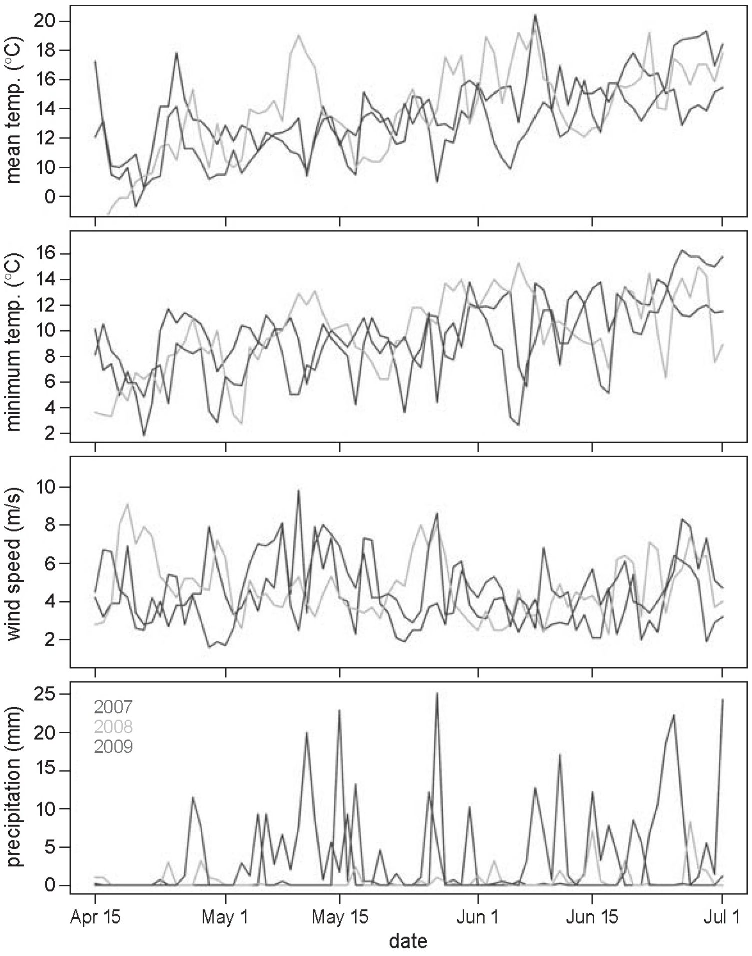


Figure VI.2 Weather conditions as a function of date during the breeding seasons of 2007–2009.

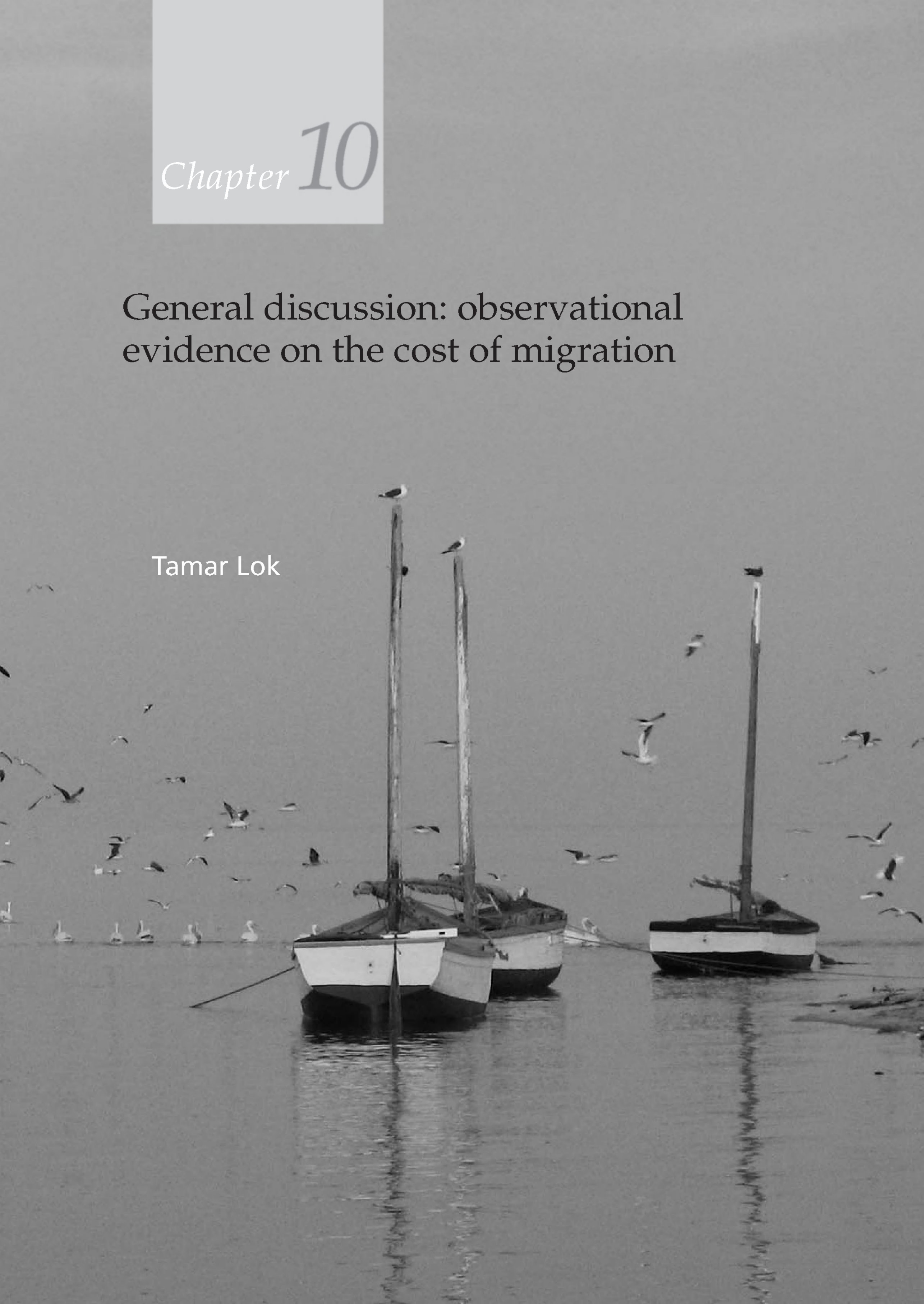
Part IV

General discussion

Chapter 10

General discussion: observational evidence on the cost of migration

Tamar Lok



FIRST SOME TECHNICAL CONCERNS[1]

In various chapters, we have applied mark-recapture analyses on the resightings (and recoveries) of colour-ringed spoonbills during different parts in their annual cycle, to estimate survival and fidelity to breeding and wintering areas (see Table 10.1 for an overview). In this section, we compare the results from the different analyses, and discuss potential explanations for apparent discrepancies.

In Chapter 5, we used all available data between 1988 and 2010, to estimate true annual survival (i.e. not confounded by permanent emigration) of different age classes of spoonbills. Using only resightings in three defined seasons of the year, we also estimated 'apparent' seasonal survival of different age classes. The annual survival, when calculated from the seasonal estimates, closely resembled the true survival estimates (Fig. 10.1). The small differences probably arose from the fact that seasonal survival has been modelled as a linear or quadratic function of population size, whereas true annual survival was estimated for each year separately. Moreover, true annual survival was estimated separately for 2^{nd} and 3^{rd} year old birds, whereas they were pooled to estimate seasonal survival (due to their low resighting probabilities in the summer periods). In Chapter 7, we estimated the population-level change in annual survival from changes in seasonal survival rates in each wintering region and the estimated changes in the number of spoonbills wintering in each region. Population-level annual survival was estimated to have decreased from 0.87 in 1994 to 0.81 in 2008, which is at the lower boundary of the estimates of true survival (Fig. 10.1). For Chapter 7, nearly the same data were used as for the seasonal survival analysis in Chapter 5, which closely resembled the true survival estimates. Therefore, the deviation cannot be explained by the difference between apparent and true survival. One other explanation is that the confidence interval for the population estimate in Chapter 7 will probably be rather large because it is based on estimates of seasonal survival per wintering area (which is less accurate than that estimated in Chapter 5, because the data is divided into three wintering regions), in combination with the estimated number of birds wintering in each area (which is based on matrix calculations using the estimated initial state and survival probabilities and assuming constant reproductive output). One other difference between Chapter 5 and 7 is that in Chapter 7, birds start their encounter history at the first observation as an adult (which is often later than at age 3), while in Chapter 5 they start their encounter history when they are born (and become automatically adult when they reach age 3 and are estimated to be still alive). When there is an age-related decline in survival, this could have resulted in lower survival estimates in Chapter 7 compared to Chapter 5.

In Chapter 8, we estimated survival during four different seasons, for three different migration strategies for a relatively short study period at high population

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[1] This is about issues of comparing results of different mark-recapture analyses. If you are interested in spoonbills or migration, skip this part.

Table 10.1 Overview of mark-recapture models and data selection used in different chapters. In grey the periods of which resightings are included.

Chapter	Parameters of interest	Mark-recapture model	Study period	Area	Month												Dead recoveries included?
					Jan	Feb	Mrt	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
5	True annual survival	Barker	1988-2010	NL				▨	▨ capture	▨	▨						Y
				All	▨	▨	▨	▨	▨	▨ interval	▨	▨	▨	▨	▨	▨	Y
	Apparent seasonal survival	CJS	1988-2010	NL		▨	▨	▨	▨		▨	▨	▨	▨			N
				EU	▨											▨	N
				M&S	▨	▨								▨	▨	▨	N
6	Fidelity and apparent annual survival per winter region	Multi-state	1992-2010	F&I	▨											▨	N
				M&S	▨	▨								▨	▨	▨	N
7	Winter site choice and per apparent seasonai survival winter region	Multi-event	1994-2010	NL			▨	▨	▨	▨	▨	▨	▨				N
				F&I	▨											▨	N
				M&S	▨	▨								▨	▨	▨	N
8	Apparent seasonal survival per migration strategy	CJS	2005-2012	NL				▨	▨	▨	▨	▨	▨				N
				W	▨	▨	▨							▨	▨	▨	N
9	Breeding propensity	CJS	2006-2010	NL				▨	▨	▨	▨	▨					N
	Post-fledging survival	CJS	2006-2012	NL								▨ age 0	▨				N
				All	▨	▨		▨	▨	▨	▨	▨	▨		▨	▨	N

NL=Netherlands, EU=Europe, F&I=France & Iberia, M&S=Mauritania & Senegal, W=winter region

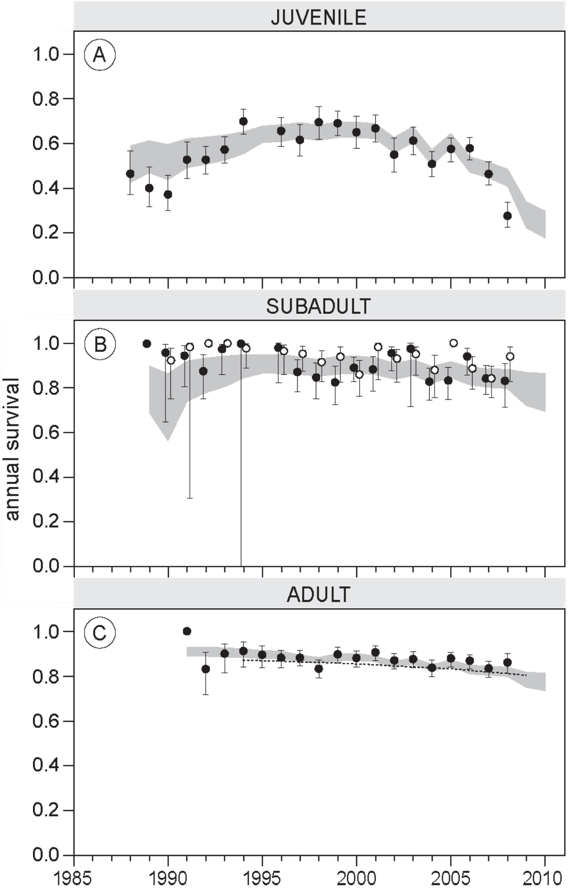

Figure 10.1 Comparison of estimates of annual survival of (A) juvenile, (B) subadult and (C) adult birds from different analyses. The black dots are the annual true survival maximum likelihood estimates of the Barker model (Chapter 5), the shaded grey area is the 95% confidence interval of annual survival when calculated from the seasonal survival estimates of the three-season CJS model (see also Fig. II.3) and the dotted line (in panel C) is the adult annual survival calculated from the winter-region specific seasonal survival estimates and the estimated number of birds wintering in each region (Chapter 7).

sizes (2005-2012). These seasonal survival estimates differ quite substantially from those in Chapter 7. In Chapter 8 we showed that survival during spring migration was much lower for birds wintering in Mauritania and Senegal, compared to those wintering in Europe, which contradicts the seasonal estimates shown in Fig. IV.2, where survival from winter to summer was estimated to be similar for the three migration strategies, and the lower annual survival appeared mainly caused by the survival from summer to winter that was lower for the birds wintering in Mauritania and Senegal. The most plausible explanation for this discrepancy seems to be that birds that were never resighted in winter were included in the analysis of Chapter 7. For those birds, summer-winter and winter-summer survival cannot be separated, which may have resulted in increased uncertainty about the season in which most mortality occurred. In contrast to the seasonal estimates, annual survival estimates were comparable (given the large confidence intervals around the estimates of Chapter 8).

The calculated annual survival estimates from Chapter 8 were 0.94, 0.89 and 0.83 for France, Iberia and Mauritania & Senegal. These estimates are higher than the apparent annual survival per winter region in Chapter 6 estimated at 0.81 in France and Iberia and 0.74 in Mauritania and Senegal. In this analysis, only winter resightings were used, so if birds permanently moved to sites with low resighting efforts, they may never be resighted again and appear dead. Despite the high fidelity at the scale of entire winter regions, small-scale movements (<100 km) were shown to be rather common (Fig. 6.4). When this happens regularly and these birds are still observed in the Netherlands, they remain alive in the analysis in Chapter 8 that used summer resightings as well.

The main aim in Chapter 6 was to estimate winter site fidelity, and therefore, only birds were included that were observed at least once in the wintering area. In this analysis, we also estimated initial state probabilities (i.e. the probability that a bird wintered in a specific region in its first year of life) and calculated the winter distribution of older birds, based on fidelity and survival estimates (Fig. 6.3). One could imagine if there is a wintering area where resighting probability is consistently lower than in other wintering regions, a bird wintering in this area has a lower probability to be observed in winter during its life, and therefore a lower probability to be included in the above described analysis. This could result in an underestimation of the initial state probability to winter in this area. When we compare the estimated probabilities of wintering in each region from this winter site fidelity analysis with those of Chapter 7 (Fig. 7.2), where also the individuals never observed in winter were included in the analysis, they are fairly comparable. This may be explained by the fact that spoonbills are long-lived and faithful to their wintering area and that in none of the wintering regions, resighting probability was low throughout the study period (see Fig. IV.2). As a result, birds in all wintering regions may have had a more or less similar chance to be observed in winter at least once during their life.

In Chapter 6 and 7, we showed that, at least the adult, spoonbills wintering in different wintering areas had different survival and different chances to be resighted in summer and winter (Chapter 6 and 7). Such migration-strategy specific differences in resighting and survival probabilities were not accounted for in the survival analysis in Chapter 5, which was one of the first written. Ignoring individual heterogeneity in resighting probability could cause a spurious positive trend in survival, which will be especially severe in short-term studies (Lebreton 1995). Given the long time series (22 years), it is unlikely that this heterogeneity in resighting probability strongly biased the results of Chapter 5.

THE EVOLUTION OF MIGRATION PATTERNS: WHAT WE LEARNT

Migration is assumed to have evolved to allow the exploitation of highly productive breeding areas and benign wintering areas, accounting for the costs of moving between them (e.g. Alerstam, Hedenstrom & Akesson 2003). To explain the enormous variation in migration patterns that exists in nature, numerous theories have been developed (Von Haartman 1968; Ketterson & Nolan 1976; Alerstam & Högsted 1980; Greenberg 1980; Alerstam, Hedenstrom & Akesson 2003; Bell 2005). All these theories are based on assumptions about the costs and benefits of migration, yet a comprehensive empirical evaluation of the magnitude of the fitness costs and benefits associated with different migration patterns has not yet been performed. This is probably due to the difficulty to collect such data, as it requires (1) that individuals are followed throughout their annual cycle, and (2) that the study covers multiple years to allow the estimation of annual and seasonal survival in relation to variation in migration strategies.

The spoonbill system is one of the few systems that meet these conditions. As part of a conservation plan and because of special personal dedication by the workers of 'Werkgroep Lepelaar', spoonbills have been individually colour-ringed for over 25 years. Probably through a combination of their conservation status, their beauty, and the immediate and enthusiastic feedback from the database managers, many enthusiastic ornithologists have read and reported their rings, which allowed us to accurately estimate annual and seasonal survival over a long period. In addition, during this period, the population has gone through a phase of steep growth, enabling us to judge the role density dependence played in shaping migration patterns on the basis of the mortality associated with different migration strategies.

In the present study, we assessed the demographic costs and benefits of migration by comparing annual and seasonal survival and reproductive performance of individuals with contrasting migration strategies, during 25 years of rapid population growth. Based on this comparative approach, we would conclude that migration is costly, as the birds that migrated the longest distances, and wintered in Mauritania or Senegal, had the lowest survival during (spring) migration (Chapter 8), bred later, which was correlated with lower reproductive output, and seemed to skip breeding more often (Chapter 9). We found no cost of wintering at temperate latitudes in Europe, as winter survival was similar (and very high) in Europe and Mauritania & Senegal (Chapter 8). As a result of this, long-distance migrants had lower annual survival than short-distance migrants (Chapter 6 and 7). Because the long-distance migrants do not compensate this lower survival by higher reproductive output (Chapter 9), their overall fitness is lower than that of short-distance migrants.

For a true assessment of the fitness costs and benefits of different migration strategies, we would have to experimentally manipulate migration strategies of individuals, to remove any confounding effects of a correlation between an individual's quality and its migration strategy. Moreover, this would provide the opportunity to include migration strategies that do not (yet) naturally exist. For example, we found no effect of wintering area on winter survival (Chapter 8), but it is very well possible that if birds would remain resident to the Netherlands, their winter survival would have been lower. Although this sounds ideal, it also appears as a challenging and tedious task. The first challenge is to manipulate an individual's migration strategy. This is possibly difficult for adult birds that are highly faithful to their wintering site and are likely to return to their original wintering area after manipulation, either directly or in the subsequent winter. One could opt to manipulate juvenile birds (that are not yet very attached to their wintering site, Chapter 6), but this would imply that the study has to wait another three years before these birds will be adult and start to migrate and breed, the point at which the costs and benefits associated with a given migration strategy only fully come to light. After these four years, these birds should be monitored for at least another couple of years to assess their seasonal survival and reproductive output. Given the intensive and long-term effort required for performing such an experiment, together with the large uncertainty about a successful outcome, comparative approaches to tackle questions about costs and benefits associated with migration seem like the best option available.

In our comparative approach, we therefore cannot entirely exclude the possibility that the long-distance migrating spoonbills were poor quality birds, for example because they were the poor competitors that were displaced from the good quality sites in Europe (Gauthreaux 1978). Yet, two important findings from the present study render this an unlikely scenario. First, we show that seasonal survival of long- and short-distance migrants only significantly differed during spring migration, with virtually all mortality of long-distance migrating birds occurring in that season (Chapter 9). During the breeding season in the Netherlands, when birds from different wintering areas come together to breed (Chapter 8), there was even some evidence (though not statistically significantly so) that birds wintering in Mauritania had higher survival than those wintering in Iberia (Chapter 9). This suggests that there are at least no major quality differences between individuals with different migration strategies.

Second, if competition would play a role in shaping the wintering distribution of spoonbills, established theories predict that an increasing part of the population would start to inhabit poorer quality sites, either through competitive displacement (Pulliam & Danielson 1991) or through interference competition (Fretwell & Lucas 1970). Such a pattern was confirmed for the rapidly growing population of Icelandic black-tailed godwits, where an increasing part of the population started occupying wintering areas associated with lower survival (Gill *et al.* 2001) and lower reproductive output (Gunnarsson *et al.* 2005a). However, the spoonbills showed the opposite pattern (Chapter 7): most birds traditionally occupied the 'lower survival' wintering areas in Mauritania and Senegal and showed a clear northward shift in winter distribution over the past 16 years, towards more birds wintering in 'high survival' areas in Europe. The most likely explanation for this observation appeared to be that conditions for wintering in Europe have improved and that we are witnessing a response to these improved conditions, rather than observing a density-dependent shift of birds toward less suitable wintering areas. This result makes it unlikely that the birds wintering in Mauritania and Senegal are poor competitors, or otherwise poor quality birds, that are forced to winter there. This is a very important finding, as this suggests that the lower survival and reproductive output of the long-distance migrating birds is not caused by differences in individual quality, but by the fact that they migrate longer distances, have to cross the Sahara during migration, and winter in different areas that offer very different resources. A schematic overview of the estimated demographic parameters in relation to migration distance, and an estimate of lifetime reproductive success of birds, given they survived until adulthood, is shown in Fig. 10.2. From this figure, it can be seen that the cost of migration is no simple linear function of migration distance, but there is a rather steep drop in fitness (expressed as lifetime recruitment success) between the Iberian and West African winterers. The fact that the birds wintering in Mauritania or Senegal have to cross the Sahara may play an important role in shaping this non-linear relationship.

Costs and benefits associated with different migration strategies may vary within and between individuals. First, the costs and benefits of wintering in a specific area may change with age. I deliberately changed here from using the term 'migration strategy' to 'wintering in a specific area', because immature spoonbills do not exhibit seasonal migration. After having migrated south during their first autumn migration, and, sometimes moving further south between their first and second winter (Chapter 6), they remain on the wintering grounds until they become adult. Therefore, immature birds do not pay the cost of migrating far in terms of reduced spring survival and delayed breeding. Consequently, wintering further south could be more beneficial (or at least less costly) for immature than for adult birds. This was supported by the fact that survival from first to second winter was not significantly different between wintering areas (Chapter 6, Table 2, model 1 was substantially less supported than model 2; $\Delta QAIC_c = 3.47$). As such, adults are expected to winter closer to the breeding grounds than immature birds, as was observed in many different species (Cristol, Baker & Carbone 1999; Marques, Sowter & Jorge 2010). However, such a pattern was not observed in this spoonbill population: juveniles on average wintered further north, and after the first year, spoonbills became highly faithful to their wintering area (Chapter 6) with no apparent shift to wintering closer the breeding grounds once birds became adult.

What we were not able to estimate, however, is the mortality cost of migrating far during the first autumn migration, because when a juvenile dies during this first migration, its winter destination will never be known. If this cost of migrating far is very high for immature birds, this could explain why juvenile birds on average wintered further north than adults in this spoonbill population (Chapter 6). That in other species juveniles winter further south than adults, could be explained by juveniles and adults facing a different cost-benefit trade-off with respect to migration strategies depending on the species, or by the fact that the role of competition in

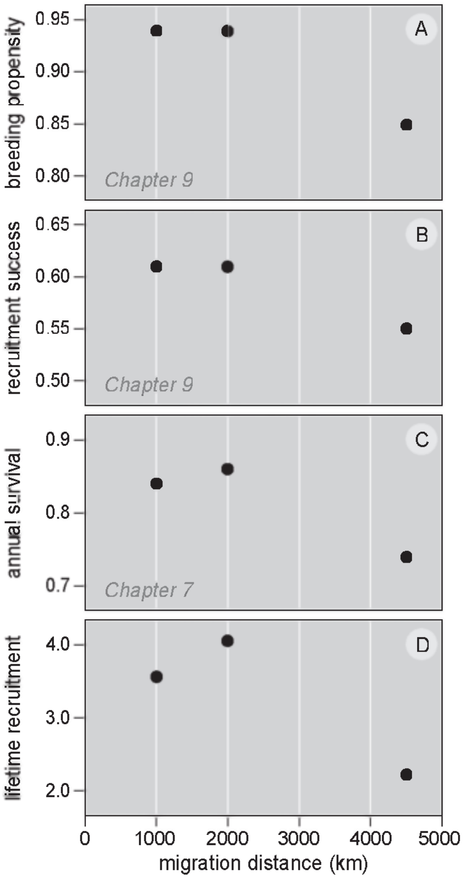

Figure 10.2 Overview of demographic parameters in relation migration distance, with (A) breeding propensity, assuming that true resighting probability of breeding birds is 1, (B) recruitment success and (C) annual survival per migration distance (the estimates for 2010 were taken). From these parameters, we calculated (D) lifetime recruitment success of adult birds (i.e. of birds that had survived until adulthood). Breeding propensity and recruitment success were estimated for France and Iberia together.

shaping current migration patterns differs among species. In species where competition for wintering sites is strong, juveniles may be forced to winter further south through competition with older, more dominant, conspecifics.

Rather than within individuals (e.g., with age), the costs and benefits of wintering in a specific area may differ between individuals, such as between males and females. For example, males, that may have to compete for good quality nest sites within the colony, may benefit more from arriving early at the breeding grounds than females. Moreover, sex-specific variation in body size could affect how well males and females can cope with harsh winter conditions. Sex-differential migration has been described for many bird species (reviewed by Cristol, Baker & Carbone 1999; Nebel 2007). In spoonbills, we found some evidence for sex-differential migration in spoonbills, with males being more likely to winter in Europe and females in Mauritania and Senegal (Chapter 9). Unfortunately, spoonbills are difficult to sex using visual cues, although reliability is considerably increased when visual sexing is done when birds are observed as a breeding pair (although still some mistakes are made then, pers. obs.). The combination of this resulted in a relatively low sample size of birds with molecularly-known sex, especially when grouped per wintering region. Explorative analyses showed that annual survival did not differ between males and females, also not when the sex effect was tested for separate wintering regions. The lack of a sex effect on annual survival could be caused by survival being truly similar for both sexes, or by low sample size. Therefore, we decided not to pay further attention to sex differences within this thesis. Nonetheless, it is an interesting future line of research to investigate whether male and female spoonbills face different constraints with respect to winter site choice. To start with, sex determination of spoonbills should be done when they are colour-ringed as a chick. This can be done using molecular sexing, but we showed that the sex of spoonbill chicks may also be fairly reliably determined from biometric measures (Chapter 3). When sample sizes are large enough, we would then be able to estimate survival during migration and winter (as in Chapter 8) for both sexes. This allows us to test whether the larger (and especially heavier) males have higher winter survival in Europe than the smaller (lighter) females (Ketterson & Nolan 1976), but that the females, potentially as a result of their lower body weight, may have higher survival during migration.

FROM DEMOGRAPHY TO MECHANISM

To understand how general our results are for other migratory species, we should know more about the mechanisms underlying the variation in seasonal survival, reproduction and density dependence. The present study revealed that survival of adult birds decreased most strongly in late winter (including spring migration) and that the decrease in annual survival was similar in all three wintering regions (Chapter 6). Combined with the fact that survival was very high in winter – estimated during a period of high population sizes (Chapter 8) – this suggests that the (density-dependent) decrease in survival was strongest during spring migration. This decrease in survival could result from carry-over effects from winter, or from factors that actually manifest during spring migration.

At present, we can only speculate about the intensity of competition for food in winter and stopover areas. It seems plausible that competition for food is higher during stopover, when spoonbills gather in high numbers in relatively small areas. For example, many spoonbills from the Netherlands make a stopover in the Santoña Marshes in northern Spain during autumn migration (Navedo *et al.* 2010a; Navedo *et al.* 2010b), but, based on the number of resightings, this area appears to be less intensively used during spring migration. The Odiel Marshes and Rocio Marshes (the latter situated in Donaña National Park) in southern Spain are used for both wintering and stopover by birds wintering further south in Mauritania and Senegal. During spring migration, these areas are probably of crucial importance for the latter group for refuelling after having crossed the Sahara. Competition for food in these areas could be strong, and cause a density-dependent decrease in spring survival. It could be imagined that this more strongly affects the birds from Mauritania and Senegal, because they have more acute energetic demands. The Iberian winterers may even have departed northward already at the time their southern conspecifics arrive. More detailed observations are needed to quantify the intensity to which the Odiel marshes and the Coto Doñana are used during autumn, and especially during spring, as these areas may be of crucial importance for spoonbills to successfully complete their seasonal migrations.

FUTURE DEVELOPMENT OF THE SPOONBILL POPULATION

The spoonbill population in The Netherlands is still growing, yet the end of this growth appears in sight (Fig. 1.2). At the same time, the population is expanding into Germany, Denmark, the United Kingdom and Belgium, but at a rather slow rate. That the expansion is so slow may be caused by a tendency to breed in The Netherlands (similar to the tendency to migrate far, Chapter 7), but could also be caused by survival being mainly density dependent away from the breeding grounds (Fig. 5.4). Density-dependent nonbreeding season mortality would limit the growth of all Northwest European breeding populations to a similar extent. Further growth of the population could be achieved by reducing the strength of density dependence in non-breeding survival. Assuming that food availability is the main limiting factor causing density dependence, management actions that increase the quality or availability of suitable foraging areas at these sites will result in an increase in the carrying capacity of the entire Northwest European breeding population.

In addition to density dependence in survival of all age classes in the non-breeding season, we also found, for juveniles, evidence of density-dependent survival in summer (i.e., on the breeding grounds) (Fig. 5.4). Moreover, the strong density-dependent decrease in juvenile survival in early winter (Fig. 5.4) could also have been caused by density-dependent carry-over effects from the breeding grounds, rather than by factors away from the breeding grounds. For example, competition with conspecifics on the breeding grounds may cause the inexperienced juvenile birds to be in poorer condition at the onset of migration, resulting in an increased risk of dying during migration. If the density-dependent decrease in juvenile survival is (mainly) driven by factors on the breeding grounds, further growth of the breeding population outside The Netherlands is to be expected and enhanced foraging conditions (assuming that food was the limiting factor) on the breeding grounds may increase juvenile summer (and potentially early winter) survival and result in an increase of the local breeding populations.

SPOONBILLS AS A MODEL SYSTEM?

We believe, and hope, to have convinced you throughout this thesis that the Eurasian spoonbill is a very suitable model system for quantifying potential costs and benefits associated with migration. In other systems, individuals have been followed throughout (part of) their annual cycle to estimate seasonal survival, mainly in geese (Clausen *et al.* 2001; Gauthier *et al.* 2001; Madsen, Frederiksen & Ganter 2002; Varner & Eichholz 2012), or to correlate individual migration distances with annual survival (Sanz-Aguilar *et al.* 2012), arrival time at the breeding grounds (Hötker 2002; Bregnballe, Frederiksen & Gregersen 2006; Gunnarsson *et al.* 2006) or breeding success (Bregnballe, Frederiksen & Gregersen 2006; Massemin-Challet *et al.* 2006). However, none were able to estimate seasonal survival for contrasting migration strategies, let alone to integrate this with estimates of individual breeding success.

While the focus has been on a within-population comparison throughout this thesis, the spoonbill system also provides the opportunity to extend the comparison among breeding populations (i.e. the Netherlands, France, Iberia and Mauritania, see Fig. 1.1), allowing the assessment of the (potential) benefits of breeding at higher latitudes. Ultimately, comparisons among different species and ecosystems are needed to verify the generality and specificity of the demographic costs and benefits of various migration patterns (e.g. Piersma 2007). Yet, this study on spoonbills has also made us realize the immense human, logistical and financial investments that are required to allow such a comprehensive comparison of the evolutionary costs and benefits of migration for any long-distance migrating bird species.

References

A

Abraham, C.L. (2008) Relative contribution of euphausiid prey species and timing of breeding to Cassin's auklet *Ptychoramphus aleuticus* growth: within-season effects. *Journal of Avian Biology*, **39**, 178-188.

Achord, S., Levin, P.S. & Zabel, R.W. (2003) Density-dependent mortality in Pacific salmon: the ghost of impacts past? *Ecology Letters*, **6**, 335-342.

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. *International Symposium on Information Theory*, 2nd edn (eds B.N. Petran & F. Csáki), pp. 267-281. Akadémiai Kiadi, Budapest.

Alerstam, T. (1990) *Bird migration*. Cambridge University Press, Cambridge.

Alerstam, T., Hedenstrom, A. & Akesson, S. (2003) Long-distance migration: evolution and determinants. *Oikos*, **103**, 247-260.

Alerstam, T. & Högsted, G. (1980) Spring predictability and leap-frog migration. *Ornis Scandinavica*, **11**, 196-200.

Alexander, R.M. (1998) When is migration worthwhile for animals that walk, swim or fly? *Journal of Avian Biology*, **29**, 387-394.

Altenburg, W. & Wymenga, E. (1997) *Voedsel voor lepelaars*. Rapport Vogelbescherming Nederland 32, Zeist.

Alves, J.A., Gunnarsson, T.G., Potts, P.M., Gelinaud, G., Sutherland, W.J. & Gill, J.A. (2012) Overtaking on migration: does longer distance migration always incur a penalty? *Oikos*, **121**, 464-470.

Anderson, D.J., Reeve, J., Gomez, J.E.M., Weathers, W.W., Hutson, S., Cunningham, H.V. & Bird, D.M. (1993) Sexual size dimorphism and food requirements of nestling birds. *Can. J. Zool.* **71**: 2541-2545.

Arcese, P., Smith, J.N.M. , Hochachka, W.M. , Rogers, C.M. & Ludwig, D. (1992) Stability, regulation, and the determination of abundance in an insular song sparrow population. *Ecology*, **73**, 805-822.

Armstrong, D.P., Davidson, R.S., Perrott, J.K., Roygard, J. & Buchanan, L. (2005) Density-dependent population growth in a reintroduced population of North Island saddlebacks. *Journal of Animal Ecology*, **74**, 160-170.

Arnason, A.N. (1973) The estimation of population size, migration rates and survival in a stratified population. *Researches in Population Ecology*, **15**, 1-8.

Arnold, T.W. (2010) Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management*, **74**, 1175-1178.

Avital, E. & Jablonka, E. (2000) *Animal traditions: behavioural inheritance in evolution*. Cambridge University Press, Cambridge.

B

Bailey, M.M., Horton, G.E. , Letcher, B.H. & Kinnison, M.T. (2010) Seasonal density dependence in Atlantic salmon over varying spatial scales. *Transactions of the American Fisheries Society*, **139**, 1642-1656.

Baker, R.R. (1978) *The evolutionary ecology of animal migration*. Holmes & Meier Publishers, New York.

Baker, R.R. (1982) *Migration: paths through space and time*. Kent: Hodder and Stoughton Educational Limited.

Barnes, G.G. & Nudds, T.D. (1991) Salt tolerance in American black ducks, mallards, and their F1-hybrids. *Auk*, **108**, 89-98.

Bates, D., Maechler, M. & Bolker, B. (2011) lme4: Linear mixed-effects models using S4 classes.

Bauchau, V., Horn, H. & Overdijk, O. (1998) Survival of spoonbills on Wadden Sea islands. *Journal of Avian Biology*, **29**, 177-182.

Bearhop, S., Thompson, D.R., Waldron, S., Russell, I.C., Alexander, G. & Furness, R.W. (1999) Stable isotopes indicate the extent of freshwater feeding by cormorants (*Phalacrocorax carbo*) shot at inland fisheries in England. *Journal of Applied Ecology*, **36**, 75-84.

Bearhop, S., Waldron, S., Votier, S.C. & Furness, R.W. (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and biochemical zoology*, **75**, 451-458.

Beaulieu, M., Spee, M., Lazin, D., Ropert-Coudert, Y., le Maho, Y., Ancel, A. & Raclot, T. (2010) Ecophysiological response of Adelie penguins facing an experimental increase in breeding constraints. *Journal of Experimental Biology*, **213**, 33-39.

Bell, C.P. (2005) Inter- and intrapopulation migration patterns. Birds of two worlds: the ecology and evolution of migration (eds R. Greenberg & P.P. Marra), pp. 41-52. Johns Hopkins University Press, Baltimore.

Berman, M., Gaillard, J.M. & Weimerskirch, H. (2009) Contrasted patterns of age-specific reproduction in long-lived seabirds. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 375-382.

Berthold, P. (2001) Bird migration: a novel theory for the evolution, the control and the adaptability of bird migration. *Journal für Ornithologie*, **142**, 148-159.

Bêty, J., Gauthier, G. & Giroux, J.F. (2003) Body condition, migration, and timing of reproduction in snow geese: A test of the condition-dependent model of optimal clutch size. *American Naturalist*, **162**, 110-121.

Birdlife Netherlands (1997) *Themanummer: lepelaars, vogelnieuws*. Birdlife Netherlands 16.

Bregnballe, T., Frederiksen, M. & Gregersen, J. (2006) Effects of distance to wintering area on arrival date and breeding performance in great cormorants *Phalacrocorax carbo*. *Ardea*, **94**, 619-630.

Brownie, C., Hines, J.E., Nichols, J.D., Pollock, K.H. & Hestbeck, J.B. (1993) Capture-recapture studies for multiple strata including non-markovian transitions. *Biometrics*, **49**, 1173-1187.

Bryant, R., Jones, I.L. & Hipfner, J.M. (1999) Responses to changes in prey availability by common murres and thick-billed murres at the Gannet Islands, Labrador. *Canadian Journal of Zoology*, **77**, 1278-1287.

Burnham, K. & Anderson, D. (2002) *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd edn. Springer-Verlag, New York.

Barbraud, C. & Weimerskirch, H. (2003) Climate and density shape population dynamics of a marine top predator. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, **270**, 2111-2116.

Barker, R.J. (1997) Joint modeling of live-recapture, tag-resight, and tag-recovery data. *Biometrics*, **53**, 666-677.

Barker, R.J., Burnham, K.P. & White, G.C. (2004) Encounter history modeling of joint mark-recapture, tag-resighting and tag-recovery data under temporary emigration. *Statistica Sinica*, **14**, 1037-1055.

Bauchau, V., Horn, H. & Overdijk, O. (1998) Survival of spoonbills on Wadden Sea islands. *Journal of Avian Biology*, **29**, 177-182.

Begon, M., Townshend, C.R. & Harper, J.L. (2006) *Ecology: from individuals to ecosystems*. Blackwell Publishing, Oxford.

Beintema, A.J. & Visser, G.H. (1989) Growth parameters in chicks of charadriiform birds. *Ardea*, **77**, 169-180.

Bell, C.P. (2005) Inter- and intrapopulation migration patterns. *Birds of two worlds: the ecology and evolution of migration* (eds R. Greenberg & P.P. Marra), pp. 41-52. Johns Hopkins University Press, Baltimore.

Benson, J., Suryan, R.M. & Piatt, J.F. (2003) Assessing chick growth from a single visit to a seabird colony. *Marine Ornithology*, **31**, 181-184.

Bêty, J., Gauthier, G. & Giroux, J.F. (2003) Body condition, migration, and timing of reproduction in snow geese: A test of the condition-dependent model of optimal clutch size *American Naturalist*, **162**, 110-121.

Bolton, M. (1995) Experimental evidence for regulation of food delivery to storm petrel, *Hydrobates pelagicus*, nestlings - the role of chick body condition. *Animal Behaviour*, **50**, 231-236.

Both, C. (1998) Experimental evidence for density dependence of reproduction in great tits. *Journal of Animal Ecology*, **67**, 667-674.

Both, C. (2010) Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Current Biology*, **20**, 243-248.

Both, C. & Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296-298.

Box, G.E.P., Jenkins, G.M. & Reinsel, G.C. (1994) Time series analysis: forecasting and control, 3rd edn. Holden-Day, San Francisco.

Boyce, M.S., Sinclair, A.R.E. & White, G.C. (1999). Seasonal compensation of predation and harvesting. *Oikos*, 87, 419-426.

Bregnballe, T., Frederiksen, M. & Gregersen, J. (2006) Effects of distance to wintering area on arrival date and breeding performance in great cormorants *Phalacrocorax carbo*. *Ardea*, **94**, 619-630.

Brook, B.W. & Bradshaw, C.J.A. (2006) Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*, **87**, 1445-1451.

Brouwer, G.A. (1964) Some data on the status of the spoonbill, *Platalea leucorodia* L., in Europe, especially in the Netherlands. *Zoologische Mededelingen*, **39**, 481-521.

Brown, J.L. (1969) Territorial behavior and population regulation in birds. *Wilson Bulletin*, **81**, 293-329.

Bryant, D. M. & Tatner, P. (1988). Energetics of the annual cycle of dippers *Cinclus cinclus*. *Ibis*, **130**, 17-38.

Burnham, K. & Anderson, D. (2002) *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd edn. Springer-Verlag, New York.

Burnham, K.P. & White, G.C. (2002) Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics*, **29**, 245-264.

C

Campos, J., Bio, A., Cardoso, J., Dapper, R., Witte, J.I.J. & van der Veer, H.W. (2010) Fluctuations of brown shrimp *Crangon crangon* abundance in the Western Dutch Wadden Sea. *Marine Ecology Progress Series*, **405**, 203-219.

Campos, J., Moreira, C., Freitas, F. & van der Veer, H.W. (2012) Short review of the eco-geography of *Crangon*. *Journal of Crustacean Biology*, **32**, 159-169.

Caswell, H. (2001) *Matrix population models: construction, analysis and interpretation*, 2nd edn. Sinauer Associates, Sunderland.

Catchpole, E.A., Morgan, B.J.T., Coulson, T.N., Freeman, S.N. & Albon, S.D. (2000) Factors influencing Soay sheep survival. *Journal of the Royal Statistical Society Series C-Applied statistics*, **49**, 453-472.

Caut, S., Angulo, E. & Courchamp, F. (2009) Variation in discrimination factors (δ^{15}N and δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology*, **46**, 443–453.

Cézilly, F., Boy, V. & Green, R.E. (1995) Interannual variation in greater flamingo breeding success in relation to water levels. *Ecology*, **76**, 20-26.

Chapman, B.B., Bronmark, C., Nilsson, J.A. & Hansson, L.A. (2011) The ecology and evolution of partial migration. *Oikos*, **120**, 1764-1775.

Chisholm, B.S., Nelson, D.E. & Schwarcz, H.P. (1982) Stable-carbon isotope ratios as a measure of marine versus terrestrial protein in ancient diets. *Science*, **216**, 1131-1132.

Choquet, R., Rouan, L. & Pradel, R. (2009) Program E-SURGE: A software application for fitting multievent models. *Modeling demographic processes in marked populations* (eds D.L. Thomson, E.G. Cooch & M.J. Conroy), pp. 845-865. Springer, New York.

Clausen, P., Frederiksen, M., Percival, S.M., Anderson, G.Q.A. & Denny, M.J.H. (2001) Seasonal and annual survival of East-Atlantic pale-bellied brent geese *Branta hrota* assessed by capture-recapture analysis. *Ardea*, **89**, 101-111.

Cooch, E. & White, G.C. (2011) *Program MARK: a gentle introduction*, 11th edn.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution*, **14**, 405-410.

Cox, C. (1998) Delta method. *Encyclopedia of Biostatistics* (eds P. Armitage & T. Colton), pp. 1125-1127. John Wiley & Sons, Chicester.

Craig, H. (1953) The geochemistry of the stable carbon isotopes. *Geochimica et Cosmochimica Acta*, **3**, 53-92.

Cramp, S. (1994) *The birds of the Western Palearctic*. Oxford University Press, Oxford.

Cramp, S. & Simmons, K.E.L. (1977) Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic, Vol. 1: Ostrich to ducks. Oxford University Press, Oxford.

Cristol, D.A., Baker, M.B. & Carbone, C. (1999) Differential migration revisited: latitudinal segregation by age and sex class. *Current Ornithology*, **15**, 33-88.

Cutts, C.J. & Speakman, J.R. (1994) Energy savings in formation flight of pink-footed geese. *Journal of Experimental Biology*, **189**, 251-261.

D

Daan, S., Dijkstra, C., Drent, R.H. & Meijer, T. (1989) Food supply and the annual timing of reproduction. *Proceedings of the XIXth International Ornithological Congress*. Ottawa Press I, Ottawa.

Davoren, G.K. & Burger, A.E. (1999) Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Animal Behaviour*, **58**, 853-863.

de Goeij, P., Kemper, J.H. & van Wetten, J.C.J. (1985) De lepelaar in het Waddengebied. *Wadden Bulletin*, **20**, 5-7.

de le Court, C. & Aguilera, E. (1997) Dispersal and migration in Eurasian spoonbills *Platalea leucorodia*. *Ardea*, **85**, 193-202.

de Naurois, R. & Roux, F. (1974). Précisions concernant la morphologie, les affinités et la position systematique de quelques oiseaux du Banc d'Arguin (Mauritanie). *L'Oiseau et la Revue Française d'Ornithologie*, **44**, 72-84.

de Voogd, M. (2005) Methods to sex juvenile spoonbills and sex-specific migration in spoonbills. Master Thesis, University of Groningen, The Netherlands.

Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Zijlstra, M. (1990) Brood size manipulations in the kestrel (*Falco tinnunculus*) – effects on offspring and parent survival. *Journal of Animal Ecology*, **59**, 269-285.

Dingle, H. (1980) Ecology and evolution of migration. *Animal migration, orientation and navigation* (ed. S.A. Gauthreaux), pp. 1-101. Academic Press, New York.

Doherty, P.F., Williams, J.B. & Grubb, T.C. (2001) Field metabolism and water flux of Carolina chickadees during breeding and nonbreeding seasons: A test of the 'peak-demand' and 'reallocation' hypotheses. *Condor*, **103**, 370-375.

Donald, P.F., Sanderson, F.J., Burfield, I.J., Bierman, S.M., Gregory, R.D. & Waliczky, Z. (2007) International conservation policy delivers benefits for birds in Europe. *Science*, **317**, 810-813.

Dosch, J.J. (1997) Salt tolerance of nestling laughing gulls: An experimental field investigation. *Colonial Waterbirds*, **20**, 449-457.

Doxa, A., Theodorou, K., Hatzilacou, D., Crivelli, A. & Robert, A. (2010) Joint effects of inverse density-dependence and extreme environmental variation on the viability of a social bird species. *Ecoscience*, **17**, 203-215.

Drent, R., Both, C., Green, M., Madsen, J. & Piersma, T. (2003) Pay-offs and penalties of competing migratory schedules. *Oikos*, **103**, 274-292.

Dugatkin, L.A. (2001) Model systems in behavioral ecology: integrating conceptual, theoretical, and empirical approaches. *Monographs in behavior and ecology*. Princeton University Press, Princeton and Oxford.

E

Eberhardt, L.L. (2002) A paradigm for population analysis of long-lived vertebrates. *Ecology*, **83**, 2841-2854.

Eggers, S. 2000. Compensatory frugivory in migratory Sylvia warblers: geographical responses to season length. *Journal of Avian Biology*, **31**, 63-74.

El-Hacen, E.M., Overdijk, O., Lok, T., Olff, H. & Piersma, T. (2013) Home range, habitat selection, and foraging rhythm in Mauritanian spoonbills (*Platalea leucorodia balsaci*): a satellite tracking study. *Waterbirds*, **36**, 277-286.

Eriksson, B.K., van der Heide, T., van de Koppel, J., Piersma, T., van der Veer, H.W. & Olff, H. (2010) Major changes in the ecology of the Wadden Sea: human impacts, ecosystem engineering and sediment dynamics. *Ecosystems*, **13**, 752-764.

Excoffier, L., Laval, G. & Schneider, S. (2005) Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47-50.

F

Ferrer, M. & Donazar, J.A. (1996) Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. *Ecology*, **77**, 69-74.

Figuerola, J., Garcia, L., Green, A.J., Ibanez, F., Manez, M., Del Valle, J.L., Garrido, H., Arroyo, J.L. & Rodriguez, R. (2006) Sex determination in glossy ibis chicks based on morphological characters. *Ardeola*, **53**, 229-235.

Fowler, C.W. (1987) A review of density dependence in populations of large mammals. *Current Mammalogy* (ed. H.H. Genoways), pp. 401-441. Plenum Press, New York.

Francis, C.M. & Cooke, F. (1986) Differential timing of spring migration in wood warblers (Parulinae). *Auk*, **103**, 548-556.

Francis, C.M., Richards, M.H., Cooke, F. & Rockwell, R.F. (1992) Changes in survival rates of lesser snow geese with age and breeding status. *Auk*, **109**, 731-747.

Frederiksen, M., Daunt, F., Harris, M.P. & Wanless, S. (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology*, **77**, 1020-1029.

Fretwell, S.D. & Lucas, H.L. (1970) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16-36.

Fridolfsson, A.K. & Ellegren, H. (1999) A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*, **30**, 116-121.

Fry, B. (2006) *Stable Isotope Ecology*. Springer, Berlin.

Fry, B., Scalan, R.S. & Parker, P.L. (1983). $^{13}C/^{12}C$ ratios in marine food webs of the Torres Strait, Queensland. *Australian Journal of Marine and Freshwater Research*, **34**, 707-715.

G

Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, **13**, 58-63.

García, L., Máñez, M., Rodríguez, R., Garrido, H., Arroyo, J.L., del Valle, J.L., Ibáñez, F., Martínez, A., Chico, A. & Martin, I.S. (2009) *Espátula común* (*Platalea leucorodia*). SEO/Birdlife, Madrid.

Gauthier, G., Pradel, R., Menu, S. & Lebreton, J.D. (2001) Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. *Ecology*, **82**, 3105-3119.

Gauthreaux, S.A., Jr. (1978) The ecological significance of behavioral dominance. *Perspectives in Ethology* (eds P.P.G. Bateson & P.H. Klopfer), pp. 17-54. Plenum Press, New York.

Gauthreaux, S. A., Jr. (1982) The ecology and evolution of avian migration systems. *Avian Biology* (eds D.S. Farner, J.R. King & K.C. Parkes), pp. 93-168. Academic Press, New York.

Gawlik, D.E. (2002) The effects of prey availability on the numerical response of wading birds. *Ecological Monographs*, **72**, 329-346.

Ghosh, M., Singh, P. & Mohan, D. (2011) Seasonal variation in foraging ecology of three species of overwintering leaf warblers (genus *Phylloscopus*) in the Himalayan foothills. *Journal of Ornithology*, **152**, 869-877.

Gill, J.A., Norris, K. , Potts, P.M., Gunnarsson, T.G., Atkinson, P.W. & Sutherland, W.J. (2001) The buffer effect and large-scale population regulation in migratory birds. *Nature*, **412**, 436-438.

Goudet, J. (2001) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available from http://www2.unil.ch/popgen/softwares/fstat.htm.

Goutte, A., Antoine, E., Weimerskirch, H. & Chastel, O. (2010) Age and the timing of breeding in a long-lived bird: a role for stress hormones? *Functional Ecology*, **24**, 1007-1016.

Greenberg, R. (1980) Demographic aspects of long-distance migration. *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation* (eds A. Keast & E.S. Morton), pp. 493-504. Smithsonian Institution Press, Washington, D.C.

Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140-1162.

Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J., Moller, A.P. & Weimerskirch, H. (2008). Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, **83**, 357-399.

Grosbois, V. & Tavecchia, G. (2003) Modeling dispersal with capture-recapture data: Disentangling decisions of leaving and settlement. *Ecology*, **84**, 1225-1236.

Groves, S. (1978) Age-related differences in ruddy turnstone foraging and aggressive behavior. *Auk*, **95**, 95-103.

Gunnarsson, T.G., Gill, J.A., Atkinson, P.W., Gélinaud, G., Potts, P.M., Croger, R.E., Gudmundsson, G.A., Appletion, G.F. & Sutherland, W.J. (2006) Population-scale drivers of individual arrival times in migratory birds. *Journal of Animal Ecology*, **75**, 1119-1127.

Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M. & Sutherland, W.J. (2005a). Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2319-2323.

Gunnarsson, T.G., Gill, J.A., Petersen, A., Appleton, G.F. & Sutherland, W.J. (2005b). A double buffer effect in a migratory shorebird population. *Journal of Animal Ecology*, **74**, 965-971.

Gutierrez, J.S., Masero, J.A., Abad-Gomez, J.M., Villegas, A. & Sanchez-Guzman, J.M. (2011) Understanding the energetic costs of living in saline environments: effects of salinity on basal metabolic rate, body mass and daily energy consumption of a long-distance migratory shorebird. *Journal of Experimental Biology*, **214**, 829-835.

H

Hamer, K.C. & Hill, J.K. (1993) Variation and regulation of meal size and feeding frequency in Cory's shearwater *Calinectris diomedea*. *Journal of Animal Ecology*, **62**, 441-450.

Hancock, J.A., Kushlan, J.A. & Kahl, M.P. (1992) *Storks, ibises and spoonbills of the world*. Academic Press, London.

Hannam, K.M., Oring, L.W. & Herzog, M.P. (2003) Impacts of salinity on growth and behavior of American avocet chicks. *Waterbirds*, **26**, 119-125.

Hargrove, J.W. & Borland, C.H. (1994) Pooled population parameter estimates from mark-recapture data. *Biometrics*, **50**, 1129-1141.

Harriman, A.E. (1967) Laughing gulls offered saline in preference and survival tests. *Physiological Zoology*, **40**, 273-279.

Harrington, B.A., Hagen, J.M. & Leddy, L.E. (1988) Site fidelity and survival differences between two groups of New World red knots (*Calidris canutus*). *Auk*, **105**, 439-445.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, **80**, 4-18.

Harrison, X.A., Tregenza, T., Inger, R., Colhoun, K., Dawson, D.A., Gudmundsson, G.A., Hodgson, D.J., Horsburgh, G.J., McElwaine, G. & Bearhop, S. (2010) Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant. *Molecular Ecology*, **19**, 5484-5496.

Henningsson, S.S. & Karlsson, H. (2009) Do adult and juvenile dunlins *Calidris alpina* form randomly mixed flocks during fall migration? *Journal of Avian Biology*, **40**, 646-649.

Hestbeck, J.B., Nichols, J.D. & Hines, J.E. (1992) The relationship between annual survival rate and migration distance in mallards – an examination of the time-allocation hypothesis for the evolution of migration. *Canadian Journal of Zoology*, **70**, 2021-2027.

Hobson, K.A. & Clark, R.G. (1992) Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. *Condor*, **94**, 181-188.

Hobson, K.A. & Welch, H.E. (1992) Determination of trophic relationships within a high artic marine food web using delta C^{13} and delta N^{15} analysis. *Marine Ecology Progress Series*, **84**, 9-18.

Holbrook, S.J. & Schmitt, R.J. (2002). Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology*, **83**, 2855-2868.

Hötker, H. (2002) Arrival of pied avocets *Recurvirostra avosetta* at the breeding site: effects of winter quarters and consequences for reproductive success. *Ardea*, **90**, 379-387.

Hufnagl, M. & Temming, A. (2011) Growth in the brown shrimp *Crangon crangon*. II. Meta-analysis and modelling. *Marine Ecology Progress Series*, 435, 155-172.

Hu, J.H., Hu, H.J. & Jiang, Z.G. (2010) The impacts of climate change on the wintering distribution of an endangered migratory bird. *Oecologia*, **164**, 555-565.

Huntingford, F.A., Chellappa, S., Taylor, A.C. & Strang, R.H.C. (2001) Energy reserves and reproductive investment in male three-spined sticklebacks *Gasterosteus aculeatus*. *Ecology of Freshwater Fish*, **10**, 111-117.

J

Jaeger, A., Connan, M., Richard, P. & Cherel, Y. (2010) Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialisation in seabirds. *Marine Ecology. Progress Series*, **401**, 269-277.

Jensen, P.M., Madsen, P., Jensen, L.S. & Pipper, C.B. (2012) Differences in carbon and nitrogen stable isotope signatures amongst wild and released pheasant populations. *European Journal of Wildlife Research*, **58**, 755-760.

Johnsen, A., Andersson, S., Fernandez, J.G., Kempenaers, B., Pavel, V., Questiau, S., Raess, M., Rindal, E. & Lifjeld, J.T. (2006) Molecular and phenotypic divergence in the bluethroat (*Luscinia svecica*) subspecies complex. *Molecular Ecology*, **15**, 4033-4047.

Johnston, J.W. & Bildstein, K.L. (1990) Dietary salt as a physiological constraint in white ibis breeding in an estuary. *Physiological Zoology*, **63**, 190-207.

Juillet, C., Choquet, R., Gauthier, G. & Pradel, R. (2011) A capture-recapture model with double-marking, live and dead encounters, and heterogeneity of reporting due to auxiliary mark loss. *Journal of Agricultural Biological and Environmental Statistics*, **16**, 88-104.

K

Kemper, J.H. (1995) Role of the three-spined stickleback (Gasterosteus aculeatus L) in the food ecology of the spoonbill *Platalea leucorodia. Behaviour*, **132**, 1285-1299.

Kentie, R., Hooijmeijer, J.C.E.W., Trimbos, K.B., Groen, N.M. & Piersma, T. (2013). Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. *Journal of Applied Ecology*, **50**, 243-251.

Kersten, M. & Brenninkmeijer, A. (1995) Growth, fledging success and postfledging survival of juvenile oystercatchers *Haematopus ostralegus. Ibis*, **137**, 396-404.

Ketterson, E.D. & Nolan, V.J. (1976) Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed junco's (*Junco hyemalis hyemalis*). *Ecology*, **57**, 679-693.

Ketterson, E.D. & Nolan, V.J. (1983) The evolution of differential bird migration. *Current Ornithology* (ed. R.F. Johnston), pp. 357-402. Plenum Press, New York.

Klaassen, M. & Ens, B.J. (1990) Is salt stress a problem for waders wintering on the Banc d'Arguin, Mauritania. *Ardea*, **78**, 67-74.

Kluyver, H.N. & Tinbergen, L. (1953). Territory and the regulation of density in titmice. *Archives Néerlandaises de Zoologie*, **10**, 266-287.

Knoff, A.J., Macko, S.A., Erwin, R.M. & Brown, K.M. (2002) Stable isotope analysis of temporal variation in the diets of pre-fledged laughing gulls. *Waterbirds*, **25**, 142-148.

Koeman, J.H. & van Genderen, H. (1966) Some preliminary notes on residues of chlorinated hydrocarbon insecticides in birds and mammals in the Netherlands. *Journal of Applied Ecology*, **3 (Suppl.)**, 99-106.

Kokko, H. (1999) Competition for early arrival in migratory birds. *Journal of Animal Ecology*, **68**, 940-950.

Kokko, H. & Lindström, J. (1998) Seasonal density dependence, timing of mortality, and sustainable harvesting. *Ecological Modelling*, **110**, 293-304.

Kopij, G. (1997) Breeding ecology of the African spoonbill *Platalea alba* in the Free State, South Africa. *Ostrich*, **68**, 77-79.

Kraan, C., van Gils, J.A. , Spaans, B., Dekinga, A., Bijleveld, A.I., van Roomen, M., Kleefstra, R. & Piersma, T. (2009) Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *Journal of Animal Ecology*, **78**, 1259-1268.

Krijgsveld, K.L., Dijkstra, C., Visser, G.H. & Daan, S. (1998) Energy requirements for growth in relation to sexual size dimorphism in marsh harrier *Circus aeruginosus* nestlings. *Physiol. Zool.* **71**: 693-702.

Kvist, L., Ponnikas, S., Belda, E.J., Encabo, I., Martinez, E., Onrubia, A., Hernandez, J.M., Vera, P., Neto, J.M. & Monros, J.S. (2011) Endangered subspecies of the reed bunting (*Emberiza schoeniclus witherbyi* and *E. s. lusitanica*) in Iberian Peninsula have different genetic structures. *Journal of Ornithology*, **152**, 681-693.

L

Lack, D. (1954) *The natural regulation of animal numbers*. Clarendon Press, Oxford.

Latta, S.C. & Faaborg, J. (2002) Demographic and population responses of Cape May warblers wintering in multiple habitats. *Ecology*, **83**, 2502-2515.

Lebreton, J.D. (1995) The future of population dynamic studies using marked individuals: A statistician's perspective. *Journal of Applied Statistics*, **22**, 1009-1030.

Lebreton, J.D., Almeras, T. & Pradel, R. (1999). Competing events, mixtures of information and multistratum recapture models. *Bird Study*, **46**, S39-S46.

Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67-118.

Lebreton, J.D. & Pradel, R. (2002) Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics*, **29**, 353-369.

Leyrer, J., Lok, T., Brugge, M., Dekinga, A., Spaans, B., van Gils, J.A., Sandercock, B.K. & Piersma, T. (2012) Small-scale demographic structure suggests preemptive behaviour in a flocking shorebird. *Behavioral Ecology*, **23**, 1226-1233.

Leyrer, J., Lok, T., Brugge, M., Spaans, B., Sandercock, B.K. & Piersma, T. (2013). Mortality within the annual cycle: seasonal survival patterns in Afro-Siberian red knots. *Journal of Ornithology*, **154**, 933-943.

Liechti, F. & Bruderer, B. (1998) The relevance of wind for optimal migration theory. *Journal of Avian Biology*, **29**, 561-568.

Lindberg, M.S., Ward, D.H., Tibbitts, T.L. & Roser, J. (2007) Winter movement dynamics of black brant. *Journal of Wildlife Management*, **71**, 534-540.

Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, **14**, 343-348.

Lindstrom, M.J. & Bates, D.M. (1990) Nonlinear mixed effects models for repeated measures data. *Biometrics*, **46**, 673-687.

Link, W.A. (1999) Modeling pattern in collections of parameters. *Journal of Wildlife Management*, **63**, 1017-1027.

Loison, A., Saether, B.E., Jerstad, K. & Rostad, O.W. (2002) Disentangling the sources of variation in the survival of the European dipper. *Journal of Applied Statistics*, **29**, 289-304.

Lok, T., Overdijk, O., Horn, H. & Piersma, T. (2009) The spoonbill *Platalea leucorodia* population of the Wadden Sea islands: does population growth level off? *Limosa*, **82**, 149-157.

Lok, T., Overdijk, O. & Piersma, T. (2013) Migration tendency delays distributional response to differential survival prospects along a flyway. *American Naturalist*, **181**, 520-531.

Lok, T., Overdijk, O., Tinbergen, J.M. & Piersma, T. (2011) The paradox of spoonbill migration: most birds travel to where survival rates are lowest. *Animal Behaviour*, **82**, 837-844.

Lok, T., Overdijk, O., Tinbergen, J.M. & Piersma, T. (2013) Seasonal variation in density dependence in age-specific survival of a long-distance migrant. *Ecology*, in press.

Lundberg, S. & Alerstam, T. (1986). Bird migration patterns - conditions for stable geographical population segregation. *Journal of Theoretical Biology*, **123**, 403-414.

M

Madsen, J., Frederiksen, M. & Ganter, B. (2002) Trends in annual and seasonal survival of pink-footed geese *Anser brachyrhynchus. Ibis*, **144**, 218-226.

Marchi, C., Sanz, I.S., Blot, E., Hansen, J., Walsh, A.J., Frederiksen, M. & Fox, A.D. (2010) Between-winter emigration rates are linked to reproductive output in Greenland white-fronted geese *Anser albifrons flavirostris. Ibis*, **152**, 410-413.

Marques, P.A.M., Sowter, D. & Jorge, P.E. (2010) Gulls can change their migratory behavior during lifetime. *Oikos*, **119**, 946-951.

Marra, P.P., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, **282**, 1884-1886.

Marthinsen, G., Wennerberg, L. & Lifjeld, J.T. (2007) Phylogeography and subspecies taxonomy of dunlins (*Calidris alpina*) in western Palearctic analysed by DNA microsatellites and amplified fragment length polymorphism markers. *Biological Journal of the Linnean Society*, **92**, 713-726.

Martin, T.E. (1987) Food as a limit on breeding birds - a life-history perspective. *Annual Review of Ecology and Systematics*, **18**, 453-487.

Massemin-Challet, S., Gendner, J.P., Samtmann, S., Pichegru, L., Wulgue, A. & Le Maho, Y. (2006) The effect of migration strategy and food availability on white stork *Ciconia ciconia* breeding success. *Ibis*, **148**, 503-508.

Massias, A. & Becker, P.H. (1990) Nutritive value of food and growth in common tern (*Sterna hirundo*) chicks. *Ornis Scandivica*, **21**, 187-194.

Matheu, E. & del Hoyo, J. (1992) Family Threskiornithidae (Ibises and Spoonbills). *Handbook of the birds of the World, vol 1.* (eds del Hoyo, J., Elliot, A. & Sargatal, J.), pp. 472-506. Lynx Edicions, Barcelona.

McCleery, R.H., Perrins, C.M., Sheldon, B.C. & Charmantier, A. (2008) Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 963-970.

McKinnon, L., Smith, P.A., Nol, E., Martin, J.L., Doyle, F.I., Abraham, K.F., Gilchrist, H.G., Morrison, R.I.G. & Bety, J. (2010) Lower predation risk for migratory birds at high latitudes. *Science*, **327**, 326-327.

Metcalfe, N.B. & Monaghan, P. (2001) Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution*, **16**, 254-260.

Miller, M.P., Haig, S.M., Gratto-Trevor, C.L. & Mullins, H.D. (2010) Subspecies status and population genetic structure in piping plover (*Charadrius melodus*). *Auk*, **127**, 57-71.

Minagawa, M. & Wada, E. (1984) Stepwise enrichment of 15N along food chains: Further evidence and the relation between δ^{15}N and animal age. *Geochimica et Cosmochimica Acta*, **48**, 1135-1140.

Mizutani, H., Fukuda, M., Kabaya, Y. & Wada, E. (1990) Carbon isotope ratio of feathers reveals feeding behavior of cormorants. *Auk*, **107**, 400-403.

Morris, D.W. (1989) Density-dependent habitat selection – testing the theory with fitness data. *Evolutionary Ecology*, **3**, 80-94.

Morris, D.W. (1991) Fitness and patch selection by white-footed mice. *American Naturalist*, **138**, 702-716.

Myers, J.P. (1981) A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Canadian Journal of Zoology*, **59**, 1527-1534.

Mylecraine, K.A., Gibbs, H.L., Anderson, C.S. & Shieldcastle, M.C. (2008) Using 2 genetic markers to discriminate among Canada goose populations in Ohio. *Journal of Wildlife Management*, **72**, 1220-1230.

N

Naef-Daenzer, B., Widmer, F. & Nuber, M. (2001) Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology*, **70**, 730-738.

Navedo, J.G. (2008) Different stopover timing in juvenile and adult spoonbills during southward migration. EUROSITE *Spoonbill Working Group Newsletter* (eds P. Triplet, O. Overdijk & M. Smart), pp. 2-5. Eurosite, http://www.eurosite.org/files/ SPOONBILL_NEWSLETTER_6.pdf.

Navedo, J.G., Masero, J.A., Overdijk, O., Orizaola, G. & Sanchez-Guzman, J.M. (2010a) Assessing the role of multiple environmental factors on Eurasian Spoonbill departure decisions from stopover sites. *Ardea*, **98**, 3-12.

Navedo, J.G., Orizaola, G., Masero, J.A., Overdijk, O. & Sanchez-Guzman, J.M. (2010) Long-distance travellers stopover for longer: a case study with spoonbills staying in North Iberia. *Journal of Ornithology*, **151**, 915-921.

Nebel, S. (2007) Differential migration of shorebirds in the East Asian-Australasian Flyway. *Emu*, **107**, 14-18.

Nelson, R.J., Demas, G.E., Klein, S.L. & Kriegsfeld, L.J. (2002) *Seasonal patterns of stress, immune function, and disease*. Cambridge University Press, Cambridge.

Nevoux, M., Gimenez, O., Arlt, D., Nicoll, M., Jones, C. & Norris, K. (2011) Population regulation of territorial species: both site dependence and interference mechanisms matter. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2173-2181.

Newton, I. (2004) Population limitation in migrants. *Ibis*, **146**, 197-226.

Newton, I. (2006) Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology*, **147**, 146-166.

Newton, I. (2007) Weather-related mass-mortality events in migrants. *Ibis*, **149**, 453-467.

Newton, I. (2008) *The migration ecology of birds*. Elsevier, Oxford.

Nichols, J.D. & Johnson, F.A. (1990) Wood duck population dynamics: A review. *Proceedings of 1988 North American Wood Duck Symposium* (eds L.H. Fredrickson, G.V. Burger, S.P. Havera, D.A. Graber, R.E. Kirby & T.S. Taylor), pp. 83-105. MO, St. Louis.

Niethammer, G., von Blotzheim, U.N.G. & Bauer, K.M. (1968) *Handbuch der Vögel Mitteleuropas*. Akademische Verlagsgesellschaft.

Nisbet, I.C.T. & Cam, E. (2002) Test for age-specificity in survival of the common tern. *Journal of Applied Statistics*, **29**, 65-83.

Novo, F.G. & Cabrera, C.M. (2006). *Doñana: water and biosphere*. Spanish Ministry of the Environment, Madrid.

O

O'Brien, S., Robert, B. & Tiandry, H. (2005) Consequences of violating the recapture duration assumption of mark-recapture models: a test using simulated and empirical data from an endangered tortoise population. *Journal of Applied Ecology*, **42**, 1096-1104.

Oro, D., Jover, L. & Ruiz, X. (1996) Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. *Marine Ecology Progress Series*, 139, 19-29.

Östlund-Nilsson, S. (2007) *Biology of the three-spined stickleback*. CRC Press, New York.

Overdijk, O., de le Court, C. & Gueye, A. (2001) *Spoonbill count on the Banc d'Arguin, Mauritania, January 2000*. WIWO report 69, Zeist, Nouakchott.

Owen-Smith, N., Mason, D.R. & Ogutu, J.O. (2005) Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. *Journal of Animal Ecology*, **74**, 774-788.

P

Parnell, A.C., Inger, R., Bearhop, S. & Jackson, A.L. (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS One*, **5**, e9672.

Peach, W., Baillie, S. & Underhill, L. (1991) Survival of British sedge warblers Acrocephalus schoenobaenus in relation to west African rainfall. *Ibis*, **133**, 300-305.

Pearce-Higgins, J.W. & Yalden, D.W. (2002) Variation in the growth and survival of golden plover Pluvialis apricaria chicks. *Ibis*, **144**, 200-209.

Pienkowski, M.W. & Evans, P.R. (1985) The role of migration in the population dynamics of birds. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (eds R.M. Sibly & R.H. Smith), pp. 331-352. Blackwell Scientific Publications, Oxford.

Piersma, T. (1980) Lepelaars op de Mokkebank. *Vanellus*, **33**, 54-57.

Piersma, T. (2007) Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology*, **148**, S45-S59.

Piersma, T. (2011) Flyway evolution is too fast to be explained by the modern synthesis: proposals for an 'extended' evolutionary research agenda. *Journal of Ornithology*, **152 (Suppl 1)**, S151-S159.

Piersma, T. (2012) What is habitat quality? Dissecting a research portfolio on shorebirds. *Birds and habitat: relationships in changing landscapes* (ed. R. Fuller), pp. 383-407. Cambridge University Press, Cambridge.

Piersma, T. & van de Sant, S. (1992) Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. *Ornis Svecica*, **2**, 55-66.

Piersma, T., van der Velde, M., El-Hacen, H.M., Lok, T. & Overdijk, O. 2012. Molecular verification of the subspecies status of the Mauritanian spoonbill *Platalea leucorodia balsaci*. *Ardea*, **100**, 131-136.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Development Core Team (2012) nlme: Linear and nonlinear mixed effects models. *R package version 3.1-104*.

Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-effects models in S and S-Plus*. Springer-Verlag, New York.

Post, D.M. (2002) Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, **83**, 703-718.

Pradel, R. (2005) Multievent: An extension of multistate capture-recapture models to uncertain states. *Biometrics*, **61**, 442-447.

Pradel, R. (2009) The stakes of capture-recapture models with state uncertainty. *Modeling demographic processes in marked populations* (eds D.L. Thomson, E.G. Cooch, & M.J. Conroy), pp. 781-795. Springer, New York.

Pulido, F. & Berthold, P. (2010). Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 7341-7346.

Pulliam, H.R. & Danielson, B.J. (1991). Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist*, **137**, S50-S66.

Q

Quaintenne, G., van Gils, J.A., Bocher, P., Dekinga, A. & Piersma, T. (2011). Scaling up ideals to freedom: are densities of red knots across western Europe consistent with ideal free distribution? *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2728-2736.

Quillfeldt, P., Masello, J.F., Strange, I.J. & Buchanan, K.L. (2006) Begging and provisioning of thin-billed prions, *Pachyptila belcheri*, are related to testosterone and corticosterone. *Animal Behaviour*, **71**, 1359-1369.

Quillfeldt, P., Voigt, C.C. & Masello, J.F. (2010) Plasticity versus repeatability in seabird migratory behaviour. *Behavioral Ecology and Sociobiology*, **64**, 1157-1164.

R

R Development Core Team (2011) R: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ratikainen, I.I., Gill, J.A., Gunnarsson, T.G., Sutherland, W.J. & Kokko, H. (2008) When density dependence is not instantaneous: theoretical developments and management implications. *Ecology Letters*, **11**, 184-198.

Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. (2003) Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology*, **72**, 36-46.

Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. (2003) Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. *Journal of Animal Ecology*, **72**, 765-776.

Richardson, D.S., Jury, F.L., Blaakmeer, K., Komdeur, J. & Burke, T. (2001) Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). *Molecular Ecology*, **10**, 2263-2273.

Ricklefs, R.E. (1968) Patterns of growth in birds. *Ibis*, **110**, 419-451.

Ricklefs, R.E. & White, S.C. (1975) A method for constructing nestling growth curves from brief visits to seabird colonies. *Bird-Banding*, **46**, 135-140.

Robertson, G. & Cooke, F. (1999) Winter philopatry in migratory waterfowl. *Auk*, **116**, 20-34.

Rodel, H.G., Bora, A., Kaiser, J., Kaetzke, P., Khaschei, M. & von Holst, D. (2004) Density-dependent reproduction in the European rabbit: a consequence of individual response and age-dependent reproductive performance. *Oikos*, **104**, 529-539.

Rodenhouse, N.L., Sherry, T.W. & Holmes, R.T. (1997). Site-dependent regulation of population size: A new synthesis. *Ecology*, **78**, 2025-2042.

Rodenhouse, N.L., Sillett, T.S., Doran, P.J. & Holmes, R.T. (2003) Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2105-2110.

Runge, M.C. & Marra, P.P. (2005) Modeling seasonal interactions in the population dynamics of migratory birds. *Birds of two worlds: the ecology and evolution of migration* (eds R. Greenberg & P.P. Marra), pp. 375-389. Johns Hopkins University Press, Baltimore.

Ruthrauff, D.R. & McCaffery, B.J. (2005) Survival of western sandpiper broods on the Yukon-Kuskokwim Delta, Alaska. *Condor*, **107**, 597-604.

S

Saether, B.E. & Bakke, O. (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**, 642-653.

Saino, N., Szép, T., Romano, M., Rubolini, D., Spina, F. & Møller, A.P. (2004) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecology Letters*, **7**, 21-25.

Sandell, M. & Smith, H.G. (1991) Dominance, prior occupancy, and winter residency in the great tit (*Parus major*). *Behavioral Ecology and Sociobiology*, **29**, 147-152.

Sandercock, B.K., Nilsen, E.B., Broseth, H. & Pedersen, H.C. (2011) Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology*, **80**, 244-258.

Sandercock, B.K. & Jaramillo, A. (2002) Annual survival rates of wintering sparrows: Assessing demographic consequences of migration. *Auk*, **119**, 149-165.

Sanz-Aguilar, A., Bechet, A., Germain, C., Johnson, A.R. & Pradel, R. (2012) To leave or not to leave: survival trade-offs between different migratory strategies in the greater flamingo. *Journal of Animal Ecology*, **81**, 1171-1182.

Sawyer, G.M. & Benjamin, R.C. (2006) Isolation and characterization of microsatellite loci for parentage assessment in captive populations of roseate spoonbill (*Ajaja ajaja*). *Molecular Ecology Notes*, **6**, 677-679.

Schaub, M., Kania, W. & Koppen, U. (2005) Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *Journal of Animal Ecology*, **74**, 656-666.

Schekkerman, H., Teunissen, W. & Oosterveld, E. (2009) Mortality of black-tailed godwit *Limosa limosa* and northern lapwing *Vanellus vanellus* chicks in wet grasslands: influence of predation and agriculture. *Journal of Ornithology*, **150**, 133-145.

Schell, D.M., Saupe, S.M. & Haubenstock, N. (1989) Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by δ^{13}C techniques. *Marine Biology*, **103**, 433-443.

Schew, W.A. & Ricklefs, R.E. (1998) Developmental plasticity. *Avian growth and development: evolution within the altricial-precocial spectrum* (eds J.M. Starck & R.E. Ricklefs), pp. 288-304. Oxford University Press, Oxford.

Schoeninger, M.J. & Deniro, M.J. (1984) Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochimica et Cosmochimica Acta*, **48**, 625-639.

Schwarz, C.J., Schweigert, J.F. & Arnason, A.N. (1993) Estimating migration rates using tag-recovery data. *Biometrics*, **49**, 177-193.

Sedinger, J.S., Ward, D.H., Schamber, J.L., Butler, W.I., Eldridge, W.D., Conant, B., Voelzer, J.F., Chelgren, N.D. & Herzog, M.P. (2006). Effects of El Niño on distribution and reproductive performance of black brant. *Ecology*, **87**, 151-159.

Shamoun-Baranes, J., Baharad, A., Alpert, P., Berthold, P., Yom-Tov, Y., Dvir, Y. & Leshem, Y. (2003) The effect of wind, season and latitude on the migration speed of white storks *Ciconia ciconia*, along the eastern migration route. *Journal of Avian Biology*, **34**, 97-104.

Shamoun-Baranes, J., Leyrer, J., van Loon, E., Bocher, P., Robin, F., Meunier, F. & Piersma, T. (2010) Stochastic atmospheric assistance and the use of emergency staging sites by migrants. *Proceedings of the Royal Society B-Biological Sciences*, **277**, 1505-1511.

Sherry, T.W., Johnson, M.D. & Strong, A.M. (2005) Does winter food limit populations of migratory birds? *Birds of two worlds: the ecology and evolution of migration* (eds R. Greenberg & P.P. Marra), pp. 414-425. Johns Hopkins University Press, Baltimore.

Sillett, T.S. & Holmes, R.T. (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*, **71**, 296-308.

Skogland, T. (1985) The effects of density-dependent resource limitations on the demography of wild reindeer. *Journal of Animal Ecology*, **54**, 359-374.

Smith, A.D., Donohue, K. & Dufty, A.M. (2008) Intrafeather and intraindividual variation in the stable-hydrogen isotope (_D) content of raptor feathers. *Condor*, **110**, 500-506.

Spaans, A.L. (1977) Are starlings faithful to their individual winter quarters? *Ardea*, **65**, 83-87.

Starck, J.M. & Ricklefs, R.E. (1998) Patterns of development: the altricial-precocial spectrum. *Avian growth and development: evolution within the altricial-precocial spectrum* (eds J.M. Starck & R.E. Ricklefs), pp. 3-30. Oxford University Press, Oxford.

Stearns, S.C. (1992) *The evolution of life histories*. Oxford University Press, Oxford.

Steenweg, R.J., Ronconi, R.A. & Leonard, M.L. (2011) Seasonal and age-dependent dietary partitioning between the great black-backed and herring gulls. *Condor*, **113**, 795-805.

Stephens, D.W. & Krebs, J.R. (1986) Foraging Theory. Princeton University Press, Princeton.

Stewart, R.L.M., Francis, C.M. & Massey, C. (2002) Age-related differential timing of spring migration within sexes in passerines. *Wilson Bulletin*, **114**, 264-271.

Stubben, C. & Milligan, B. (2007) Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, **22**, 1-23.

Studds, C.E. & Marra, P.P. (2005) Nonbreeding habitat occupancy and population processes: An upgrade experiment with a migratory bird. *Ecology*, **86**, 2380-2385.

Sutherland, W.J. (1996) Predicting the consequences of habitat loss for migratory populations. *Proceedings of the Royal Society of London B*, **263**, 1325-1327.

Sutherland, W.J. (1998) Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*, **29**, 441-446.

T

Tank, A., Wijngaard, J.B., Konnen, G.P., Bohm, R., Demaree, G., Gocheva, A., Mileta, M. et al. 2002. Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment. *International Journal of Climatology*, **22**, 1441-1453.

te Marvelde, L., Meininger, P.L., Flamant, R. & Dingemanse, N.J. (2009) Age-specific density-dependent survival in Mediterranean gulls *Larus melanocephalus*. *Ardea*, **97**, 305-312.

Thompson, D.R. & Furness, R.W. (1995) Stable-isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in northern fulmars. *Auk*, **112**, 493-498.

Tinbergen, J.M. & Williams, J.B. (2002) Energetics of incubation. *Avian incubation: behaviour, environment and evolution*. (ed. D.C. Deeming), pp. 299-313. Oxford University Press, Oxford.

Tjorve, K.M.C. & Tjorve, E. (2010) Shapes and functions of bird-growth models: how to characterise chick postnatal growth. *Zoology*, **113**, 326-333.

Tøttrup, A.P., Klaassen, R.H.G., Kristensen, M.W., Strandberg, R., Vardanis, Y., Lindström, Å., Rahbek, C., Alerstam, T. & Thorup, K. (2012) Drought in Africa caused delayed arrival of European songbirds. *Science*, **338**, 1307.

Townshend, D.J. (1985) Decisions for a lifetime: establishment of spatial defence and movement patterns of juvenile grey plovers (*Pluvialis squatarola*). *Journal of Animal Ecology*, **54**, 267-274.

Triplet, P., Overdijk, O., Smart, M., Nagy, S., Schneider-Jacoby, M., Karauz, E.S., Pigniczki, C., El Din, S.B., Kralj, J., Sandor, A. & Navedo, J.G. (2008) *International single species action plan for the conservation of the Eurasian spoonbill*. Bonn.

Tulp, I., Bolle, L.J., Meesters, E. & de Vries, P. (2012) Brown shrimp abundance in northwest European coastal waters from 1970 to 2010 and potential causes for contrasting trends. *Marine Ecology Progress Series*, **458**, 141-154.

V

Valera, F., Wagner, R.H., Romero-Pujante, M., Gutierrez, J.E. & Rey, P.J. (2005) Dietary specialization on high protein seeds by adult and nestling serins. *Condor*, **107**, 29-40.

van de Pol, M., Ens, B.J., Heg, D., Brouwer, L., Krol, J., Maier, M., Exo, K.M., Oosterbeek, K., Lok, T., Eising, C.M. & Koffijberg, K. (2010) Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology*, **47**, 720-730.

van de Pol, M. & Verhulst, S. (2006) Age-dependent traits: A new statistical model to separate within- and between-individual effects. *American Naturalist*, **167**, 766-773.

van de Pol, M. & Wright, J. (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, **77**, 753-758.

van der Hut, R.M.G. (1992) *Biologie en bescherming van de Lepelaar* Platalea leucorodia. Vogelbescherming, Zeist.

van der Jeugd, H.P. & Larsson, K. (1998) Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. *Journal of Animal Ecology*, **67**, 953-966.

van Gils, J.A., Piersma, T., Dekinga, A., Spaans, B. & Kraan, C. (2006) Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS Biology*, **4**, 2399-2404.

van Gils, J.A., Spaans, B., Dekinga, A. & Piersma, T. (2006) Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. *Ecology*, **87**, 1189-1202.

van Gils, J.A., van der Geest, M., Jansen, E.J., Govers, L.L., de Fouw, J. & Piersma, T. (2012) Trophic cascade induced by molluscivore predator alters pore-water biogeochemistry via competitive release of prey. *Ecology*, **93**, 1143-1152.

van Wetten, J.C.J. & Wintermans, G.J.M. (1986) *The food ecology of the spoonbill*. Verslagen en technische gegevens, University of Amsterdam, Amsterdam.

Varner, D.M. & Eichholz, M.W. (2012) Annual and seasonal survival of trumpeter swans in the upper midwest. *Journal of Wildlife Management*, **76**, 129-135.

Velando, A., Graves, J. & Freire, J. (2000) Sex-specific growth in the European shag *Stictocarbo aristotelis*, a sexually dimorphic seabird. *Ardea*, **88**, 127-136.

Visser, M.E., Perdeck, A.C., van Balen, J.H. & Both, C. (2009) Climate change leads to decreasing bird migration distances. *Global Change Biology*, **15**, 1859-1865.

Von Haartman, L. (1968) The evolution of resident versus migratory habit in birds. Some considerations. *Ornis Fennica*, **45**, 1-7.

W

Wassenaar, L.I. & Hobson, K.A. (2006) Stable-hydrogen isotope heterogeneity in keratinous materials: mass spectrometry and migratory wildlife tissue subsampling strategies. *Rapid Communications in Mass Spectrometry*, **20**, 2505-2510.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S., Holmes, R.T. (2002) Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution*, **17**, 76-83.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, S120-S139.

Wiersma, P. & Piersma, T. (1994) Effects of microhabitat, flocking, climate and migratory goal on energy-expenditure in the annual cycle of red knots. *Condor*, **96**, 257-279.

Wiley, A.E., Ostrom, P.H., Stricker, C.A., James, H.F. & Gandhi, H. (2010) Isotopic characterization of flight feathers in two pelagic seabirds: sampling strategies for ecological studies. *Condor*, **112**, 337-346.

Wiley, A.E., Welch, A.J., Ostrom, P.H., James, H.F., Stricker, C.A., Fleischer, R.C., Gandhi, H., Adams, J., Ainley, D.G., Duvall, F., Holmes, N., Hu, D.C., Judge, S., Penniman, J. & Swindle, K.A. (2012) Foraging segregation and genetic divergence between geographically proximate colonies of a highly mobile seabird. *Oecologia*, **168**, 119-130.

Williams, C.K., Samuel, M.D., Baranyuk, V.V., Cooch, E.G. & Kraege, D. (2008) Winter fidelity and apparent survival of lesser snow goose populations in the Pacific Flyway. *Journal of Wildlife Management*, **72**, 159-167.

Wilson, A.J. & Nussey, D.H. (2010) What is individual quality? An evolutionary perspective. *Trends in Ecology & Evolution*, **25**, 207-214.

Wright, S. (1951) The genetical structure of populations. *Annals of Eugenics*, **15**, 323-354.

Y

Yeung, C.K.L., Hsu, Y.-C., Yao, C.-T. & Li, S.-H. (2009) Isolation and characterization of 23 microsatellite loci in the black-faced spoonbill (*Platalea minor*) and amplification in other Ciconiiformes waterbirds. *Conservation Genetics*, **10**, 1081–1084.

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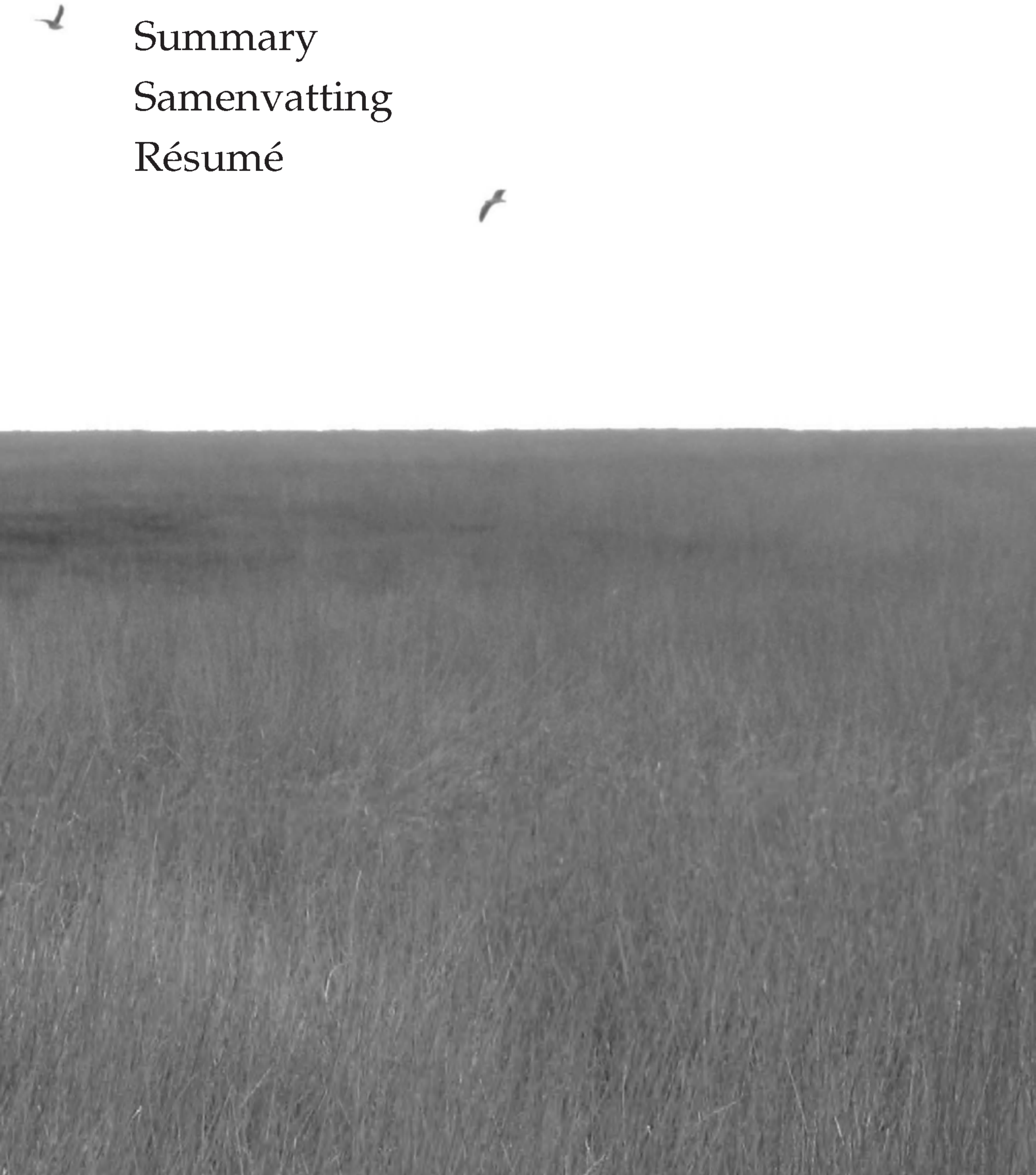

Summary

In February, when it is still cold, and most plants are still a long way from turning green, the first ones return. Balancing on one leg, bill covered in the softly white feathers, the elegant crown feathers waving in the wind, sleeping. Tired from a long journey. Spoonbills. Like many other birds, they leave our country in autumn to spend the winter somewhere in the south and come back to the Netherlands to breed in spring. But why do they do that?

The answer may seem obvious: conditions in winter in the Netherlands are too harsh for them to survive, so they have to leave. Yet, many other bird species, including quite some waterbirds, do stay here in winter. Why do they stay, and do others, like spoonbills, go? And why do some birds commute over only a couple of 100 kilometers between breeding and wintering grounds, whereas others, like Arctic terns, cross the entire globe to breed in the Arctic and winter in the Antarctic? These differences are not only seen among different species, but may even occur between individuals from a single breeding population. This tremendous variation in migration habits has intrigued biologists for many decades and led to the proposal of a variety of hypotheses to seek for potential explanations. All hypotheses share the assumption that the migratory journey itself must be costly, but differ in their presumed role of competition, and about the (individual differences in) benefits of breeding in seasonally productive high latitude areas and wintering in more benign low latitude areas.

Despite the existence of many theories, it has proven very difficult to empirically quantify the demographic costs and benefits associated with migration. With 'demographic costs and benefits' we here refer to a comparison of the demography (survival and reproduction) of individuals with contrasting migration strategies. The main difficulty is that such a comparison requires that individuals must be followed throughout their annual cycle. Only then, we can determine the breeding and wintering areas of individual birds, and assess their survival in different seasons, as well as their reproductive performance during the breeding season. This is quite a challenge for migratory species, as they often span a large geographical range throughout the year. Moreover, for accurate (seasonal) survival estimates, long-term studies are required: at least three years of data collection to derive an estimate of survival over one year.

Spoonbills (more precisely, Eurasian spoonbills, *Platalea leucorodia*) turned out to provide such an exceptional system. Already in the 1980's, Werkgroep Lepelaar has started in the Netherlands to provide spoonbill chicks with unique colour-ring combinations to make them individually recognizable. Through a combination of their conservation status, their beauty and the immediate and enthusiastic feedback from the database managers, many enthusiastic ornithologists have read and reported their rings, which resulted in an accumulation of over 100,000 resightings in the past 25 years. Due to this colour-ringing, it was recognized that important wintering areas of 'our' spoonbills were the Banc d'Arguin (Mauritania) and the Senegal river estuary (on the border of Mauritania and Senegal). As these are very remote areas, only very few

resightings were performed there, and expeditions with the specific aim to read the colour-rings of wintering spoonbills were organized in 1997–2001 (financed by WIWO and Natuurmonumenten), and, as part of this study, in 2005–2012. In addition to Mauritania and Senegal, 'our' spoonbills were also resighted in winter in France, Spain and Portugal. Hence, there was considerable variation in the distance travelled from the breeding grounds in the Netherlands to the wintering grounds and vice versa, varying from less than 2,000 km per year to winter in France, to nearly 10,000 km to winter in Senegal.

To investigate whether survival and breeding success correlate with migration distance and wintering area, we first need to know whether individuals spend the winter in the same area each year. Based on the resightings of colour-ringed spoonbills in the winter months between 1992 and 2010, we were able to assess the fidelity of spoonbills to a single wintering area (Chapter 6). We found that, while juveniles were still likely to move further south after their 1st winter, spoonbills became very faithful to their wintering area thereafter (distinguishing three main regions: France, Iberia (Spain & Portugal) and Mauritania & Senegal). Their probability of returning to the same wintering area the next year was about 93%. This meant that we are fairly safe by using a single resighting of an individual in winter (in its 2nd winter or later) to determine where this individual will spend the winter for the rest of its life.

Most spoonbills breed on the Wadden islands (Chapter 1). In the past 15 years, most spoonbill chicks have been colour-ringed on the island Schiermonnikoog. As most spoonbills return to their natal colony to breed (Chapter 2), the number of colour-ringed individuals is highest in the colony of Schiermonnikoog, which makes this colony the most suitable to investigate the relationship between an individual's migration strategy and its timing of breeding and breeding output. Whereas of many migratory bird species, either the wintering area or the breeding area is known, there are only very few of which both wintering and breeding area are known at the individual level. The Eurasian spoonbill is one of them. In combination with the already existing long-term dataset of colour-ring readings, this sets the solid basis for a comparison of (seasonal) survival and breeding success of individuals wintering in different areas, hence, migrating different distances.

The spoonbill population has been growing rapidly over the past 25 years, which allowed us to assess whether this growth was associated with a decrease in survival, indicative of density-dependent processes. A decrease in survival was observed in all age classes. In contrast to juvenile survival, which decreased mainly during summer and early winter, adult survival mainly decreased in the season of late winter and spring migration (Chapter 5). This suggests that for the adult birds that migrate and breed, in contrast to immature birds that stay at the wintering grounds year-round, density dependence, potentially driven by competition for resources (e.g. food), is strongest at the wintering areas or at stopover sites during spring migration. Two main mechanisms have been proposed that may underlie density dependence. The first mechanism is *site dependence*, where animals may use sites in a preemptive manner, meaning that first the best sites are occupied, while, as more individuals enter the population, poor sites become increasingly occupied, leading to a decrease in vital rates at the population level because of an increasing proportion of animals in the population that are forced to occupy poor quality sites and hence have lower fitness. The second mechanism that can lead to density dependence is *interference*: the more animals, the more they interfere, which may lead to decreased fitness of all animals.

In Chapter 7, we aimed to distinguish between *site dependence* and *interference* as the mechanism underlying the observed density-dependent decrease in late winter and spring survival. For this, we estimated the changes over a period of 16 years in the proportion of the population wintering in each region as well as in the survival in each winter region. Survival decreased at a similar rate in all three wintering regions but was consistently lower in Mauritania & Senegal. Surprisingly, at the onset of our study most spoonbills wintered in Mauritania & Senegal. This result cannot be explained by either of the two mechanisms of density dependence. We argue that the most likely explanation is that the relative suitability of different wintering areas has changed prior to the onset of our study. Either conditions in Mauritania & Senegal have deteriorated (potentially through density dependence) or conditions in Europe have improved, e.g. through increased protection of wetlands or climate change. Spoonbills do seem to respond to these changed wintering suitabilities as an increasing part of the population now chooses Europe as their winter destination, yet their distributional response is slower than optimal and seems somehow constrained by a tradition to migrate far.

In Chapter 8, we investigated whether migrating far leads to increased mortality during migration, and whether this is (partially) compensated by higher survival during the winter. To do so, we estimated seasonal survival in four seasons (summer (the breeding season), autumn migration, winter and spring migration) for birds with different migration distances (birds wintering in France, Iberia and Mauritania) which required resighting periods at the start and end of winter in each wintering region, as well as at the start and end of the summer. Data was only sufficient for doing this, especially for the Mauritanian winterers, in the past 7 years (2005–2012). We showed that survival during migration was indeed lower for the birds wintering in Mauritania, compared to those wintering in Europe, but only during spring migration. The higher mortality during migration was not compensated by lower mortality in the winter, as survival rates during summer, autumn migration and winter were similar for the three migration strategies.

So far, we have only looked at survival (on an annual and seasonal basis), yet the other important component of the fitness of an individual is breeding success. An individual's wintering area (and migration distance) may affect its timing of arrival at the breeding grounds, its condition at arrival, and hence the timing of breeding. In many bird species, later breeding is associated with lower breeding success. Our study population on Schiermonnikoog holds about 200 breeding pairs, of which about 30% was colour-ringed. Winter destination was known of ca. 60% of the colour-ringed birds. Considerable variation in migration strategies exists between individuals, sometimes even between breeding partners. Spoonbills do not pair for life, but generally have a different partner each year. Pair bonds are formed at the breeding colony. To be able to estimate chick age and condition, we have measured several chicks multiple times during their development to estimate growth curves for several morphometric measurements and body mass (Chapter 3). These results revealed that age can be reliably estimated from head-bill length (and 8th primary, for older chicks). In addition, a measure of chick body condition was proposed, which turned out an important predictor of the survival of a chick after fledging (Chapter 9). In Chapter 4, we showed that the diet of spoonbill chicks raised in this estuarine breeding colony changed throughout the breeding season, from a more freshwater to a more marine diet. This was very presumably associated with the availability of freshwater (mainly sticklebacks) and marine food sources (mainly shrimps). It has been hypothesized that having a salty diet may impose costs of physiological nature for chicks, as their salt glands are still being developed, resulting in reduced chick condition and increased mortality. Although we could not detect a direct relationship between a chick's diet and its body condition in this study, this may have been due to the small sample size. Between 2006 and 2009 we have monitored timing of breeding and breeding success at the individual level, and specifically investigated whether breeding birds from different wintering areas differed in their timing of breeding and breeding success. The main results are that long-distance migrants breed later and that later breeding is associated with lower breeding success and chick body condition. This could be associated with the change in diet as shown in Chapter 4. Long-distance migrants were also more likely to skip breeding in a given year.

To conclude, long-distance migrants have lower annual survival (mainly driven by spring migration mortality), and because they breed later in the season and seem to more often skip breeding, they probably also produce less offspring per year. Despite the convincing results, it is still somewhat premature to conclude that migration is costly (as both survival and breeding success were lower for long-distance migrants), as we did not manipulate the migration strategies of individual birds. In theory, it is possible that the birds wintering in Mauritania and Senegal are 'poor quality' birds that would also have had lower survival and breeding success if we would have forced them to winter in Europe. Yet, we did find strong suggestive evidence against this, as we showed that historically, when population sizes were still very low, most spoonbills wintered in Mauritania & Senegal, and that this proportion of birds is now decreasing. This suggests that the survival in Mauritania & Senegal is lower not because the birds wintering there are of 'poorer quality' but because these birds show traditional behaviour which is no longer optimal. Therefore, although we do not claim that we did measure true costs and benefits of migration, our estimates of demographic costs and benefits are likely a close approximation.

Throughout this thesis, we have focussed on a single breeding population that uses different wintering areas. For a full assessment of the demographic costs and benefits of migration, this comparison should be extended to different breeding populations using the same wintering area, to investigate the theory that breeding success is higher at higher (more seasonal) latitudes. The suitability of the spoonbill system extends here, as there are many different breeding populations along the East-Atlantic Flyway, breeding from Denmark in the north to Mauritania (where the resident Mauritanian spoonbill *P.l. balsaci* breeds, a genetically recognized subspecies of 'our' Eurasian spoonbill *P.l. leucorodia*, Chapter 2) in the south, providing a unique opportunity to compare breeding output along a huge latitudinal gradient.

Although the number of breeding pairs of spoonbills in Northwest Europe is still increasing, the growth appears to level off. In addition to the rapid growth of the Dutch spoonbill population, spoonbills also started to breed along the coasts of Germany, Denmark, England and Belgium, but in much lower numbers than you would expect based on the apparent wealth of suitable yet unoccupied breeding sites. This may partly be caused by the tendency of spoonbills to breed in their natal colony, but is probably also explained by the fact that further growth of the Northwest European breeding population appears to be mainly limited by factors in stopover and wintering areas (Chapter 5). Protection and measures to increase the availability and quality of stopover and wintering areas will then turn out to be most effective to achieve further growth of the Northwest European spoonbill population.

Samenvatting

In februari, als het nog koud is en grauw, keren de eersten terug. Balancerend op één been, de snavel verstopt tussen de roomwitte veren, de elegante kroonveren wuivend in de wind, in diepe slaap. Moe van een lange reis. Lepelaars. Zoals veel andere vogels, verlaten ze ons land in het najaar om de winter in zuidelijkere streken door te brengen om in het voorjaar weer terug te keren om te broeden. Maar waarom doen ze dat eigenlijk?

Het antwoord lijkt voor de hand te liggen: de omstandigheden in de winter in Nederlandse zijn zo bar dat ze niet zouden overleven, en daarom moeten ze wel vertrekken. Echter, veel andere vogelsoorten, waaronder ook veel watervogels (eenden, meeuwen) blijven wel hier in de winter. Waarom blijven zij, terwijl anderen, zoals de lepelaars, weggaan? En waarom vliegen sommige vogels maar enkele honderden kilometers tussen broed- en overwinteringsgebied, terwijl bijvoorbeeld Noordse Sterns de hele wereld overvliegen om te broeden rond de Noordpool en te overwinteren rond de Zuidpool. Zulke verschillen bestaan niet alleen tussen soorten, maar ook binnen soorten en soms zelfs tussen individuen uit dezelfde broedpopulatie. Biologen zijn al decennialang gefascineerd door deze enorme variatie in trekgedrag, en hebben allerlei hypotheses opgesteld om dit te verklaren. Deze hypotheses hebben gemeen dat ze de aanname doen dat de trek een kost met zich meebrengt, maar verschillen in de veronderstelde rol van competitie, over de voordelen van broeden in gematigde ten opzichte van tropische streken, en omgekeerd, over de voordelen van overwinteren in tropische ten opzichte van gematigde gebieden, en over de rol van individuele verschillen in deze voor- en nadelen van trek.

Ondanks de vele theorieën is het heel moeilijk gebleken om empirisch vast te kunnen stellen wat de demografische kosten en baten van trek zijn. Met 'demografische kosten en baten' doelen we hier op een vergelijking van de demografie (overleving en reproductie) van groepen vogels met een bepaalde trekstrategie. De belangrijkste horde voor een dergelijke vergelijking is dat individuen zowel in hun broed- als overwinteringsgebied gevolgd moeten kunnen worden. Alleen dan kunnen we op individueel niveau trekstrategieën relateren aan voortplantingssucces en aan overleving tijdens verschillende seizoenen (zomer, winter en tijdens de voorjaars- en najaarstrek). Voor trekvogels die vaak een enorme geografische verspreiding hebben door het jaar heen is dit een grote uitdaging. Daarnaast zijn langetermijn datareeksen nodig om nauwkeurige schattingen van overleving te kunnen krijgen: er moet tenminste drie jaar lang gegevens verzameld worden om een schatting te krijgen van de overleving over één jaar.

Lepelaars (*Platalea leucorodia*) blijken hiervoor uitermate schikt te zijn. In de jaren '80 is de Werkgroep Lepelaar in Nederland gestart met het kleurringen van Lepelaar kuikens, waardoor ze individueel herkend konden worden. De combinatie van hun beschermingsstatus, hun schoonheid en de enthousiaste feedback van de database beheerders, werden door vele enthousiaste vogelaars de kleurringen van lepelaars afgelezen en doorgegeven. Tot op heden heeft dit geresulteerd in meer dan 100,000 aflezingen. Dankzij dit kleurring-programma werd ontdekt dat de Banc d'Arguin in Mauretanië en de monding van de Senegal rivier op de grens tussen Mauretanië en Senegal belangrijke overwinteringsgebieden voor onze lepelaars waren. Omdat dit vrij afgelegen gebieden zijn waar weinig mensen wonen, werden hier weinig afgezingen gedaan en zijn er speciale expedities georganiseerd om de kleurringen van de hier overwinterende lepelaars af te lezen, in 1997-2001 (gefinancierd door WIWO en Natuurmonumenten) en, als onderdeel van dit promotieonderzoek, in 2005-2012. Naast waarnemingen uit Mauretanië en Senegal, werden ook veel van 'onze' gekleurringde lepelaars in de winter afgelezen in Frankrijk, Spanje en Portugal. Er was dus aanzienlijke variatie in de afstand die lepelaars afleggen tussen hun broedgebied in Nederland en hun overwinteringsgebieden en terug, varierend van minder dan 2,000 km per jaar om in Frankrijk te overwinteren tot bijna 10,000 km om in Senegal te overwinteren.

Om te kunnen onderzoeken of overleving en voortplantingssucces verschilt tussen indviduen met verschillende trekstrategieën, moeten we eerst weten of individuen ieder jaar op dezelfde plek overwinteren. Op basis van aflezingen van gekleurringde lepelaars in de wintermaanden tussen 1992 en 2010, konden we bepalen hoe plaatstrouw lepelaars aan hun overwinteringsgebied zijn (Hoofdstuk 6). We vonden dat, hoewel veel lepelaars in hun eerste jaar nog verder naar het zuiden afzakten, lepelaars vanaf hun 2^{e} winter heel plaatstrouw waren aan hun overwinteringsgebied (waarbij we onderscheid hebben gemaakt tussen drie geografische gebieden: Frankrijk, het Iberisch Schiereiland en Mauretanië & Senegal). De kans dat een vogel in hetzelfde gebied overwintert in twee opeenvolgende winters was rond de 93%. Dit betekent dat we aan de hand van één winterwaarneming van een (2^{e} jaars of oudere) lepelaar met behoorlijke zekerheid kunnen zeggen waar hij zijn de rest van zijn leven overwintert.

De meeste lepelaars broeden op de Waddeneilanden (Hoofdstuk 1). De afgelopen 15 jaar zijn de meeste jongen gekleurringd op Schiermonnikoog. Aangezien de meeste lepelaars naar hun geboortekolonie terugkeren om te broeden (Hoofdstuk 2), is het aantal gekleuringde vogels hier het hoogst en is deze kolonie daarom het meest geschikt om de relatie tussen de trekstrategie van een individu en zijn timing van broeden en voortplantingssucces te onderzoeken. Terwijl van de meeste trekvogels óf het overwinteringsgebied óf het broedgebied bekend is, zijn er maar weinig soorten waarbij zowel broed- als overwinteringsgebied bekend is op individueel niveau. De lepelaar is er één van. In combinatie met de reeds bestaande langetermijn dataset met kleurring aflezingen is dit een hele sterke basis voor de vergelijking van seizoensoverleving en voortplantingssucces van individuen die in verschillende gebieden overwinteren en dus verschillende afstanden trekken.

De afgelopen 25 jaar is de lepelaar populatie in Nederland hard gegroeid. Dit gaf ons de mogelijkheid om te kijken of deze groei gepaard ging met een afname in overleving, wat een aanwijzing zou zijn voor dichtheidsafhankelijke processen. We vonden inderdaad een afname in overleving in zowel onvolwassen als volwassen vogels. De sterkste afname in de overleving van volwassen vogels vonden we in het seizoen dat de late winter en de voorjaarstrek omvatte (Hoofdstuk 5). Dit suggereert dat voor volwassen vogels die trekken en broeden, in tegenstelling tot de onvolwassen vogels die het hele jaar in hun overwinteringsgebieden blijven, dichtheidsafhankelijkheid, mogelijk gestuurd door competitie voor (voedsel)bronnen, het sterkst is in de overwinteringsgebieden of in opvetplaatsen tijdens de (voorjaars)trek. Twee belangrijke mechanismen zouden aan de basis van deze dichtheidsafhankelijkheid kunnen liggen. Het eerste mechanisme is *plaatsafhankelijkheid*, waarbij de dieren gebieden gebruiken op een 'wie het eerst komt, wie het eerst maalt' basis. Dit betekent dat de beste plekken eerst worden bezet, en dat, naarmate er meer individuen in de populatie komen en de beste plekken vol beginnen te raken, ook de slechtere plekken worden bezet, wat leidt tot verminderde populatiegroei omdat er steeds meer dieren zijn die slechte plekken bezetten en dus een lagere fitness hebben. Het tweede mechanisme dat tot dichtheidsafhankelijkheid kan leiden is *interferentie*: hoe meer dieren, hoe meer last ze van elkaar hebben, wat leidt tot een afname in de fitness van alle dieren.

In Hoofdstuk 7 hebben we gekeken of *plaatsafhankelijkheid* of *interferentie* de afname in overleving tijdens de late winter en voorjaarstrek kon verklaren. Hiervoor hebben we een schatting gemaakt van de veranderingen over een periode van 16 jaar in het deel van de populatie dat in elk gebied overwintert en in de overleving in elk overwinteringsgebied. We vonden dat de mate van afname in overleving gelijk was in alle drie overwinteringsgebieden, maar dat de overleving consistent lager was in Mauretanië & Senegal. Verrassend genoeg overwinterden aan het begin van de studie de meeste lepelaars in Mauretanië en Senegal. Dit resultaat kan door geen van beide mechanismen van dichtheidsafhankelijkheid verklaard worden. De meest aannemelijke verklaring voor dit onverwachte resultaat is dat de geschiktheid van de verschillende gebieden is veranderd voordat we onze studie begonnen (in 1994). De omstandigheden in Mauretanië zijn mogelijk verslechterd (wellicht door dichtheidsafhankelijkheid), of de omstandigheden in Europe zijn beter geworden, bijvoorbeeld door verbeterde bescherming van wetlands of door klimaatsverandering. Lepelaars lijken wel te reageren op deze veranderde omstandigheden aangezien steeds meer lepelaars voor Europa kiezen als overwinteringsgegbied, maar de verandering in de winterverspreiding is langzamer dan wat optimaal zou zijn en lijkt te worden tegengehouden door de drang om verder te trekken.

In Hoofdstuk 8 hebben we onderzocht of de dieren die verder trekken een verhoogde kans hebben om het loodje te leggen tijdens de trek, en of dit wordt gecompenseerd door hogere overlevingskansen in de winter (die dan in relatief warmere streken wordt doorgebracht). Hiertoe hebben we de overleving geschat in vier seizoenen: de zomer (het broedseizoen), de najaarstrek, de winter en de voorjaarstrek voor vogels met verschillende trekafstanden (die in Frankrijk, het Iberisch Schiereiland of Mauretanië overwinteren). Hiervoor moesten vogels afgelezen worden aan het begin en einde van de zomer en de winter. Voor de lepelaars die in Mauretanië overwinteren hadden we hiervoor alleen genoeg gegevens in de afgelopen zeven jaar (2005–2012). De overleving tijdens de trek blijkt inderdaad lager te zijn voor Mauretaanse overwinteraars dan voor de Europese overwinteraars, maar alleen tijdens de voorjaarstrek. Deze hogere sterfte werd niet gecompenseerd door hogere overleving in de winter: we vonden geen verschillen in overleving tijdens de zomer, najaarstrek en winter waren tussen de drie trekstrategieën.

Tot nu toe hebben we alleen gekeken naar overleving (op jaar- en seizoensbasis). Echter, de andere belangrijke component van de fitness van een individu is voortplantingssucces. Het overwinteringsgebied (en de trekafstand) van een individu kan effect hebben zijn aankomstdatum in het broedgebied, zijn conditie bij aankomst, en daarmee op de datum waarop begonnen kan worden met broeden. In veel vogelsoorten is later broeden geassocieerd met lager voortplantingssucces. Tijdens de onderzoeksperiode (2006–2009) huisvestte onze studiepopulatie op Schiermonnikoog zo'n 200 broedparen lepelaars, waarvan ongeveer 30% is gekleurringd. Van zo'n 60% van de gekleurringde vogels weten we ook waar ze overwinteren, omdat ze als 2^{e} jaars of oudere vogel in hun overwinteringsgebied zijn waargenomen. Er was aanzienlijke variatie in trekstrategieën tussen individuen, soms zelfs tussen partners. Lepelaars vormen geen paarband voor het leven, maar hebben meestal elk jaar een nieuwe partner die ze na aankomst in de broedkolonie uitkiezen. Om de leeftijd en conditie van kuikens te schatten, hebben we een aantal kuikens meerdere malen tijdens het opgroeien gemeten om zo voor een aantal lichaamsmaten groeicurves te krijgen (Hoofdstuk 3). Hieruit bleek dat leeftijd nauwkeurig kan worden geschat aan de hand van de lengte van de kop-snavel, en voor oudere kuikens ook aan de hand van de 8ste slagpen. Daarnaast lijkt de relatieve afwijking van het voorspelde leeftijds- en geslachtsafhankelijke lichaamsgewicht een goede maat te zijn voor de lichaamsconditie van een kuiken, aangezien dit een goede voorspeller was voor de overleving van kuikens na uitvliegen (Hoofdstuk 9). In Hoofdstuk 4 laten we zien dat het dieet van lepelaarkuikens op Schiermonnikoog verandert gedurende het broedseizoen, van een dieet dat voor het merendeel uit zoetwater bronnen bestaat aan het begin van het seizoen naar een veelal zoutwater-dieet later in het seizoen. Dit is waarschijnlijk gerelateerd aan veranderingen in de beschikbaarheid van voedsel in het zoetwater (vooral stekelbaarsjes) en zoutwater (vooral garnalen). Een zout dieet kan kosten van fysiologische aard met zich meebrengen voor kuikens met nog niet volgroeide zoutklieren, wat zou kunnen resulteren in verlaagde conditie en overleving. We vonden geen directe relatie tussen het dieet van de kuikens en hun lichaamsconditie, maar mogelijk was de steekproef hiervoor te klein. In Hoofdstuk 9 vonden we namelijk wel dat later geboren kuikens een lagere conditie hadden en dat voortplantingssucces van late nesten lager was. Lepelaars die in Mauretanië & Senegal overwinteren broedden later dan lepelaars die in Europa overwinteren. Ook lijken ze vaker een broedseizoen over te slaan.

De over lange afstanden trekkende lepelaars hebben een lagere jaarlijkse overleving (vooral veroorzaakt door lage overleving tijdens de voorjaarstrek) dan de korteafstandstrekkers. Omdat ze later in het jaar broeden, en vaker een broedseizoen overslaan, produceren ze gemiddeld ook minder jongen per jaar. Hoe overtuigend dit ook lijkt, het is nog steeds wat voorbarig om nu te concluderen dat we de kosten (zowel lagere overleving als voortplantingssucces) van lange afstandstrek hebben getoond. Dit komt omdat we de trekstrategieën van individuen niet experimenteel hebben gemanipuleerd. In theorie zou het kunnen dat de overwinteraars in Mauretanië en Senegal 'lagere kwaliteit' vogels zijn die het ook slechter zouden hebben gedaan als we ze (op wat voor manier dan ook) hadden gedwongen om in Europa te overwinteren. Wel hebben we sterke aanwijzingen gevonden dat dit erg onwaarschijnlijk is. Toen de populatie nog klein was, overwinterden de meeste lepelaars in Mauretanië en Senegal, maar over de tijd zijn er steeds meer lepelaars in Europa gaan overwinteren (Hoofdstuk 7). Dit suggereert dat de overleving in Mauretanië en Senegal lager is, niet omdat de vogels daar van slechtere kwaliteit zijn maar omdat deze vogels traditioneel gedrag vertonen wat niet langer optimaal is. Hoewel we dus niet echt de individuele kosten en baten van trek hebben aangetoond, zullen onze schattingen van de demografische kosten en baten wel heel dichtbij komen.

In dit proefschrift lag de nadruk op de vergelijking van individuen uit één broedpopulatie (de Nederlandse) die op verschillende afstanden van het broedgebied overwinteren. Voor een compleet plaatje van de demografische kosten en baten van trek zou een soortgelijke vergelijking moeten worden gemaakt van voortplantingssucces op verschillende breedtegraden, om te kijken of de aanname klopt dat lepelaars meer jongen grootbrengen in meer gematigde (noordelijkere) streken. Ook hier is de (meta)populatie van lepelaars geschikt voor, aangezien er veel verschillende broedpopulaties zijn langs de Oost-Atlantische vliegroute, met als noordelijkste broedgebied Denemarken en als zuidelijkste Mauretanië, waar de niet trekkende (residente) Mauretaanse lepelaar *P.l. balsaci* broedt, een genetisch vastgestelde ondersoort van 'onze' Europese lepelaar *P.l. leucorodia* (Hoofdstuk 2). Dit biedt een unieke mogelijkheid tot het vergelijken van voortplantingssucces over een enorme gradient van breedtegraden.

Hoewel het aantal broedparen lepelaars in Noordwest Europa nog steeds toeneemt lijkt de hardste groei er wel uit. Naast de sterke groei van de Nederlandse populatie zijn er ook wat lepelaars in Duitsland, Denemarken, Engeland en België gaan broeden, maar minder dan je zou verwachten op basis van de ogenschijnlijke overvloed aan geschikte broedplaatsen. Dit kan komen doordat lepelaars geneigd zijn te gaan broeden waar ze geboren zijn, maar het kan ook te maken hebben met het feit dat verdere groei van de Noordwest-Europese broedpopulatie vooral beperkt wordt door factoren in gebieden die gebruikt worden tijdens de trek en in de winter (Hoofdstuk 5). Bescherming en maatregelen ter bevordering van de beschikbaarheid en kwaliteit van opvet- en overwinteringsgebieden zullen dan het meest effectief zijn om verdere groei van de Noordwest Europese lepelaarpopulatie te bewerkstelligen.

Résumé

En février, lorsqu'il fait encore froid et que la plupart des plantes sont encore sans feuilles, on les voit revenir. Se balançant sur une patte, le bec caché dans les douces plumes blanches, les élégantes couronnes de plumes ondulant dans le vent, elles dorment. Les spatules blanches. Comme beaucoup d'autres oiseaux, les spatules quittent les Pays Bas à l'automne pour passer l'hiver ailleurs, dans le sud, et reviennent au printemps pour se reproduire. Mais pourquoi donc?

La réponse parait évidente : pour survivre ! Les conditions hivernales des Pays Bas ne permettent pas en effet aux spatules de survivre et les obligent à partir. Cependant, beaucoup d'autres espèces d'oiseaux, y compris des espèces de milieu aquatique, restent en hiver. Alors pourquoi certaines espèces, comme les spatules, migrent-elles alors que d'autres restent ? Et pourquoi certains oiseaux ne parcourent qu'une centaine de kilomètres pour rejoindre leur site hivernal alors que d'autres, comme la sterne arctique, traversent le globe entier pour se reproduire en arctique et hiverner en antarctique ? D'ailleurs, ces incroyables différences comportementales ne se retrouvent pas seulement entre espèces mais également entre individus d'une même population. Une telle variabilité intrigue les biologistes depuis de nombreuses décennies et les a conduit à formuler de nombreuses hypothèses expliquant ce phénomène. Si toutes les hypothèses partagent le même postulat, à savoir que la migration est en elle-même coûteuse, elles divergent en revanche sur d'autres aspects. Ces aspects incluent un rôle plus ou moins important de la compétition et des différences dans les (différences individuelles dans les) bénéfices attribués au fait de se reproduire dans les zones de hautes latitudes à productivité saisonnière et au fait d'hiverner dans les zones plus stables des basses latitudes.

Malgré l'existence de nombreuses théories, il s'avère très difficile de quantifier les coûts et bénéfices démographiques associés à la migration. Par « coûts et bénéfices démographiques », il est fait référence ici à la comparaison de la démographie (survie et reproduction) d'individus adoptant des stratégies de migration différentes. Une grande difficulté réside donc dans le fait que cette comparaison nécessite que les individus soient suivis tout au long de leur cycle annuel. Alors seulement, il devient possible de déterminer quelles sont les aires de reproduction et d'hivernage des individus et d'accéder à leur survie au cours des différentes saisons, ainsi qu'à leur succès reproducteur. Accéder à ces données pour les espèces migratrices constitue un défi car ces espèces sont souvent réparties tout au long de l'année sur de grandes aires géographiques. De plus, l'obtention d'estimées précises de survie (saisonnières) nécessite des études à long terme : il faut au minimum 3 ans de données pour obtenir l'estimée de survie d'une année.

Les spatules blanches (*Platalea leucorodia*) se trouvent être un modèle biologique exceptionnel. Dans les années 80, le groupe de recherche néerlandais travaillant sur les spatules (« Werkgroep Lepelaar ») baguait déjà des poussins avec des combinaisons uniques de couleur dans le but de les identifier individuellement. Puis, grâce au statut protégé des spatules, à leur beauté et aux retours immédiats et enthousiastes des coordinateurs de la base de données, de nombreux ornithologistes ont lu et reporté les bagues de ces oiseaux, permettant d'accumuler ainsi plus de 100,000 observations au cours de ces 25 dernières années. Ces campagnes de baguage ont permis d'identifier le Banc d'Arguin (Mauritanie) et l'estuaire de la rivière Sénégal (à la frontière entre la Mauritanie et le Sénégal) comme étant des aires d'hivernage importantes pour « nos » spatules. Comme ces aires sont très isolées, les observations d'individus bagués sont restées longtemps très rares. C'est pourquoi, des expéditions ayant pour objectif principal de lire les bagues des spatules hivernantes ont été organisées en 1997–2001 (grâce aux financements de WIWO et Natuurmonumenten) et en 2001–2012 (cette étude). Au delà de la Mauritanie et du Sénégal, des observations de « nos » spatules ont aussi été reportées en France, Espagne et Portugal. Les distances parcourues entre les sites de reproduction aux Pays Bas et les sites d'hivernage (et vice versa) varient donc considérablement : de moins de 2000 km par an jusqu'à la France à quasiment 10,000 km jusqu'au Sénégal.

Afin de pouvoir étudier si la survie et le succès reproducteur sont corrélés avec la distance migratoire et les sites d'hivernages, il est indispensable de savoir si les individus hivernent dans le même endroit chaque année. Sur la base des lectures de bagues colorées obtenues en hiver (entre 1992 et 2010), nous avons été capables de déterminer la fidélité des spatules à leur site d'hivernage (chapitre 6). Notre étude montre qu'après leur premier hiver, les juvéniles se déplacent généralement plus au sud, alors que plus tard, les spatules deviennent très fidèles à leur site d'hivernage (définissant ainsi trois régions principales : la France, l'Ibérie (Espagne & Portugal) et la Mauritanie & Sénégal). Nous avons trouvé que la probabilité de retourner dans le même site hivernage l'année suivante est d'environ 93%. Ceci signifie qu'il est donc raisonnable de déterminer le site d'hivernage à vie d'un individu sur la base d'une seule observation (de son deuxième hiver ou plus).

La plupart des spatules se reproduisent dans les îles Wadden (chapitre 1). Durant les 15 dernières années, la plupart des poussins de spatules de l'île de Schiermonnikoog ont été équipés de bagues colorées. Comme les spatules reviennent généralement se reproduire sur leur site de naissance (chapitre 2), cela signifie que le nombre d'individus bagués sur la colonie de Schiermonnikoog est très élevé. Cette colonie est donc adaptée à l'étude liant stratégies migratoires, timing de la reproduction et succès reproducteur. Ceci est un grand avantage car il existe très peu d'espèces pour lesquelles les sites de reproduction ou d'hivernage sont connus à l'échelle individuelle. Ces données, en association avec la base de données à long terme des relectures de bagues, constituent une base solide pour comparer la survie (saisonnière) et le succès reproducteur des individus hivernant dans des sites différents, c.à.d. migrant à des distances différentes.

Les populations de spatules ont crû rapidement ces 25 dernières années, ce qui nous a permis d'étudier si cette croissance était associée à une diminution de la survie, indicative de processus densité-dépendants. Les résultats montrent une diminution de la survie dans toutes les classes d'âge, avec cependant une diminution plus prononcée dans la survie des adultes en fin d'hiver et pendant la migration au printemps (chapitre 5). Ces résultats suggèrent donc que pour les adultes qui migrent et se reproduisent (en contraste avec les oiseaux immatures qui restent toute l'année en hivernage), la dépendance à la densité est plus forte dans les aires d'hivernage ou dans les sites de halte migratoire. Cette dépendance à la densité est probablement causée par la compétition pour l'accès aux ressources (par ex. la nourriture). Deux mécanismes principaux ont été suggérés afin d'expliquer cette dépendance à la densité. Le premier mécanisme est dépendant du site (*site dependence*) : les animaux utilisent les sites d'une manière préemptive, c-à-d que les meilleurs sites sont occupés en premier alors que les moins bons ne sont occupés que lorsque le nombre d'individus entrant dans la population augmente. Par conséquent, les taux vitaux de la population diminuent car un nombre de plus en plus élevé d'individus est forcé d'occuper des sites de mauvaise qualité, ce qui leur diminue leur fitness (ou aptitude phénotypique). Le second mécanisme est appelé interférence (*interference*): plus il y a d'animaux, plus ils interfèrent les uns avec les autres, ce qui diminue la fitness de tous.

Le but du chapitre 7 de cette thèse fut d'identifier le mécanisme responsable de la diminution densité-dépendante de la survie hivernale et printanière (*site dependence* versus *interference*). Pour cela, nous avons estimé, pour chaque aire d'hivernage et sur une période de 16 ans, les changements dans la proportion de la population hivernante et les changements de survie. Notre étude montre que la survie diminue à un taux similaire entre les trois aires d'hivernage mais que cette survie est en général plus basse pour la Mauritanie et pour le Sénégal. Etonnamment, au début de notre étude une grande majorité des spatules hivernaient en Mauritanie et au Sénégal. Ce résultat ne peut être expliqué par aucuns des deux mécanismes dépendant de la densité. L'hypothèse la plus plausible est donc la qualité relative des différentes régions d'hivernage a changé avant le début de notre étude. Soit les conditions de la Mauritanie et du Sénégal se sont détériorées (potentiellement au travers de processus densité-dépendant), soit les conditions en Europe se sont améliorées au travers par ex. de la protection de régions humides ou du changement climatique. Les spatules semblent répondre à ces variations des conditions hivernales car une partie croissante de la population choisit maintenant d'hiverner en Europe. Cependant, cette réponse populationnelle est plus lente que la réponse optimale et semble être contrainte, d'une façon ou d'une autre, par « l'habitude » de migrer loin.

Dans le chapitre 8, nous avons étudié si le fait de migrer sur de longues distances conduisait à une augmentation de la mortalité pendant la migration et si cela était compensé (partiellement) part une survie plus élevée en hiver. Pour cela, nous avons estimé la survie d'oiseaux migrant sur des distances différentes (oiseaux hivernant en France, en Ibérie et en Mauritanie) pendant les différentes saisons (été (saison reproductrice), automne, hiver et migration printanière). Ces estimées nécessitent des périodes d'observations au début et à la fin de l'hiver dans chaque région d'hivernage et au début et à la fin de chaque été. Les données obtenues n'ont permis ces calculs que sur les 7 dernières années (2005–2012), en particulier pour la Mauritanie. Notre étude monte que la survie pendant la migration est en effet plus basse pour les oiseaux hivernant en Mauritanie que pour ceux hivernant en Europe. La plus grande mortalité pendant la migration n'est pas compensée par une mortalité plus faible en hiver car les taux de survie en été, automne et hiver sont similaires pour les trois stratégies de migration.

Jusqu'à présent, nous avons seulement étudié les taux de survie (sur des bases annuelles et saisonnières). Cependant un autre composant important de la fitness d'un individu se trouve être son succès reproducteur. L'aire d'hivernage (et la distance de migration) d'un individu est susceptible d'affecter le timing de son retour sur les sites de reproduction, sa condition à son arrivée et, par conséquent, le timing en lui-même de sa reproduction. Chez beaucoup d'espèces d'oiseaux, une reproduction tardive est associée à un succès reproducteur faible. Notre population d'étude sur Schiermonnikoog contient environ 200 couples reproducteurs dont 30% sont bagués. Les sites d'hivernage de ces couples sont connus dans 60% des cas. Il existe une variabilité considérable dans les stratégies de migration entre individus et même parfois entre les partenaires d'un même couple. Les spatules ne s'apparient pas à vie et changent en général de partenaire tous les ans. Les liens entre partenaires se forment sur la colonie de reproduction. Afin d'estimer l'âge et la condition des poussins, nous avons mesuré plusieurs poussins de façon répétée pendant la phase de développement. Ces mesures permettent d'estimer les courbes de croissance et les masses corporelles (chapitre 3). Notre étude révèle que l'âge des spatules peut être estimé de façon fiable à partir de la longueur tête-bec (et 8ème primaire pour les poussins plus âgés). De plus, nous proposons une mesure de la condition des poussins qui s'avère être un prédicteur important de la survie des poussins après l'envol (chapitre 9). Dans le chapitre 4, nous montrons que le régime alimentaire des poussins de spatule, élevés dans les colonies estuaires, change au cours de la saison de reproduction : il passe d'une nourriture d'eau douce à une nourriture d'eau salée. Ce changement de régime alimentaire est très certainement associé à la disponibilité des ressources alimentaires des milieux d'eau douce (principalement des épinoches) et des milieux marins (principalement des crevettes). Il a été proposé qu'avoir un régime salé impose aux poussins des coûts physiologiques car leurs glandes à sel ne sont pas encore totalement développées, ce qui réduirait leur condition corporelle et augmenterait leur mortalité. Dans cette étude, nous n'avons pas détecté de relation directe entre le régime alimentaire des poussins et leur condition corporelle, mais ceci est peut être le résultat d'une taille d'échantillon trop faible. Entre 2006 et 2009, nous avons suivi le timing de reproduction et le succès reproducteur des individus et avons étudié si ces paramètres différaient entre les oiseaux reproducteurs provenant de différents sites d'hivernage. Les résultats principaux de cette étude révèlent que les oiseaux qui migrent sur de grandes distances se reproduisent plus tard et qu'une reproduction tardive est associée à un faible succès reproducteur ainsi qu'à une condition corporelle des poussins réduite. Ces résultats pourraient s'expliquer par à un changement de régime alimentaire, comme nous l'avons montré dans le chapitre 4.

Enfin, les oiseaux migrant sur de grandes distances sont également plus susceptibles de sauter un événement de reproduction dans une année donnée.

En conclusion, cette thèse montre que les spatules qui migrent sur de grandes distances ont une survie annuelle réduite (dû principalement à la mortalité pendant la migration printanière) et que ces individus produisent probablement moins de descendants par an car ils se reproduisent tardivement et sont plus susceptibles de sauter un événement de reproduction. Cependant, malgré ces résultats convaincant, il reste tout de même prématuré de conclure que la migration est coûteuse (c.-à-d. associée à une survie et une reproduction réduite) car nous n'avons pas manipulé les stratégies de migration des individus. En théorie, il est possible que les oiseaux qui hivernent en Mauritanie et au Sénégal soient de plus « mauvaise qualité » et qu'en les forçant à hiverner en Europe, nous aurions diminué leur survie et leur succès reproducteur. Malgré tout, nos résultats suggèrent que ce scénario est très peu probable. Nous avons en effet montré qu'auparavant (quand les tailles de population étaient encore très basses) la plupart des spatules hivernaient en Mauritanie et au Sénégal mais que maintenant cette proportion d'oiseaux est en diminution. Ce résultat suggère que la survie des spatules en Mauritanie et au Sénégal est plus faible non pas parce que les oiseaux qui hivernent là-bas sont de « mauvaise qualité » mais parce que ces oiseaux expriment un comportement qui n'est plus optimal à l'heure actuelle. C'est pourquoi, bien que nous ne pouvons pas prétendre avoir mesuré les vrais coûts et bénéfices associés à la migration, nos estimées des coûts et bénéfices démographiques en sont une approximation très proche.

Dans cette thèse, nous nous sommes concentrés sur une seule population reproductrice utilisant des aires d'hivernage différentes. Pour une évaluation complète des coûts et bénéfices démographiques associés à la migration, cette comparaison doit être étendue à d'autres populations reproductrices utilisant les mêmes aires d'hivernage. Ceci permettrait de tester la théorie selon laquelle le succès reproducteur augmente avec les latitudes (plus saisonnières). La pertinence du choix des spatules comme système d'étude demeure car il existe de nombreuses populations reproductrices situées le long du couloir de migration atlantique-est. Ces populations de spatules se reproduisent depuis le Danemark, au nord, jusqu'à la Mauritanie, au sud (où nichent les spatules mauritaniennes résidentes *P.l. balsaci*, reconnue génétiquement comme étant une sous-espèce de « nos » spatules blanches *P.l. leucorodia*, chapitre 2), ce qui fournit une opportunité unique de comparer le succès reproducteur le long d'un gradient latitudinal énorme.

Bien que le nombre de couples reproducteurs de spatules soit toujours en augmentation dans le nord ouest de l'Europe, la croissance des populations semble avoir atteint un plateau. En plus d'une croissance rapide des populations des Pays Bas, les spatules commencent à coloniser les côtes de l'Allemagne, du Danemark, de l'Angleterre et de la Belgique, mais en nombre beaucoup plus faible que ce qui est attendu sur la base des sites apparemment propices à la reproduction et encore disponibles. Ce phénomène peut s'expliquer en parti par la grande fidélité qu'ont les spatules à leur site de naissance mais probablement aussi par le fait que la croissance démographique des populations reproductrices du nord ouest de l'Europe est limitée par des facteurs associés aux sites d'hivernage et des haltes migratoires (chapitre 5). La protection et la mise en place de mesures permettant d'augmenter la disponibilité et la qualité des sites des haltes migratoires et d'hivernage apparaissent comme étant le moyen le plus efficace pour permettre la croissance des populations de spatules blanches du nord ouest de l'Europe de continuer.

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List of publications

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El-Hacen, H.M., Overdijk, O., **Lok, T.**, Olff, H. & Piersma, T. (2013) Home range, habitat selection, and foraging rhythm in Mauritanian spoonbills (*Platalea leucorodia balsaci*): A satellite tracking study. *Waterbirds*, in press.

Leyrer, J., **Lok, T.**, Brugge, M., Spaans, B., Sandercock, B.K. & Piersma, T. (2013) Mortality within the annual cycle: seasonal survival patterns in Afro-Siberian red knots. *Journal of Ornithology*, **154**, 933-943.

Lok, T., Overdijk, O. & Piersma, T. (2013) Migration tendency delays distributional response to differential survival prospects along a flyway. *American Naturalist*, **181**, 520-531.

Piersma, T., Van der Velde, M., El-Hacen, H.M., **Lok, T.** & Overdijk, O. (2012) Molecular verification of the subspecies status of the Mauritanian spoonbill *Platalea leucorodia balsaci. Ardea*, **100**, 131-136.

Leyrer, J., **Lok, T.**, Brugge, M., Dekinga, A., Spaans, B., Van Gils, J.A., Sandercock, B.K. & Piersma, T. (2012) Small-scale demographic structure suggests preemptive behavior in a flocking shorebird. *Behavioral Ecology*, **23**, 1226-1233.

Lok, T., Overdijk, O., Tinbergen, J.M. & Piersma, T. (2011) The paradox of spoonbill migration: most birds travel to where survival rates are lowest. *Animal Behaviour*, **82**, 837-844.

van de Pol, M., Ens, B.J., Heg, D., Brouwer, L., Krol, J., Maier, M., Exo, K.M., Oosterbeek, K., **Lok, T.**, Eising, C.M. & Koffijberg, K. (2010) Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology*, **47**, 720-730.

Lok, T., Overdijk, O., Horn, H. & Piersma, T. (2009) The spoonbill *Platalea leucorodia* population of the Wadden Sea islands: does population growth level off? *Limosa*, **82**, 149-157.

Vahl, W.K., **Lok, T.**, van der Meer, J., Piersma, T. & Weissing, F.J. (2005) Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behavioral Ecology*, **16**, 834-844.

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